Variation in diversity among Laurales, Early Cretaceous to Present

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Molecular data accumulated since 1999 have shown that monophyletic Laurales consist of Calycanthaceae, 10 species, ((Siparunaceae, 70 spp., (Atherospermataceae, 14 spp., Gomortegaceae, 1 sp.)), (Lauraceae, 2500-3000 spp., Hernandiaceae, 50 spp., Monimiaceae, 195 spp.)). As assessed by Guyer and Slowinski's imbalance metric, Lauraceae and Siparunaceae are significantly more species rich than if populations/species in Laurales families had proliferated with some random equal likelihood. Four of these families have fossil records that go back to the Cretaceous, one goes back to the Oligocene, and two are unknown as fossils (Hernandiaceae, Siparunaceae). All have multi-locus molecular phylogenies that together include representatives of 79 of the 92 genera, permitting the calibration of local molecular clocks and the comparison of families in terms of the geological periods during which they accumulated most of their extant net diversity. Most data sets exhibit sufficient heterogeneity in substitution rates to warrant semiparametric models of sequence evolution in which different rates are assumed between ancestral and descendent branches, but excessive heterogeneity is penalized. A comparison of penalized likelihood chronograms for the six families with more than one species suggests that at the relatively deep level of the analysis, climate change did not affect related families in similar ways. On the other hand, the raise of the Andes appears to relate to bursts of species accumulation in both, Lauraceae and Siparunaceae. To explain the observed low species numbers in ancient families, such as Atherospermataceae, Gomortegaceae, and Calycanthaceae, one needs to postulate extinction rates that left fewer than 10% of species surviving at any one time or accept the alternative possibility of (some) species persisting for 80-100 my, basically without proliferating.

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Introduction

Species accumulation and extinction both take time, and the asymmetry between the two processes has long been recognized (Darwin 1859). Darwin argued that complete extinction would take longer than species accumulation, except in the case of catastrophic mass extinctions. "There is reason to believe that the complete extinction of the species of a group is generally a slower process than their production: if the appearance and disappearance of a group of species be represented, as before, by a vertical line of varying thickness, the line is found to taper more gradually at its upper end, which marks the progress of extermination, than at its lower end, which marks the first appearance and increase in numbers of the

species. In some cases, however, the extermination of whole groups of beings, as of ammonites towards the close of the secondary period, has been wonderfully sudden." The persistence of species-poor lineages that appear to have been around for millions of years is a phenomenon as difficult to study as the opposite, the existence of groups in which accumulation of species appears to far outweigh extinction. With the advent of molecular phylogenetics and sophisticated approaches to extracting information about time from molecular data, plus the recent increase in early angiosperm fossils, it has become possible to better relate persistence and diversity to absolute lineage age and to particular geological times during which lineages diversified. For flowering plants, such analyses suggest that speciation rates likely increased during their evolution (Magallón & Sanderson 2001; Barraclough & Savolainen 2001), resulting in the net accumulation of diversity in the more derived clades if extinction rates stayed roughly the same.

By contrast, basal groups of angiosperms are significantly less rich than expected, suggesting an increased susceptibility to extinction and/or slowdown in speciation. Of the basal dicot lineages, only Annonaceae (2300 species), Piperaceae (2000 species), and Lauraceae (2500-3000 species) are species rich. However, as Darwin described, lineages accumulate and lose diversity slowly, and the question therefore arises when Lauraceae accumulated the bulk of their extant diversity and how they might differ from their closest relatives in terms of diversity, geographic range, or the impact of extinction. Depending on the geological period or place at which the majority of living Lauraceae originated, one may be able to identify geographic or environmental factors that could have mitigated the loss of diversity suffered by their relatives among basal angiosperms.

Lauraceae are a member of the order Laurales, which comprises seven families, 92 genera, and between 2840 and 3340 species, depending on the species numbers assumed for Lauraceae (Rohwer 1993; Chanderbali *et al.* 2001). The monophyly of the order and its sister group relationship to the Magnoliales receive strong bootstrap support in a 9-gene data set (87%; Y.-L. Qiu, personal communication, May 2003; see also the 5-gene data set of Qiu *et al.* 2000), and family relationships within the order are clear except for a trichotomy of Hernandiaceae, Lauraceae, and Monimiaceae (Renner & Chanderbali 2000). Laurales are particularly suited for a comparative study of net diversities because of the group's unusually good fossil record (below) and level of molecular phylogenetic exploration. Of the 92 genera, all but 13 (three of Monimiaceae and ten of Lauraceae) have been included in phylogenetic analyses based on more than one gene region, and six of the families have had between 17% and 100% of their species sequenced. (However, Lauraceae have only 4-5% of their species sampled.) This level of taxon sampling allows in-depth study of the relative ages of clades of contrasting net species-richness; it also assures that paraphyly, the single largest problem for diversity comparisons of higher taxa, is not a concern. Moreover, because of the exceptional fossil record of Laurales, the possibility exists to translate relative ages into absolute ages based on local molecular clocks. This solid phylogenetic and paleobotanical framework allows the tackling of questions about differences in species richness among contemporary clades that are of central importance in evolutionary biology (Ricklefs & Schluter 1993), but that have become stalled by issues relating to statistical analysis of trait correlations (*e.g.*, Ricklefs & Renner 1994, 2000; Dodd *et al.* 1999; Isaac *et al.* 2003). While sophisticated analyses of trait correlations can incorporate change over time and heteroge-

neous branch lengths in trees (Isaac *et al.* 2003), the data for such analyses need to come from well resolved and supported topologies, fossils, and molecular clock-based estimates of branch lengths.

The present review of relevant available data for Laurales contributes towards this goal. It starts with brief summaries of the extant diversity, oldest fossils, and molecular-clock derived major node ages for each of the seven families (based on published and unpublished data sets) and then compares results from the family analyses to an analysis of the order, which is based on a different set of genetic markers and a much smaller sample of taxa. The effects on age estimation of using fewer taxa, but more nucleotides, are insufficiently understood. Results of the seven family analyses and the overall Laurales-analysis are used to address four questions about net diversity differences between major lineages of Laurales: Did they accrue over greatly different lengths of times? Did events affect related clades in similar ways? Did certain ecological settings favor speciation over extinction? And, are there traits that correlate with net species accumulation and that deserve further study as perhaps enhancing speciation?

Materials and Methods

Laurales diversity and its imbalance

The software program Mesa (Agapow & Purvis 2002) was used to test whether a null model of Markovian evolution (each descendent lineage splitting or going extinct at random, with the probabilities of either event constant for all species) could generate species diversities similar to those seen in the seven families of Laurales. Species numbers for the seven families come from the sources cited under the family accounts (Results). Mesa calculates several tree imbalance statistics of which I report the metric suggested by Guyer and Slowinski (Slowinski & Guyer 1989; Guyer & Slowinksi 1993). To account for the Hernandiaceae, Lauraceae, Monimiaceae trichotomy, the test for significant imbalance was run for all three possible resolutions.

Time estimates

Likelihood ratio tests were used to assess the severity of rate heterogeneity among sequences (Sanderson 1998). Maximum likelihood (ML) scores of models with and without a clock were obtained from PAUP (Swofford 2002) after exclusion of all gapped or ambiguous characters from the data sets, using PAUP's character exclusion option. Model parameters were estimated simultaneously, usually on one of the most parsimonious trees obtained from the same data before exclusion of gapped or ambiguous characters.

