ORIGINAL ARTICLE

Biogeography of the Monimiaceae (Laurales): a role for East Gondwana and long-distance dispersal, but not West Gondwana

Susanne S. Renner[1]*, Joeri S. Strijk[2], Dominique Strasberg[3] and Christophe Thébaud[2]

[1]*Systematic Botany and Mycology, Department of Biology, University of Munich, Menzinger Str. 67, D-80638 Munich, Germany,* [2]*Laboratoire Evolution et Diversité Biologique (UMR 5174), Université Paul Sabatier and CNRS, F-31062 Toulouse Cedex 9, France,* [3]*Université de La Réunion, Unité Mixte de Recherche Peuplement Végétaux et Bioagresseurs en Milieu Tropical, 15 avenue René Cassin, 97715 Saint-Denis, Cedex 9, France*

ABSTRACT

Aim The biogeography of the tropical plant family Monimiaceae has long been thought to reflect the break-up of West and East Gondwana, followed by limited transoceanic dispersal.

Location Southern Hemisphere, with fossils in East and West Gondwana.

Methods We use phylogenetic analysis of DNA sequences from 67 of the *c.* 200 species, representing 26 of the 28 genera of Monimiaceae, and a Bayesian relaxed clock model with fossil prior constraints to estimate species relationships and divergence times. Likelihood optimization is used to infer switches between biogeographical regions on the highest likelihood tree.

Results *Peumus* from Chile, *Monimia* from the Mascarenes and *Palmeria* from eastern Australia/New Guinea form a clade that is sister to all other Monimiaceae. The next-deepest split is between the Sri Lankan *Hortonia* and the remaining genera. The African Monimiaceae, *Xymalos monospora*, then forms the sister clade to a polytomy of five clades: (I) *Mollinedia* and allies from South America; (II) *Tambourissa* and allies from Madagascar and the Mascarenes; (III) *Hedycarya*, *Kibariopsis* and *Leviera* from New Zealand, New Caledonia and Australia; (IV) *Wilkiea*, *Kibara*, *Kairoa*; and (V) *Steganthera* and allies, all from tropical Australasia.

Main conclusions Tree topology, fossils, inferred divergence times and ancestral area reconstruction fit with the break-up of East Gondwana having left a still discernible signature consisting of sister clades in Chile and Australia. There is no support for previous hypotheses that the break-up of West Gondwana (Africa/South America) explains disjunctions in the Monimiaceae. The South American *Mollinedia* clade is only 28–16 Myr old, and appears to have arrived via trans-Pacific dispersal from Australasia. The clade apparently spread in southern South America prior to the Andean orogeny, fitting with its first-diverging lineage (*Hennecartia*) having a southern-temperate range. The crown ages of the other major clades (II–V) range from 20 to 29 Ma, implying over-water dispersal between Australia, New Caledonia, New Zealand, and across the Indian Ocean to Madagascar and the Mascarenes. The endemic genus *Monimia* on the Mascarenes provides an interesting example of an island lineage being much older than the islands on which it presently occurs.

Keywords

Bayesian relaxed clock, East Gondwana, Indian Ocean, long-distance dispersal, Monimiaceae, Sri Lanka, West Gondwana.

*Correspondence: Susanne Renner, Systematic Botany and Mycology, Department of Biology, University of Munich, Menzinger Str. 67, D-80638 Munich, Germany.
E-mail: renner@lrz.uni-muenchen.de

INTRODUCTION

Molecular clock-based dating has become a standard tool of historical biogeography. Between 1995 and 2005, some 100 plant biogeographical studies used molecular dating, and all inferred long-distance dispersal as the most plausible explanation of remote or disjunct organismal ranges (Renner, 2005a). The trend in animal biogeography is similar (de Queiroz, 2005). A recent analysis of disjunctions in Southern Hemisphere vascular plants reported 226 transoceanic dispersal events between Africa, Madagascar, Australia/New Guinea, New Caledonia, New Zealand and South America (Crisp *et al.*, 2009), and a search in Web of Science (26 February 2009) for the string 'long-distance dispersal' in titles, abstracts, or key words yielded well over 1000 hits. The resurrection of transoceanic dispersal as an explanation for range disjunctions has become so pervasive that long-distance dispersal (LDD) now seems a more plausible *a priori* explanation for most disjunctions than does continental drift (cf. de Queiroz, 2005). Nevertheless, there are some widespread angiosperm clades that pre-date the break-up of Gondwana, and it is such clades that present intriguing problems for historical biogeography. A classic example of such a clade is the angiosperm family Monimiaceae (Money *et al.*, 1950; Mädel, 1960; Axelrod, 1971; Raven & Axelrod, 1974; Lorence, 1985; Poole & Gottwald, 2001).