Where data rejected the assumption that substitution rates could be modeled as approximately equal over the tree, Sanderson's penalized likelihood approach (implemented in the software package 'r8s'; Sanderson 2002) was used to obtain age estimates. The approach involves a semi-parametric model of evolution that assumes different substitution rates along the tree and that then reduces the resulting enormous number of more or less arbitrary alternatives by assigning penalties that increase with the abruptness of rate change between adjacent branches. The relative contributions of the two components of the model are determined by a "smoothing" parameter, calculated by sequentially removing part of the data (*e.g.*, one branch at a time), re-estimating the remaining model parameters, and then using the fitted model parameters to predict the data that were removed (*i.e.,* the expected number of substitutions on the pruned branch). This is repeated with different smoothing values; the one that best predicts the removed data is considered optimal (Sanderson 2002). Advantages of the r8s software are that it not only allows

incorporating multiple calibration points but that these can take two forms. Ages of particular nodes can be fixed, or nodes can be assigned minimal and/or maximal ages, with the program calculating the most likely age, given the remaining age constraints and substitutions in the data set.

Input data for the r8s software are branch lengths calculated under some model of evolution. Models that fit the specific data sets used here were developed using likelihood ratio testing. Usually, the best fitting model was the general-time-reversible model (GTR Yang 1994), which assumes that all substitution probabilities are independent and accounts for unequal base frequencies (I used the empirically observed frequencies), a possible transition/transversion bias, and variable substitution rates among sites, which can be described by a gamma distribution with four rate categories (the default in PAUP). The proportions of invariable sites and the shape parameters of the gamma distributions were estimated using the implementation of Yang's model in PAUP. Starting trees for ML searches were obtained via neighbor joining or parsimony; the swapping strategy employed was tree bisection-reconnection swapping.

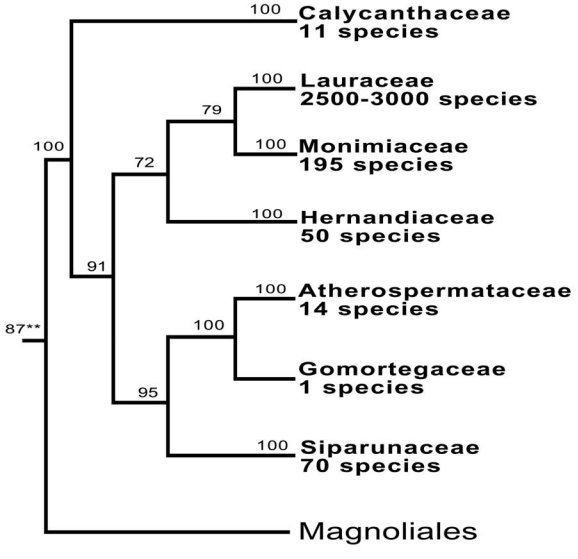

Fig. 1. Family relationships in the order Laurales based on combined sequences from six cpDNA introns and spacers (modified from Renner 1999). Bootstrap values (on branches, from 1000 pseudo-replicates) are slightly higher than in the original paper because of the inclusion of formerly missing sequence sections. The bootstrap value marked with two asterisks comes from an ongoing 9-gene data set (Y.-L. Qiu, personal communication, May 2003).

Absolute times

Absolute times scales are those of Gradstein *et al.* (1995) for the Cretaceous and Berggren *et al.* (1995) for the Lower Tertiary. Progress in geochronology during the past years has resulted in striking (to non-paleobiologists) changes in the absolute ages given for the geological periods of the Cretaceous and Tertiary, and this obviously determines the resulting estimates.

Results

Species diversity imbalance

Based on the metric of Slowkinski and Guyer (1989), the observed imbalance in species numbers between the seven families of Laurales is too great to be ascribed to a constant-rates Markov null model (statistics not shown). The polytomy of Hernandiaceae, Lauraceae, and Monimiaceae required that the test be carried out three times: As long as either Hernandiaceae (50 species) or Monimiaceae (192 species) are the sister clade to Lauraceae (2500-3000 species), Lauraceae are significantly more species-rich than expected. However, if the two families together are assumed to be the sister clade of Lauraceae, then the latter are not significantly richer in species than their closest relative. Siparunaceae (70 species) are always significantly more species-rich than their sister clade Gomortegaceae (1 species) plus Atherospermataceae (14 species).

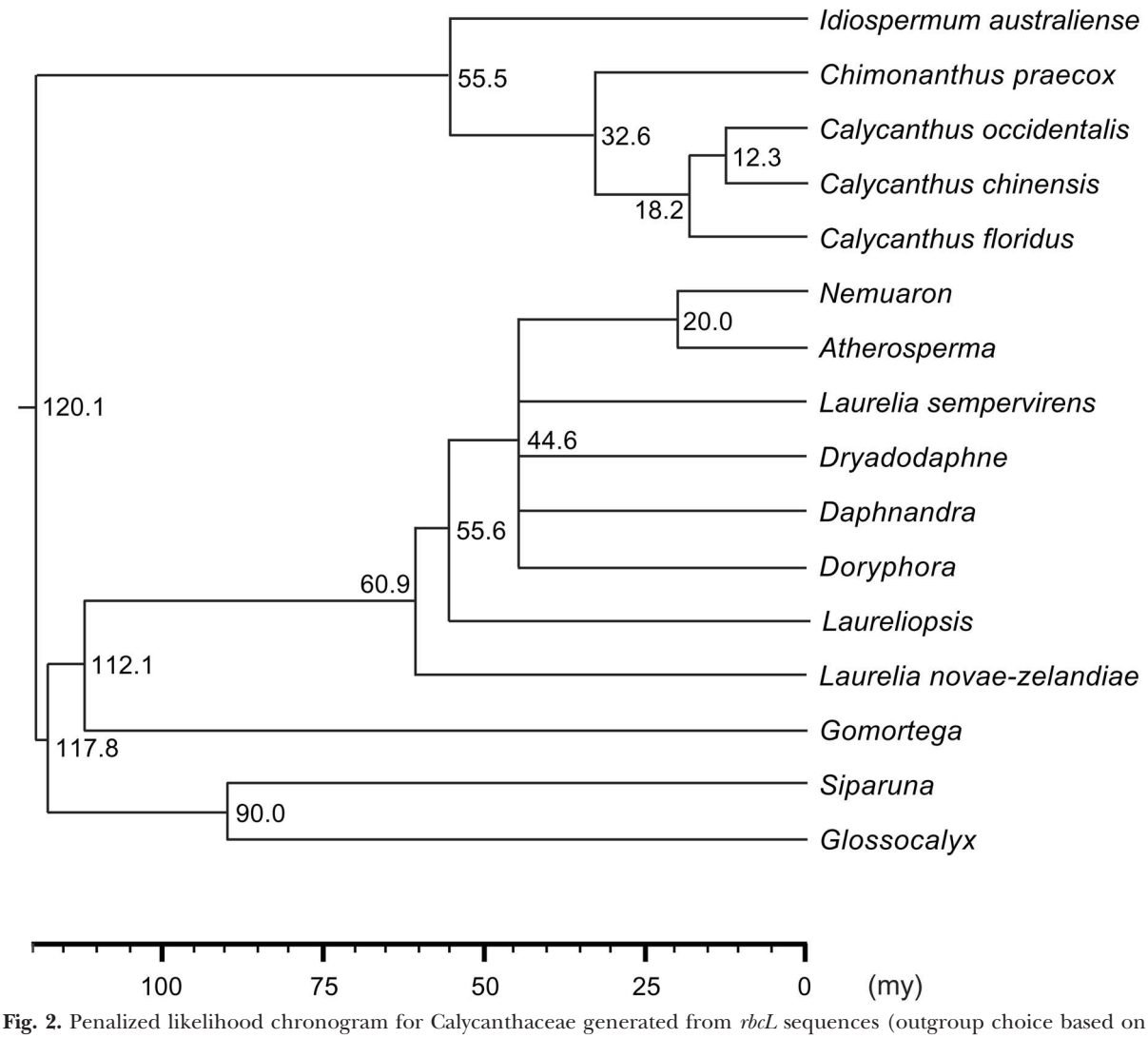

Fig. 2. Penalized likelihood chronogram for Calycanthaceae generated from *rbcL* sequences (outgroup choice based on Fig. 1). Compare Fig. 3 for strikingly different time estimates for the same outgroup taxa, but using different DNA regions. Representatives of Magnoliales served to root the tree, but were pruned from the analysis (Sanderson 2002). Branch lengths were obtained under the GTR + G + Pinv model of evolution and calibrated by constraining the stem of Calycanthaceae to a minimum age of 110 my, based on Early Cretaceous *Virginianthus calycanthoides* flowers, and a maximum age of 120 million years, based on an assumed age of 140 my for the onset of flowering plant divergence (see text for references and for alternative placements of constraints). The age of the split between *Calycanthus* and *Chimonanthus* was constrained to minimally 24 my old, based on Miocene *Calycanthus* fruits, and the most recent common ancestors of Siparunaceae and of Atherospermataceae/Gomortegaceae were constrained to minimally 90 my old, based on fossils and results shown in Fig. 3.

Relative and absolute times of diversity accumulation in Laurales

The result that extant species numbers of Laurales families are significantly imbalanced, at least against a Markovian null model, clearly does not address differences in speciation and extinction rates through time. The following sections report results of age estimations for the major lauralean clades and address the issues of persistence and diversity accumulation. Ways to explore extinction rates are taken up in the Discussion.

The relative time that the different families have had to accumulate and lose species can be gauged firstly from their fossil record, secondly by their phylogenetic relationships, and thirdly from their genetic distances. Most directly relevant are the oldest fossils of each family, which are cited in the following accounts. The phylogenetic relationships of the seven families are shown in Fig. 1 and imply that the stem lineage of the six core lauralean families is exactly as old as the stem of Calycanthaceae. The six core families then split into two main lineages, one comprising Siparunaceae and their sisters, Atherospermataceae plus Gomortegaceae (making Siparunaceae as old as the stem of these two families); the other comprising Hernandiaceae, Lauraceae, and Monimiaceae, which seem to have diverged from their common ancestor over a short period of time, judging by extremely short branches separating the three (Renner & Chanderbali 2000).

Calycanthaceae

Calycanthaceae contain three genera and 10 species (Kubitzki 1993a, Zhou, Renner, and Wen, unpublished work). Of the three genera, the morphologically most divergent is *Idiospermum australiense* (Diels) S. T. Blake, which is a rain forest tree in Queensland with three to four large (4.5-5 x 5.5-6.5 cm) fleshy cotyledons that completely fill out the mature seeds and that are poisonous, at least to cattle (Endress 1983). Each *Idiospermum* seed is enclosed in a dry receptacle. The remaining members of Calycanthaceae have seeds enclosed in juicy poly-carpellate receptacles and comprise six species of *Chimonanthus* in China, *Calycanthus chinensis* Cheng & S. Y. Chang (*Sinocalycanthus chinensis* (Cheng & S. Y. Chang) Cheng & S. Y. Chang) also in China, and *Calycanthus occidentalis* Hook. & Arn. in northern California and *C. floridus* L. in Florida.

The earliest fossil of Calycanthaceae is the flower *Virginianthus calycanthoides* Friis, Eklund, Pedersen & Crane from the Puddledock flora in Virginia, which dates at least to the Albian (112-105 my) or possibly Aptian (Friis *et al.* 1994; Crane *et al.* 1994; E. M. Friis, personal communication, May 2003). A recently described Brazilian fossil from the Aptian or Albian that includes flowers, buds, and leaves (Mohr and Eklund 2003) shares several flower features with Calycanthaceae and may represent the common stem lineage of Calycanthaceae and remaining Laurales. Another calycanthaceous flower comes from the Turonian of New Jersey (K. Nixon, personal communication, May 2003). *Calycanthus* itself is known from fruits described from Miocene strata in eastern Germany (Mai 1987).

All 10 species of Calycanthaceae have been sequenced for three chloroplast loci (*trnL-trnF* spacer, *trnL* intron, *trnC-trnD* spacer) and the nuclear ITS region (Zhou, Renner, and Wen, unpublished). The three genera are highly distinct from each other, suggesting lengthy separation. Branch lengths between the Chinese *Chimonanthus* species by contrast are extremely short. Age estimation in the present study relies on the relatively slowly mutating chloroplast gene *rbcL*, and Fig. 2 shows a penalized likelihood chronogram based on branch lengths from that gene obtained under the GTR + G + Pinv model of evolution (data from Renner 1999 and unpublished). Three representatives of Magnoliales were included as

'extra' outgroups to root the tree and were then pruned from the analysis (Sanderson 2002). Four nodes were constrained as follows. The stem of Calycanthaceae either was constrained to a minimum age of 90 my, based on the fossil flower from New Jersey, or to 110 my, based on the fossil flower from Virginia, which shows a mosaic of features today seen in *Idiospermum*, *Calycanthus*, and *Chimonanthus*. The age of the split between *Calycanthus* and *Chimonanthus* was constrained to minimally 24 my old, based on the Miocene *Calycanthus* fruit. This, however, might be too conservative, and perhaps the fruit fossil should instead be associated with the divergence between Chinese and American *Calycanthus* (Fig. 2). The final climatic deterioration of the Bering region began in the Miocene and, from then on, most of the plants and mammals that dispersed between the two continents appear to have been cold-tolerant forms.

While the precise placement of Calycanthaceae constraints is problematic (above), results reported in the next section allowed constraining the most recent common ancestors of the outgroups Siparunaceae, Atherospermataceae, and Gomortegaceae as at least 90 my old. However, this was found to make little difference for ages obtained within Calycanthaceae.

The chronogram (Fig. 2) suggests that *Idiospermum australiense* could be as young as 55 my old, which is too young for it to have reached its present range in Queensland before the break-up of East Gondwanaland, which began some 130 my ago (Li & Powell 2001). Error margins around this estimate, however, are ± 30% since it is based on the limited information contained in a single gene. There are modern bird flyways that connect Queensland and China (Feduccia 2003), but it is unlikely that birds would carry the fruits of *Idiospermum*, which weigh up to 130 g (Endress 1983; S. Worboys, Cook University, Cairns, Australia, personal communication), across any such distance. *Idiospermum* is locally common where it occurs, and all populations known are found in creeks near sea level (Endress 1983). Dispersal by water (in a geographically very different Malaysian region 55 my ago) is thus a possibility.