Monimiaceae is a pantropical family in the order Laurales that comprises 195–200 species in 28 genera (Philipson, 1993; Renner, 1998, 1999; Whiffin, 2007; Peixoto & Leite Pereira-Moura, 2008). The family is of disproportionate biogeographical interest because of its highly disjunct range and deep fossil record (Fig. 1). Extant Monimiaceae are distributed in Central and South America (*c.* 30 species in five genera), tropical Africa (the monotypic genus *Xymalos*), Madagascar and the Mascarenes (63 species in the genera *Decarydendron*, *Ephippiandra*,

Tambourissa and *Monimia*), Sri Lanka (*Hortonia*), New Caledonia (10 species in two genera, one of them endemic), New Zealand (one species), Australia (26 species, one reaching Tasmania), and the Malesian region. New Guinea, which has 75 species in 10 genera, is the centre of species and genus diversity (Takeuchi & Renner, 2002; Renner & Takeuchi, 2009). The family clearly occurs on fragments of the former Gondwana continent [South America, Africa, Madagascar, India/Sri Lanka, Australia/New Guinea; and Antarctica (as documented by fossils, see Materials and Methods)].

The austral distribution of Monimiaceae resembles that of other basal angiosperm families, such as Amborellaceae, Trimeniaceae, Hydatellaceae and Austrobaileyaceae, as well as basal eumagnoliid families (e.g. Degeneriaceae, Winteraceae, Atherospermataceae). Because of their Gondwanan range, Monimiaceae have figured prominently in discussions of the history of this continent. Specifically, their distribution has been linked to the break-up of West Gondwana, that is, the separation of Africa and South America at about 100–110 Ma (Money *et al.*, 1950; Mädel, 1960; Raven & Axelrod, 1974; Lorence, 1985), which was thought to explain the occurrence of the family in tropical America and Africa.

The break-up of East Gondwana, which comprised Australia, Antarctica, Madagascar and India, began playing a role in the family's biogeography with the discovery of Monimiaceae wood fossils near Seymour Island in the Antarctic Peninsula (Poole & Gottwald, 2001). Full South Atlantic Ocean spreading occurred 120–100 Ma, severing the former link between East and West Gondwana near the Antarctic Peninsula (Somoza & Zaffarana, 2008). The separation of India from Antarctica and Australia began 130–124 Ma (Gaina *et al.*, 2007), while Australia–Antarctica began separating at about 90 Ma (Li & Powell, 2001). Seafloor spreading between Australia and Antarctica remained slow until *c.* 45 Ma, with land contact maintained via the South Tasman Rise until 40 Ma (Li &
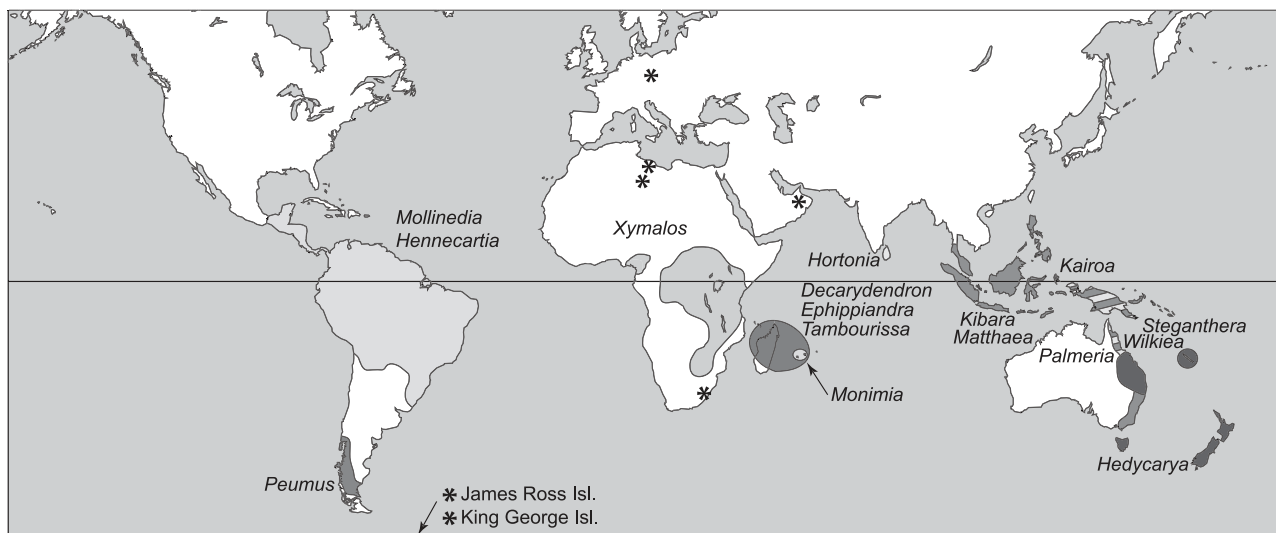

Figure 1 The geographical distribution of the Monimiaceae. For a complete list of the family's genera, see Fig. 2 and Materials and Methods. Asterisks indicate the locations of the oldest fossils (see Introduction). The wood fossil from Germany is of doubtful identity (see Materials & Methods).