Atherospermataceae and Gomortegaceae

Gomortega comprises a single species in northern Chile. Atherospermataceae consist of 11 species, two (in two genera) in Chile and the remainder (in five genera) in Tasmania, Australia, New Zealand, New Caledonia, and New Guinea (Renner *et al.* 2000). All species have been sequenced for five chloroplast loci (*rpl16*, *trnT-trnL*, *trnL-trnF*, *atpB-rbcL*, *psbA-trnH*) and most also for the *rbcL* gene. Ecologically, Atherospermataceae are prominent elements of south Chilean laurel forests and temperate evergreen forests of New Zealand and Tasmania where they grow on well-drained or humid sites mainly between 800 m and 2400 m elevation. Different from other Laurales, their achenes are dry and wind-dispersed.

Gomortega is only known from the Late Oligocene-Early Miocene (24-21 Ma; Nishida *et al.* 1989) but Atherospermataceae go back to the Campanian, Paleocene, and Eocene of Antarctica (Dusén 1908; Poole & Francis 1999; Poole & Gottwald 2001), the Upper Eocene of Germany (Gottwald 1992), the Lower Oligocene of the eastern Cape Province and Egypt (Mädel 1960), and the Oligocene of New Zealand (Mildenhall 1980 and references therein). The oldest record of the family, however, is pollen found in Kerguelen plateau material (Ocean Drilling Program, leg 120) dated to the Coniacian at 86-88 my ago (Mohr 1998).

Fig. 3 shows a penalized likelihood chronogram that reflects input branch lengths from substitutions in combined sequences of six cpDNA introns and spacers comprising 4203

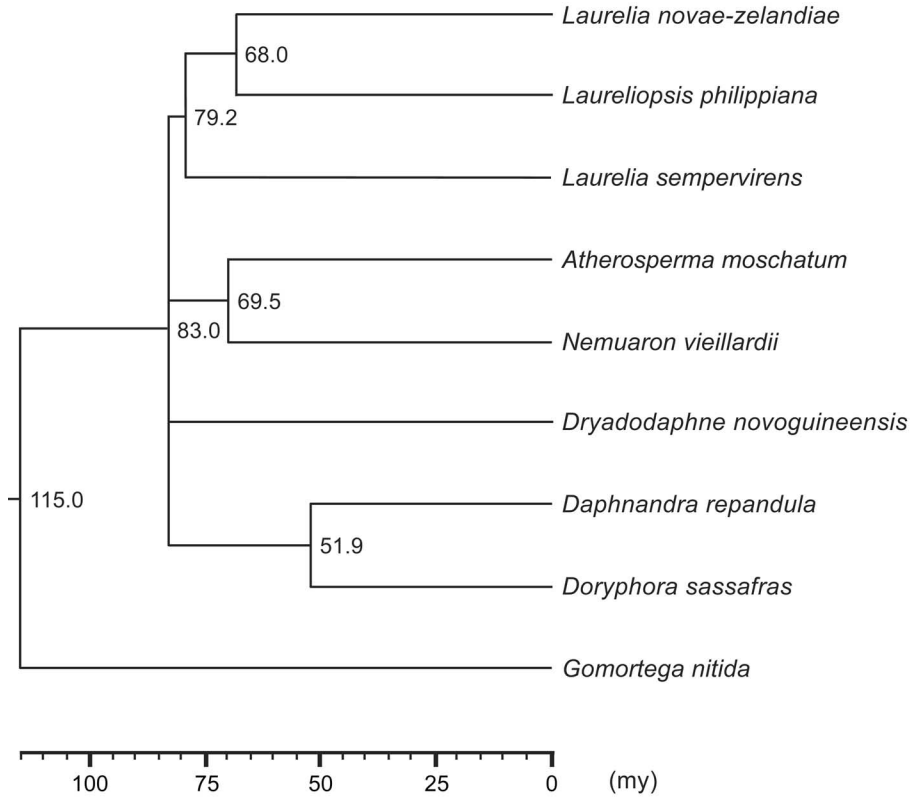

Fig. 3. Penalized likelihood chronogram for Atherospermataceae and Gomortegaceae reflecting branch lengths from substitutions in combined sequences of six cpDNA regions (see text; data modified from Renner *et al.* 2000). Siparunaceae served to root the tree and were then pruned (compare Figs. 1 and 2). Branch lengths were obtained under the GTR + G + Pinv model of evolution and calibrated by constraining the stem of Atherospermataceae to a maximum age of 115 my and a minimum age of 88 my, and the age of the split between *Laurelia/Laureliopsis* and the remaining genera to minimally 83 my old (references to fossils, see text).

nucleotide positions after exclusion of all gapped characters (data modified from Renner *et al.* 2000). Branch lengths were obtained under the GTR + G + Pinv model of evolution and calibrated by constraining the stem of Atherospermataceae as having a minimum age of 88 my, based on the Coniacian pollen, and a maximum age of 115 my. (The latter is based on widely held views about the age of angiosperms overall; cf. Discussion). The age of the split between *Laurelia/Laureliopsis* and the remaining genera was constrained to minimally 83 my old based on Campanian Laureliopsis-like wood (Poole & Francis 1999). The resulting absolute ages suggests that *Atherosperma*, a monotypic genus endemic on Tasmania is 69.5 my old and could thus have arrived overland from Antarctica or Australia, which maintained land contact via the South Tasman Rise up to 40 my ago (Li & Powell 2001). By contrast, *Laurelia novae-zelandiae* Cunn. dated as perhaps 68 my old, must have reached New Zealand via long distance dispersal because seafloor spreading between Antarctica and New Zealand started at 96 my ago, with New Zealand reaching its present day position 2000 km from Australia and Antarctica, by 60 my ago. As indicated above, seed dispersal in Atherospermataceae is by wind.

Siparunaceae

Siparunaceae consist of about 70 species in two genera, tropical American *Siparuna* with 69 species and West African *Glossocalyx longicuspis* Benth. (Renner & Hausner, in press). The family has no fossil record (Renner & Won (2001)