Powell, 2001). The northward movement of India, by contrast, was very rapid, and by 83 Ma the distance between India and Antarctica was at least 2100 km (Ali & Aitchison, 2009). India and Madagascar broke apart *c.* 90 Ma (Raval & Veeraswamy, 2003), and Antarctica and New Caledonia *c.* 83 Ma (Neall & Trewick, 2008).

Because the Monimiaceae have *c.* 83-Myr-old fossils from both Africa and the Antarctic Peninsula (for details on these fossils see Materials and Methods), which was the last connection between East and West Gondwana, it is possible that the break-up of parts of Gondwana may have influenced the family's earliest evolution. The closest relatives of Monimiaceae are the Lauraceae and Hernandiaceae, of which the former also have an extensive Cretaceous fossil record (Eklund, 2000; von Balthazar *et al.*, 2007 and references therein), while the latter have no known fossils (Michalak *et al.*, 2010). The trichotomy between these families has not yet been resolved (Renner & Chanderbali, 2000). With the exception of the Sri Lankan *Hortonia* (one or two species), the *c.* 200 species of Monimiaceae have unisexual, usually small flowers that often are brown-red or greenish and look like immature fruits. In addition, about half the species are dioecious, with male plants usually much less conspicuous than female plants. All these traits have contributed to the family being underrepresented in collections, resulting in poor understanding of variation and, as a corollary, a tendency to recognize monotypic genera (12 out of 28 genera currently recognized). Many of the species, and even some genera, are known only from one or two collections worldwide.

Here we use nuclear and plastid DNA sequences from 34% of the family's extant species to infer the spatial and temporal unfolding of the Monimiaceae clade from the Upper Cretaceous onwards. Particular interests were the detection of any Gondwanan signal in today's clade ranges, the origin of the endemic Monimiaceae of Madagascar and the Mascarene Islands, and the explanation of the relationships of the monotypic *Peumus* from Chile, *Hortonia* from Sri Lanka and *Xymalos* from Africa. This study concludes a series of biogeographical analyses of the order Laurales, which comprises some 3000 species in 92 genera and seven families: Calycanthaceae (Zhou *et al.*, 2006), Atherospermataceae (Renner *et al.*, 2000), Gomortegaceae (with just one species in Chile), Siparunaceae (Renner, 2005b), Lauraceae (Chanderbali *et al.*, 2001), Hernandiaceae (Michalak *et al.*, 2010) and Monimiaceae. Most of the Laurales clade appears to have evolved in the Southern Hemisphere, a pattern that is tested further here.

MATERIALS AND METHODS

Taxon sampling, DNA sequencing, alignment and phylogenetic analyses

We included 67 species from 26 of the 28 currently recognized genera of Monimiaceae (Philipson, 1986, 1987, 1993; Whiffin, 2007; Peixoto & Leite Pereira-Moura, 2008). The monotypic genus *Lauterbachia* has not been collected since its original

discovery in 1899, and the type in Berlin appears to have been destroyed (Philipson, 1985, 1986). *Parakibara* from the Moluccas is also only known from the holotype (in the Bogor herbarium) and was not available for sequencing. Madagascan, Comoros and Mascarene species were collected during extensive fieldwork in 2006 and 2008 (vouchers stored at the University of Toulouse DNA bank). Trees were rooted with representatives of Hernandiaceae and Lauraceae selected to span the roots of these families (Chanderbali *et al.*, 2001; Michalak *et al.*, 2010).

DNA isolation and sequencing followed standard procedures, using the universal primers of Taberlet *et al.* (1991) for amplifying and sequencing the *trn*L–*trn*F intergenic spacer. The *rbc*L gene was amplified with the external primers 1F (Fay *et al.*, 1997) and 1460R (Olmstead *et al.*, 1992), and the internal primers 636F, 724R and 724F (complement to 724R; Lledó *et al.*, 1998). The entire 5.8S gene, nuclear ribosomal internal transcribed spacer 2 (ITS-2), 669 nt of ITS-1, 18 nucleotides of the 3′ end of the 18S gene, and 30 nucleotides of the 5′ end of the 25S gene were amplified using the primers of von Balthazar *et al.* (2000). Direct amplification via polymerase chain reaction (PCR) always yielded single bands and unambiguous base calls, and we therefore refrained from cloning. In all, 104 sequences were newly generated for this study. Appendix S1 in the Supporting Information lists all DNA sources, species names with authorities, and GenBank accession numbers. Sequencing relied on Big Dye Terminator kits (Applied Biosystems, Foster City, CA, USA) and an ABI 3100 Avant capillary sequencer (Applied Biosystems). Sequence assembly of forward strands and reverse strands was carried out in Sequencher (version 4.6; Gene Codes, Ann Arbor, MI, USA), all sequences were Blast-searched in GenBank, and sequences were then aligned by eye. No program was required to align the *rbc*L gene, and the *trn*L and ITS data could also easily be aligned except for the Hernandiaceae and Lauraceae ITS1 and ITS2, which were too distant from the ingroup sequences. We therefore included only the 5.8S region for this locus, replacing ITS1 and ITS2 with question marks.

The aligned *trn*L matrix comprised 512 nucleotides, of which we excluded 26 in a microsatellite region. The aligned ITS matrix comprised 784 nucleotides, and the *rbc*L matrix comprised 1323 nucleotides. Analyses of the individual matrices revealed no contradictory phylogenetic groupings, and the chloroplast and nuclear data were therefore combined, yielding a matrix of 2619 characters. All tree searches relied on maximum likelihood (ML) as implemented in RAxML (Stamatakis, 2006; Stamatakis *et al.*, 2008) and the GTR + G model with eight gamma rate categories and separate partitions for the nuclear and chloroplast data. Statistical support for nodes was assessed by bootstrap resampling of the data under the same model (100 replicates).

Molecular clock analyses

Divergence dating relied on beast v. 1.4.8 (Drummond *et al.*, 2006; Drummond & Rambaut, 2007), which employs a

Bayesian Markov chain Monte Carlo (MCMC) approach to co-estimate topology, substitution rates and node ages. Posterior probability distributions of node ages were obtained from the concatenated alignment, but excluding the Hernandiaceae outgroups, which constituted the longest branches in the analysis, and a few species that differed from each other only in one or two substitutions. This left 53 taxa and 2593 nucleotides. All dating runs relied on the GTR + G model (again with eight rate categories), a Yule tree prior, with rate variation across branches uncorrelated and lognormally distributed. MCMC chains were run for 5–10 million generations (burn-in 20%), with parameters sampled every 1000th step. Results from individual runs were combined as recommended, and effective sample sizes for all relevant estimated parameters and node ages were well above 100.

The oldest monimiaceous woods are from the Upper Senonian (87–83 Ma) Umzamba beds of the Eastern Cape Province (*Hedycaryoxylon hortonioides*; Mädel, 1960; Müller-Stoll & Mädel, 1962) and the Campanian (83–71 Ma) of James Ross Island in Antarctica (*Hedycaryoxylon tambourissoides*; Poole & Gottwald, 2001). Other fossil woods attributed to the family come from the Late Lutetian to Late Eocene Graret el Gifa Formation in Libya [*Flacourtioxylon* (*Monimiaxylon*) *gifaense* Louvet; Louvet, 1971, 1974] and the Early Miocene of Djebel Zelten, likewise in Libya [*Xymaloxylon* (*Monimiaxylon*) *zeltenense*; Louvet, 1971, 1974]. A similar type of wood has been described from the Early Oligocene (34–28 Ma) of Oman (Privé-Gill *et al.*, 1993), and all three of these wood samples may represent a single species (Privé-Gill *et al.*, 1993, p. 554). Besides these African and Antarctic woods, there are leaves from Palaeocene/Eocene boundary strata (*c.* 57 Ma) on King George Island, Antarctic Peninsula (*Monimiophyllum antarcticum* Zastawniak; Birkenmajer & Zastawniak, 1989). *Hedycaryoxylom subaffine* (Vater) Süss and *Hortonioxylon henericiungeri* Gottwald, woods from the Late Eocene of Germany, have also been interpreted as Monimiaceae (Süss, 1960; Gottwald, 1992; these strata were originally dated to the Lower Senonian, but are now dated to the Upper Eocene). However, the wood anatomist E. Wheeler (Department of Wood and Paper Science, North Carolina State University, email to S.R. on 7 March 2006) has indicated that these woods might instead belong to Icacinaceae.