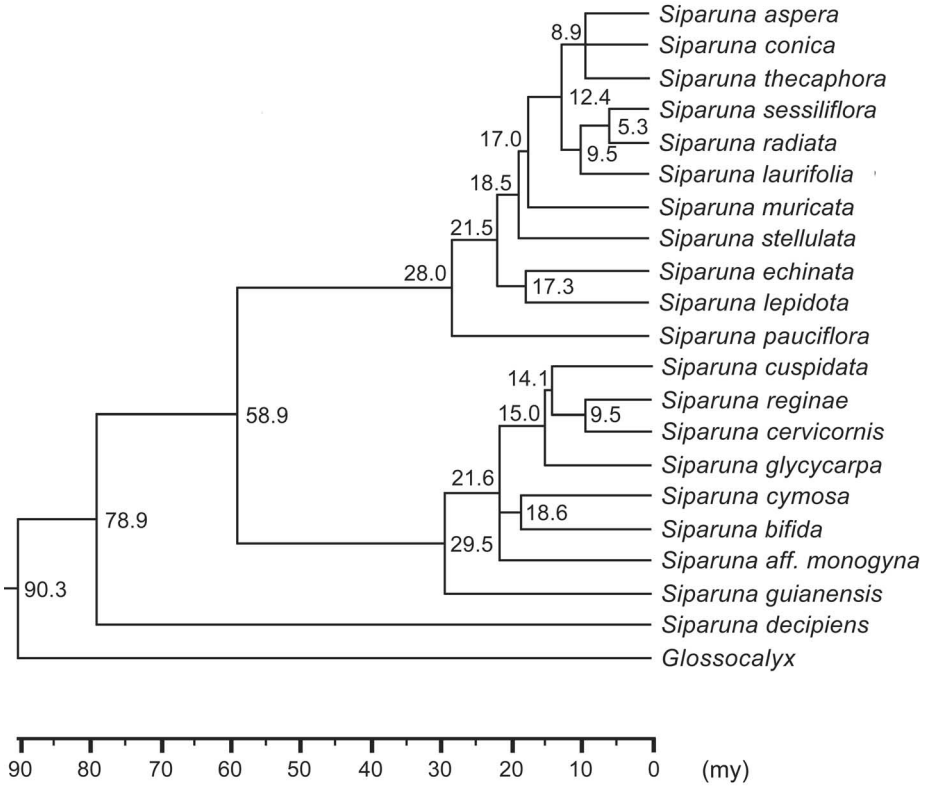

Fig. 4. Penalized likelihood chronogram for Siparunaceae reflecting branch lengths from substitutions in combined nuclear and chloroplast sequences (see text; data modified from Renner & Won 2001). Gomortegaceae served to root the tree and were then pruned (compare Figs. 1 and 2). Branch lengths were obtained under the GTR + G + Pinv model and calibrated by constraining the stem of Siparunaceae to a minimum age of 88 my based on oldest fossils of their sister clade (Fig. 3). Note that an age of 90 my would have permitted relatively easy crossing of a still narrow Atlantic between West Africa (*Glossocalyx*, today 1 species) and South America (*Siparuna*, today 69 species).

re-evaluated two supposed fossil Siparunaceae after receiving them on study loan). Fig. 4 shows a penalized likelihood chronogram for Siparunaceae reflecting branch lengths from substitutions in nuclear ITS sequences and cpDNA *trnL-trnF* spacer sequences comprising a combined 1040 nucleotide positions after exclusion of all gaps (data modified from Renner & Won 2001). Gomortegaceae served to root the tree and were then pruned (compare Figs. 1 to 3). Branch lengths were calibrated by constraining the stem of Siparunaceae to minimally 88 my old based on the oldest fossils of their sister clade (previous family account). Note that such an age would have permitted overland passage or island hopping between a still close West Africa and South America, which fits the finding that the single African member of the family is sister to all tropical American ones rather than being embedded among them as would be expected if it were the result of long distance dispersal.

Results suggest a minimum age of 59 my for the initial divergence of an Andean clade from a lowland clade and an age of around 28 my for the onset of major species accumulation in the Andean clade.

Monimiaceae

Monimiaceae consist of 195 species in 25 genera of which all but three have at least one species sequenced (Renner 1998, 1999, and unpublished). The family's phylogenetic circumscription and placement have been problematic (Philipson 1987, 1993; Renner 1999), but are gradually becoming clear, with the molecular data corroborating many of Philipson's groups. Thus, his subfamily of *Peumus* (1

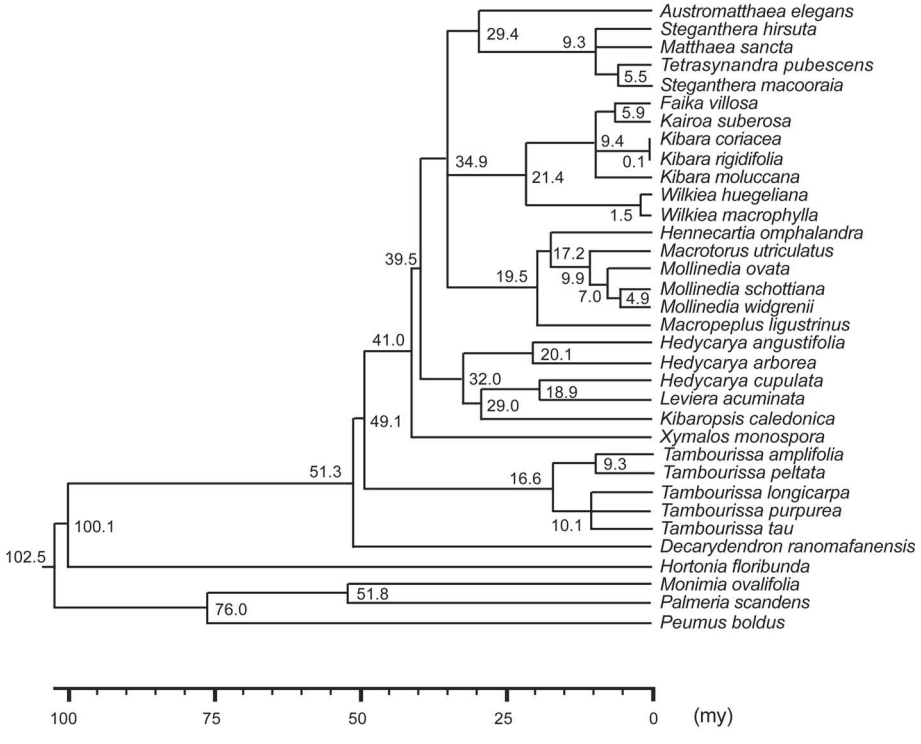

Fig. 5. Penalized likelihood chronogram for Monimiaceae reflecting branch lengths from substitutions in combined nuclear and chloroplast sequences (Renner, unpublished). A basal taxon of Lauraceae (*Hypodaphnis zenkeri*) served to root the tree and was then pruned (compare Fig. 1). Branch lengths were obtained under the GTR + G + Pinv model and calibrated by constraining the stem of Monimiaceae as having a minimum age of 90 my based on Maastrichtian or Campanian *Hedycaryoxylon* wood (Mädel 1960, Poole & Gottwald 2001).

species in Chile), *Monimia* (3 species in Mauritius and Réunion), and *Palmeria* (14 species mainly in New Guinea, but one species westward to east Sulawesi and three in eastern Australia) is supported and is sister to all other Monimiaceae (Fig. 5). The first-branching taxon in this latter clade ('all other Monimiaceae') is *Hortonia*, with a single species on Sri Lanka. Wood characteristic of Monimiaceae is assigned to the form genus *Hedycaryoxylon* and is known from the Campanian of Antarctica (Poole & Gottwald 2001), the Upper Eocene of Germany (Süss 1960; Gottwald 1992), and the Lower Oligocene of the Cape Province (Mädel 1960). A leaf (*Monimiophyllum*) has also been reported from the Paleocene/Eocene of Antarctica (Birkenmajer & Zastawniak 1989). Monimiaceae thus were widespread by the Early Tertiary, and Raven and Axelrod (1974) hypothesized that they migrated between South America and Africa, and between West Gondwana, Madagascar, India, and Australia across a still narrow Indian Ocean, which would require a minimum age of 120 my (Li & Powell 2001). The sole extant Monimiaceae in Africa is *Xymalos monospora*.

Fig. 5 shows a penalized likelihood chronogram for Monimiaceae reflecting branch lengths from substitutions in combined nuclear ITS and cpDNA trnL-trnF spacer sequences comprising 983 nucleotide positions after exclusion of all gaps (Renner, unpublished). A basal taxon of Lauraceae (*Hypodaphnis zenkeri* (Engl.) Stapf) served to root the tree and was then pruned (compare Fig. 1). Branch lengths were calibrated by constraining the stem of Monimiaceae as having a minimum age of 90 my, based on the oldest *Hedycaryoxylon* woods, and a maximum age of 120 my, based on an assumed age of 140 my for the

flowering plants. (The earliest fossils generally accepted as angiosperms are pollen records from 141-132 my ago (Brenner 1996; Hughes 1994)).