Using undoubted Monimiaceae fossils, we designed two calibration schemes for cross-validation. In scheme 1, we placed a normally distributed prior of 83 Ma with an SD of 1.5 and a 95% confidence interval (CI) of 80.5–85.5 on the crown group node of Momimiaceae, based on the oldest woods of Monimiaceae from the Upper Senonian (87–83 Ma) and the Campanian (83–71 Ma). In addition, we placed a normally distributed prior of 30 Ma on the divergence of *Xymalos*, with an SD of 1.5 and a 95% CI interval of 33–28, based on *Xymaloxylon zeltenense* and the woods from Oman, dated to 34–28 Ma. In scheme 2, we left *Xymalos* unconstrained and placed the 83 Ma-prior on the divergence of *Hortonia* from the remaining Monimiaceae, based on the rationale that the oldest woods have been likened to *Hortonia*, *Hedycarya* and *Xymalos*, but not *Peumus*, *Monimia* and *Palmeria* (which diverge below

Hortonia; see Results). *Peumus* has relatively narrow phloem rays and non-septate fibres, while *Xymalos*, *Hortonia* and *Hedycarya* (and other 'higher' Monimiaceae) have broader rays and septate fibres (Money *et al.*, 1950). The unusually broad rays are the most important character for palaeobotanists to assign fossil woods to Monimiaceae.

To convert stratigraphic ages into absolute ages, we used the geological time scale of Ogg (2008).

Biogeographical analyses

To reconstruct shifts between biogeographical regions we used ML as implemented in Mesquite v. 2.72 (Maddison & Maddison, 2009; http://mesquiteproject.org/mesquite/mesquite.html). The ML model incorporated information from genetic branch lengths and used the Markov *k*-state one-parameter model, which assumes a single rate for all transitions between character states (Lewis, 2001). Analyses were carried out on the highest likelihood tree with GTR + G branch lengths and transition parameters estimated based on the tip trait states (for the 67 taxa). Geographical regions were coded as an unordered multi-state character using seven states that present a balance between circumscribing geologically meaningful areas and not introducing too many states: (1) Australasia (which included Australia, New Guinea, Malesia and, for one outgroup, the Philippines), (2) New Zealand and New Caledonia, (3) South America, (4) Africa, (5) Madagascar and the Comoros, (6) the Mascarenes, and (7) Sri Lanka. The outgroup *Caryodaphnopsis bilocellata* from Vietnam was coded as '?' instead of introducing an autapomorphic character state for Laurasia. A finding is that the *Monimia* lineage is older than the islands it currently occurs on (see Results); we therefore re-coded all *Monimia* species as '?' to explore how this would affect the inferred ancestral ranges.

RESULTS

Main phylogenetic results

Maximum likelihood analysis of the 67-species matrix resulted in the tree shown in Fig. 2. Monimiaceae are monophyletic, and the deepest divergence in the family is that between a clade comprising *Peumus* (Chile), *Monimia* (Mascarenes) and *Palmeria* (eastern Australia and New Guinea), and a clade including all other Monimiaceae. In the latter, the first divergence involves *Hortonia* on the one hand and the remaining Monimiaceae on the other. The next split consists of the sole African Monimiaceae, *Xymalos monospora*, which is sister to a polytomy of (I) *Mollinedia* and allies from South America; (II) *Tambourissa* and allies from Madagascar and the Mascarenes; (III) *Hedycarya*, *Kibariopsis* and *Leviera* from New Zealand, New Caledonia and Australia; (IV) *Wilkiea*, *Kibara*, *Kairoa*; and (V) *Steganthera* and allies, all from tropical Australasia. (These clade numbers are used in Figs 2–4.) Several of the genera, including *Mollinedia*, *Steganthera* and *Wilkiea*, appear to be paraphyletic (Fig. 2), requiring future nomenclatural adjustments.
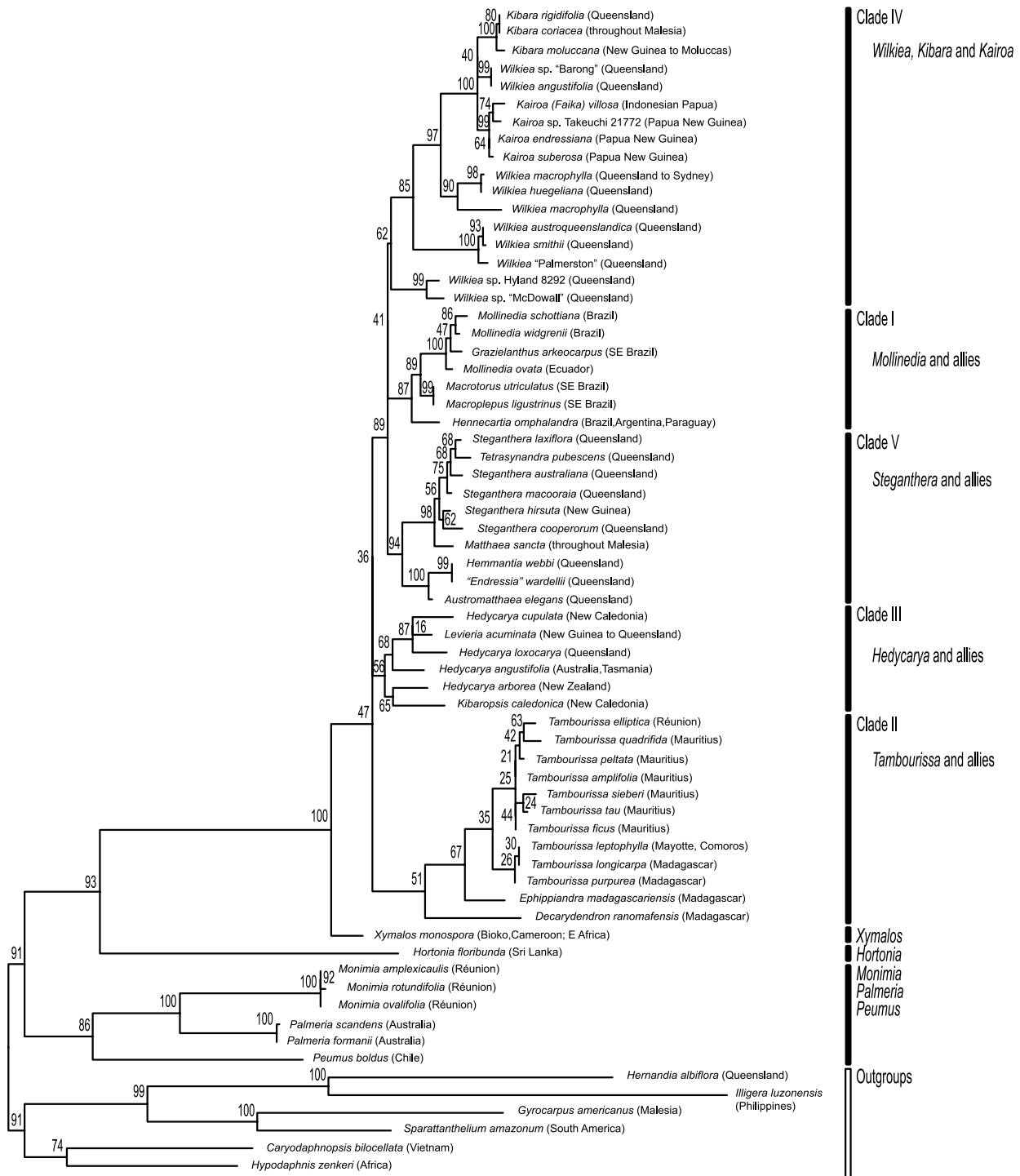
Figure 2 Phylogenetic relationships in the Monimiaceae as inferred from the combined chloroplast and nuclear data under maximum likelihood (ML) optimization (67 species, 2593 aligned nucleotides; the sequences of *Wilkiea hylandii* and *W. austroqueenslandica* are exactly identical and only one of these two species is shown here); numbers at nodes are ML bootstrap support values from 100 replicates. Numbers I–V mark five clades of geographical interest. Note that the recently described Australian *Endressia* Whiffin is illegitimately named because of the older *Endressia* J. Gay, which is an Apiaceae (Renner & Takeuchi, 2009).