Results suggest that the Chilean *Peumus* diverged from the *Monimia/Palmeria* line some 76 my ago, perhaps by disruption of a once continuous range that stretched from Chile across Antarctica and the Kerguelen plateau to Madagascar. Indo-Madagascar and eastern Antarctica were connected until 120 my, and a link via the Kerguelen outcrops seems to have persisted as late as 80 my ago (Sampson *et al.* 1998). Former presence of *Monimia* ancestors on Madagascar has to be postulated to explain the occurrence of the genus on the islands of Mauritius and Réunion, east of Madagascar, which are only 7.8 and 2.5-3 my old. The split between *Monimia* and *Palmeria* in turn is dated to 52 my ago, which would make *Palmeria* old enough to have reached Queensland and New Guinea overland from Antarctica. As mentioned above, Antartica and Australia maintained land contact via the South Tasman Rise up to 40 my ago (Li & Powell 2001).

The further biogeographic history of Monimiaceae, especially their Eocene entry into Laurasia (documented by fossil woods from Germany) and subsequent entry into South America, which appears to have occurred quite recently (as indicated by the short branch length of the clade that comprises all South American Monimiaceae, Fig. 5), are the subject of an ongoing study.

Lauraceae

The Lauraceae comprise 2500-3000 species in about 50 genera of which 44 (and 122 species) have had representatives included in molecular phylogenetic studies (Rohwer 2000; Chanderbali *et al.* 2001). Chanderbali *et al.*'s conclusions were based on phylogenies from four cpDNA regions plus nuclear ITS and 26S rDNA sequences. Two of the DNA regions (*rpl16* and ITS) satisfied the molecular clock as assessed by likelihood ratio testing, and these branch lengths then formed the basis for age estimation, with calibration coming from a geological event, the separation of Africa and South America at 90 my. Together, the topologies and calibrated branch lengths indicated that Lauraceae radiated when trans-Tethyean migration was relatively easy, and basal lineages were clearly established on Gondwanan or Laurasian terrains by the Late Cretaceous. *Caryodaphnopsis* and *Neocinnamomum* may be the only extant representatives of the ancient Lauraceae flora documented in Middle to Late Cretaceous Laurasian strata (below). The bulk of today's genera is concentrated in a terminal 'Perseeae-Laureae' clade that radiated in Early Eocene Laurasia. Several genera and their immediate satellites, for example the *Persea* cluster and the *Cinnamomum* cluster, show tropical amphi-Pacific disjunctions that Chanderbali *et al.* credited to the disruption of Boreotropical ranges by Eocene-Oligocene climatic cooling. By contrast, the *Ocotea* genus complex shows a trans-Atlantic disjunction possibly derived from a Madrean-Tethyan ancestral distribution. Overall, findings supported morphology-based hypotheses (Rohwer & Kubitzki 1993) of a Laurasian ancestry for most of today's tropical American diversity of Lauraceae, with molecular-clock based estimates for the arrival of the *Ocotea* complex in South America sometime during the Miocene.

Although Lauraceae fossils cannot unambiguously be assigned to nodes on current trees, it is clear that the family was both widespread and diverse by the Early Cretaceous (Upchurch & Dilcher 1990; Drinnan *et al.* 1990; Herendeen *et al.* 1994; Eklund & Kvacek 1998; Eklund 1999, for a summary). Well-preserved flowers with the general floral structure of genera in the *Persea* group (but unfortunately also some genera in Cinnamomeae) have been described from Eocene deposits in

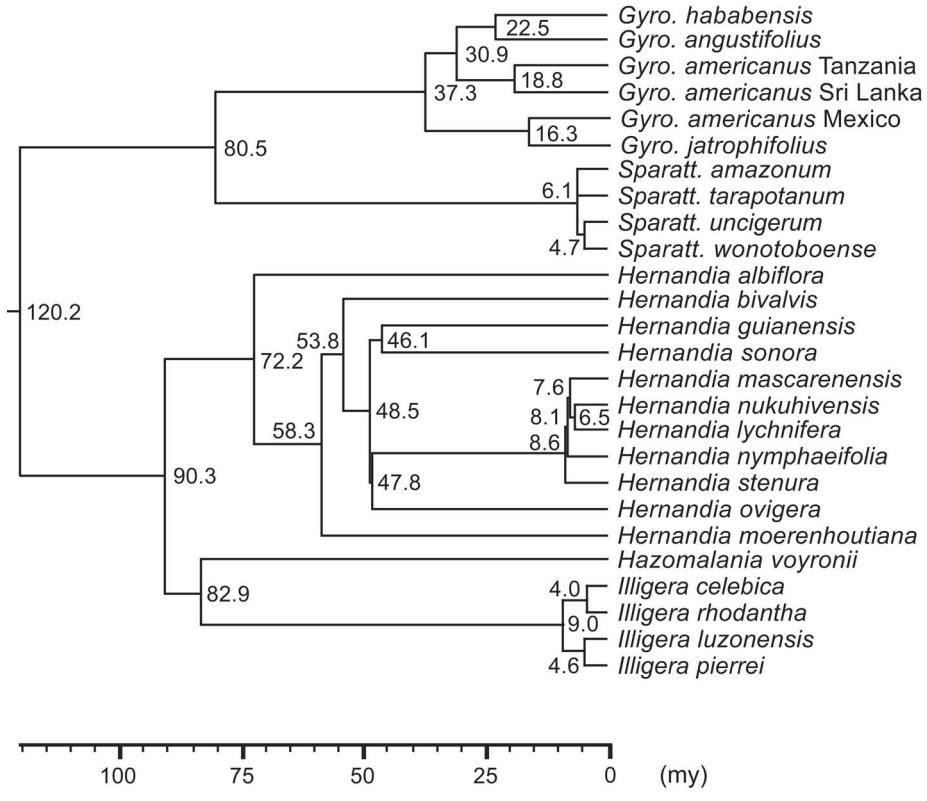

Fig. 6. Penalized likelihood chronogram for Hernandiaceae reflecting branch lengths from substitutions in three cpDNA spacer and intron regions (Renner & Zhang, submitted). Six basal taxa of Lauraceae and Monimiaceae served to root the tree and were then pruned (compare Fig. 1). Branch lengths were obtained under the GTR + G + Pinv model and calibrated by constraining the stem of Hernandiaceae to a minimum age of 90 my, based on Campanian fossils of Lauraceae and Monimiaceae (compare text and Fig. 5), and a maximum age of 120 my, based on an assumed age of 140 my for the flowering plants. Sparatt = *Sparattanthelium*, Gyro = *Gyrocarpus*.

North America and Late Eocene Baltic amber and even the Turonian and Cenomanian (Drinnan *et al.* 1990; Herendeen *et al.* 1994 and references therein).