Dating analyses and ancestral area reconstruction

The ages inferred for nodes of biogeographical interest under the two calibration schemes are shown in Table 1, which also shows 95% highest posterior density (HPD) intervals on the estimates (i.e. the shortest intervals in parameter space that contain 95% of the posterior probability). Figure 3 shows the
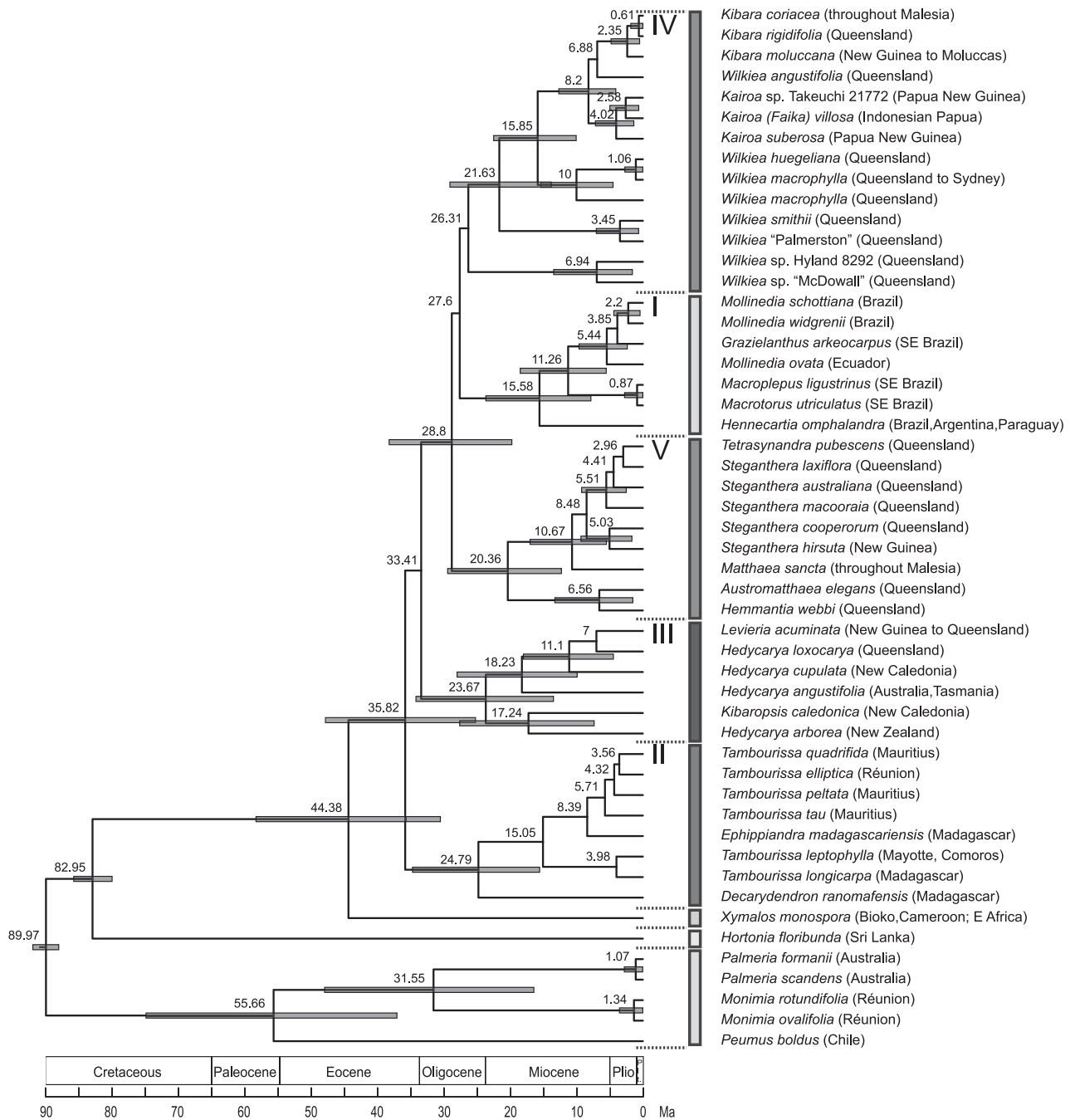
Figure 3 Chronogram for the Monimiaceae obtained under a Bayesian relaxed clock with lognormally distributed rates (51 species, 2570 aligned nucleotides). Bars around node ages indicate the 95% highest posterior density (HPD) intervals for nodes with a posterior probability >0.9. Numbers I–V mark five clades of geographical interest.

chronogram (i.e. the maximum clade credibility tree with mean node ages from the several thousand trees included in the post-burn-in sample) resulting from calibration scheme 2 (see Materials and Methods). In calibration scheme 1, the crown age of Monimiaceae was constrained to minimally 83 Ma, while in calibration scheme 2, it was left unconstrained and then dated to about 90 Ma. The split between *Hortonia* and the remaining genera is dated to 71 (57–84) Ma (Table 1), the split between *Peumus* and *Monimia/Palmeria* to 57 (37–75)

Ma, and that between *Xymalos* and clades I–V to 44 (31–58) Ma. The crown age of the Madagascan Monimiaceae clade is *c.* 25 Myr old, with the diversification of *Tambourissa* starting around 15 Ma. Most surprising is the young inferred age for the *Mollinedia* clade, the ancestor of which diverged from Asian relatives *c.* 28 Ma and which has a crown group age of only 16 Ma.