Hernandiaceae

Hernandiaceae comprise five genera and 50 species, several only known from their types (Kubitzki 1969, 1993b; Renner & Zhang, submitted). Seven species occur in Africa, four in Madagascar, 22 in the neotropics, 21 in Indochina, Malesia and throughout the Pacific, and three in Australia; one species (*Gyrocarpus americanus* Jacq.) is supposed to have a pantropical range. Twenty-four species, and several accessions of the pantropical taxon, have been sequenced for three cpDNA regions (*trnL-trnF* spacer, *trnL* intron, *rpl16* intron) amounting to 2265 aligned base pairs. As predicted by morphology, there is a deep split between an ancestrally African-Madagascan-Malesian lineage comprising *Hazomalania*, *Illigera*, and *Hernandia*, and an African-tropical American lineage comprising *Gyrocarpus* and *Sparattanthelium*. The basal splits between these genera relate parsimoniously to the break-up of Gondwana (Fig. 6).

For *Hernandia*, with c 20 species, Kubitzki (1969) proposed three dispersal events from Polynesia to Central America and subsequent dispersal from the West Indies or Guianas to the West African offshore islands São Tome and Bioko. Current topologies (Fig. 6) support minimally two arrivals in tropical America, but minute sequence divergences within tropical American/Polynesian clades make it difficult to resolve details. African accessions of the supposedly pantropical species *Gyrocarpus ameri-*

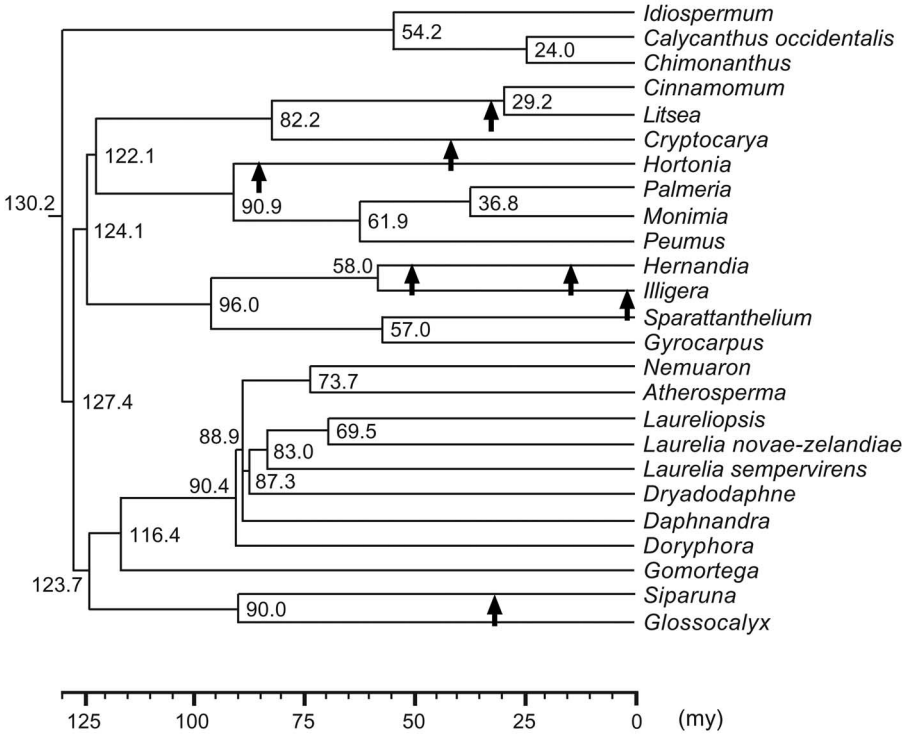

Fig. 7. Penalized likelihood chronogram for the order Laurales reflecting branch lengths from substitutions in six combined cpDNA regions (data modified from Renner 1999). Three representatives of Magnoliales served to root the tree and were then pruned. Branch lengths were obtained under the GTR + G + Pinv model and calibrated by constraining the stem of Laurales to a minimum age of 110 my, based on the oldest fossils of Calycanthaceae, and a maximum age of 130 my, based on an assumed age of 140 my for the flowering plants (compare text). In addition, the stem lineages were constrained of *Calycanthus/ Chimonanthus* to minimally 24 my old (compare Fig. 2), *Laurelia/ Laureliopsis* to minimally 83 my old (compare Fig. 3), Siparunaceae to minimally 90 my old (compare Fig. 4), and Monimiaceae to minimally 90 my old (compare Fig. 5). Arrows mark major bursts of extant species accumulation identified in the family analyses (Figs. 3-6 and text).

canus group with the other African species of *Gyrocarpus* rather than tropical American *G. americanus*, casting doubt on the current wide concept of *G. americanus* (Kubitzki 1969).

Fig. 6 shows a penalized likelihood chronogram for Hernandiaceae reflecting branch lengths from substitutions in three combined cpDNA gene, spacer, and intron sequences comprising 1892 nucleotide positions after exclusion of most gapped characters (Renner & Zhang, submitted). Six basal taxa of Lauraceae and Monimiaceae served to root the tree and were then pruned (compare Fig. 1). Branch lengths were calibrated by constraining the stem of Hernandiaceae as having a minimum age of 90 my, based on Campanian fossils of Lauraceae and Monimiaceae (*cf.* family accounts and Fig. 5), and a maximum age of 120 my, based on an assumed age of 140 my of the angiosperm crown group (Brenner 1996; Hughes 1994).

Laurales

A penalized likelihood chronogram for the order Laurales is shown in Fig. 7. It is based on a sample of 25 genera that optimally represent the families, meaning that small families are represented by most or all their genera and large families by genera selected to span their root. It reflects branch lengths from substitutions in six combined cpDNA spacer and intron regions (*rbcL*, *rpl16*, *trnT-trnL*, *trnL-trnF*, *atpB-rbcL*, *psbA-trnH*) comprising 3176 nucleotide positions after exclusion of all gaps

(data modified from Renner 1999). The data used are thus not exactly the same as in the individual analyses because as taxon representation changes, so do insertions and deletions in the alignments and therefore gapped characters excluded from branch length estimation under maximum likelihood (Methods). Three representatives of Magnoliales served to root the Laurales tree and were then pruned. Branch lengths were calibrated by constraining the stem of Laurales as having a minimum age of 110 my, based on the oldest fossils of Calycanthaceae (above and Fig. 2), and a maximum age of 130 my, based on an assumed age of flowering plants of 140 my (Brenner 1996; Hughes 1994). In addition, the stem lineages were constrained in *Laurelia/Laureliopsis* to minimally 83 my old (cf. Fig. 3), Siparunaceae to minimally 90 my old (cf. Fig. 4), Monimiaceae to minimally 90 my old (Fig. 5), and *Calycanthus/Chimonanthus* to minimally 24 my old (Fig. 2).

Results suggest that sparser taxon sampling consistently yields younger ages. For example, the splits between *Peumus/Monimia/Palmeria* vs. the remaining Monimiaceae, *Peumus* vs. *Monimia/Palmeria*, *Monimia* vs. *Palmeria*, *Sparattanthelium* vs. *Gyrocarpus*, and *Hernandia* vs. *Illigera* all are 10-20 my older in the order analysis than in the denser-sampled family analyses. Sampling in Atherospermataceae is the same in family and order analyses, and ages are nearly identical between analyses. An estimate that stays unaffected is the basal split in Calycanthaceae; *Idiospermum* always comes out as around 55 my old.

Fig. 7 shows the major bursts of extant species accumulation identified in the family analyses. Except for Lauraceae, genus and species sampling is dense enough to ensure that there are no unrecognized additional bursts of extant diversity accumulation in Laurales. Of the 92 genera of Laurales all have been sampled except ten small genera of Lauraceae, one small genus of Monimiaceae, and two Monimiaceae only known from type collections. Comparison of lineage ages with bursts of species accumulation (indicated by the arrows) shows that extant diversity in the order goes back to periods spread out over the Upper Tertiary.

Discussion

Effect of taxon sampling on age estimation

Taxon sampling is expected to affect genetic distances (branch lengths) and, thus, age estimates based on branch lengths. This is because the addition of sequences to an alignment has the effect of creating (or masking) shared or unique substitutions, which in turn affects model estimation for the evolution of the sequences. Branches rich in unique substitutions will appear as 'long' and will cluster with other long, isolated branches. Attempts to remedy the situation via denser taxon sampling often will not work, unless the amount of DNA sampled is also increased, because of the impact of substitution stochasticity, which is expected to be strongest for sequences differing by few substitutions such as those of closely related taxa. In other words, sampling error in age estimation is bad in data sets with isolated long branches but equally (?) bad in data sets with very short branches. An example of such sampling effects comes from a comparison of age estimates for the split between *Nemuaron* and *Atherosperma* from 1323 nucleotides of just the *rbcL* gene (20 my, Fig. 2), 3176 nucleotides of combined spacers and introns (74 my, Fig. 7), or 4303 nucleotides of even more spacers/introns (70 my, Fig. 3). The young estimate almost certainly is an artifact because *rbcL* sequences of *Nemuaron* and *Atherosperma* differ in a single base pair, which is too little information for a statistically reliable estimate.

Results of the present comparison of Laurales diversities as they relate to absolute ages

and geological times of major bursts of diversity accumulation fit with Darwin's impression that species loss and accumulation – seen from the present – appear to be asymmetric. It can be argued that this asymmetry is real. Taking Atherospermataceae, for example, their current 14 species appear to have diverged from each other 60-80 my ago. Yet, the family must have accumulated 'sufficient' species early on during its 100 my-long history for populations to occur in southern South America, Antarctica, New Zealand, the Kerguelen plateau, the Cape region, Egypt, and central Europe (references, see respective family account above). Conceivably, Atherospermataceae built up great species diversity sometime in the beginning of their history, with massive extinction then outweighing speciation following the end of the Eocene warm-tropical climate peak. An alternative scenario for atherosperms and similarly species-poor families is developed below. Large build-up followed by large-scale extinction might also have occurred in Monimiaceae, which have a fossil family range similar to that of atherosperms. However, different from Calycanthaceae (today 11 species), atherosperms (14 species), and Hernandiaceae (today 50 species), Monimiaceae have at least some medium-diverse genera, such as *Tambourissa*, with 49 species on Madagascar and the Mascarenes, and Kibara with 40 species in the Malesian region.

Magallón and Sanderson (2001) compared standing species diversity among angiosperm orders that have good fossil records with 'expected' species diversities, given each order's age and assuming constant speciation and extinction rates. Which groups are ranked as orders obviously affects results. For example, Magallón and Sanderson rank Calycanthales as an order, sister to Laurales, rather than as part of Laurales. This significantly increases the number of species-poor orders of basal angiosperms because overall there are few orders of basal angiosperms. The matter illustrates the difficulty of quantifying biological diversity, whether or not one relies on Linnean ranks.

Magallón and Sanderson's 'expected' ordinal diversities came from a Markovian birth/death model that either disregarded extinction or, in other runs, assumed high extinction rates. A high extinction rate corresponded to a species having a lower than 10% chance of survival to the present. Under this high extinction rate, the background diversification rate for all angiosperms (assuming an age of 132 my and a total number of 262,196 species) is 0.08 per my, and Calycanthales (= Calycanthaceae, 11 species) are 'extremely species-poor' compared to other angiosperm clades of the same age, while Laurales (= six families) have the statistically expected diversity. The few angiosperm orders/clades with extremely low apparent rates of diversification include, besides Calycanthales, Nymphaeales, Ceratophyllaceae, and Chloranthales (the last usually classified in Laurales before the advent of molecular data). Molecular-clock based estimates of the onset of species accumulation in Chloranthaceae suggest that most extant species-level diversity in that family is quite young and linkable to the raise of the Andes (genus *Hedyosmum*; Zhang & Renner, 2003).

Computer simulations similar to those of Magallón and Sanderson of stochastic birth/death models for Laurales show that a homogeneous process cannot produce the range of diversity values (1 to 2500-3000 spp.) observed among the seven Laurales families. No combination of species birth and extinction rates at the same time yields families as species-poor (Atherospermataceae, Calycanthaceae, Gomortegaceae) and as species-rich (Lauraceae, Siparunaceae) as actually exist. Perhaps then, speciation rates and accumulation of persisting entities among Laurales changed over time, with a dramatic increase in

Lauraceae and Siparunaceae, likely concomitant with the raise of the Andes.

The other side of the coin, extreme species-poverty in Atherospermataceae, Calycanthaceae, and Gomortegaceae, is more difficult to understand. Did these families suffer extremely high extinction rates – but why? Or were they in ecological settings unfavorable to speciation? To explore this latter hypothesis, namely that some lineages (essentially populations) in these families persisted for 100 my without proliferating much, one might try to relate species persistence to kind of habitat occupied by sister clades. Additionally, by mapping the total range and then roughly categorizing the diversity of habitats within the range in which a species or genus occurs, one might quantify and then compare habitat niche breadth between diverse and non-diverse clades. At least for one clade of Laurales, namely the clade formed by atherosperms, *Gomortega*, and Siparunaceae, the necessary data are available; range sizes for all species of *Siparuna* could be calculated from coordinates available for 8011 collections (Renner & Hausner, in press). Such a comparison of kind and number of habitat types occupied would permit testing the hypothesis that ancient lineages persist in habitats where they experience limited biological competition, such as on extreme soils or on oceanic or terrestrial islands, and from where they cannot readily 'escape' via species proliferation into better habitats (because of their physiological and morphological close local adaptation). An example of an ancient species that has been tracking a local habitat may be *Gomortega nitida*, the sole species of Gomortegaceae and apparently 100 my old. *Gomortega* is restricted to a few forest patches in Chile and is currently at risk of extinction. However, it is difficult to assess the impact of over-harvesting of timber on the current small range of *Gomortega*.

The four questions about Laurales net species diversity posed at the outset can thus be answered as follows. The seven families accrued their extant diversity over quite different lengths of time, and sister families do not appear to have accumulated diversity in significantly similar ways (compare Fig. 7). A geological event that appears to have had a consistent effect is the raise of the Andes: Lauraceae and Siparunaceae both experienced bursts of species accumulation in the mid-Tertiary and precisely in clades that are concentrated in the northern Andean foothills. Although not a main focus, results of this study do not point to morphological or ecological traits correlating positively with net species accumulation. All Laurales are insect-pollinated (flies, beetles, bees) and 2795 to 3295 species are animal-dispersed, while only 44 are wind-dispersed (Renner 1999 and references therein). Laurales thus exhibit the typical reproductive strategy of tropical tree lineages (*i.e.*, animal pollination and dispersal). They lack unusual defense compounds (Gottlieb in Rohwer 1993). Together these findings suggest that, in Laurales, habitats and geology played a more important role in diversity accumulation than did pollinators and dispersers.

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