The ancestral area reconstruction is shown in Fig. 4. Both outgroups, the Lauraceae and the Hernandiaceae, are pan-
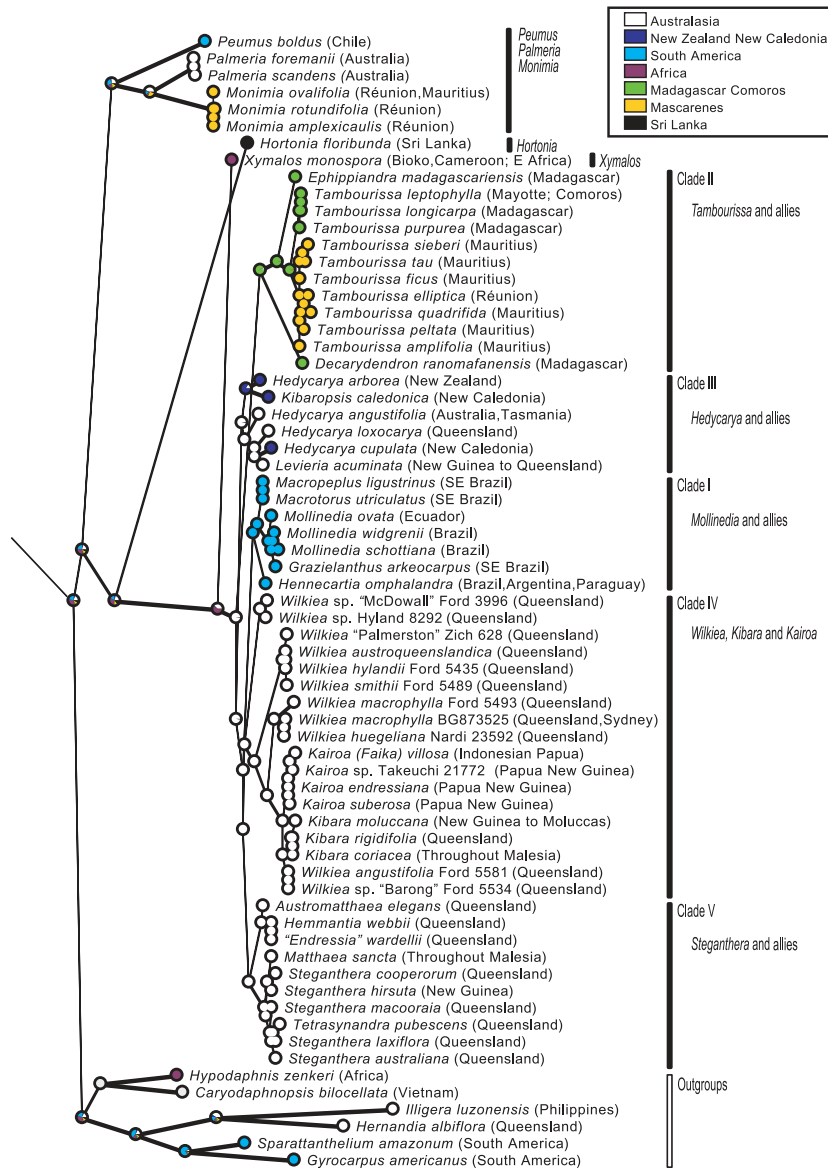
Figure 4 Ancestral area reconstruction for Monimiaceae on the maximum likelihood tree (Fig. 2), under the Markov *k*-state one-parameter model (see Materials and Methods).

Table 1 Estimated node ages (Ma) for the crown groups or splits shown in Fig. 3 under the two calibration schemes described in the Materials and Methods; 95% highest posterior density (HPD) confidence intervals are given in parentheses.

Calibrations	Peumus vs. *Monimia*, *Palmeria*	*Monimia* vs. *Palmeria*	*Hortonia* vs. remainder	*Xymalos* vs. remainder	*Monimia* crown group	*Decarydendron* divergence (clade I)	*Hedycarya* crown (clade II)	*Steganthera* clade (clade III)	*Wilkiea* crown (clade IV)	*Hennecartia* divergence (clade V)
Scheme 1	52 (34–70)	29 (14–42)	71 (57–84)	Set to 30 ± 1.5 SD	1 (0–2.4)	20 (14–27)	17 (11–23)	15 (10–20)	19 (16–25)	11 (6–16)
Scheme 2	57 (37–75)	32 (16–48)	Set to 83 ± 1.5 SD	44 (31–58)	1.3 (0–3.5)	23 (16–35)	24 (14–34)	20 (12–29)	16 (20–38)	16 (8–24)

tropically distributed and of unknown geographical origin; an ambiguous reconstruction of the ancestral distribution of Monimiaceae is thus expected. The Neotropical *Mollinedia*

clade, however, is unambiguously reconstructed as coming from Australasia, and the New Caledonia and New Zealand species are reconstructed as having arrived from Australia. The

geographical origins of the Sri Lankan *Hortonia* and the African *Xymalos* cannot be inferred with certainty (Fig. 4). Given that the *Monimia* lineage is older than the Mascarene Islands to which it is now endemic (Table 1 and Discussion), we also ran an ancestral area reconstruction with the *Monimia* range coded as '?'. This slightly shifted the relative probabilities at the two nodes below *Monimia* (Fig. 4), but did not change the unclear geographical origin of the family.

DISCUSSION

Reliability of the molecular clock estimates

The present study employed two calibration points, used in different ways for cross-validation, and the estimates obtained agree well with two other studies. One is the angiosperm-wide dating effort of Wikström *et al.* (2001), which employed nonparametric rate smoothing and the split between Fagales and Cucurbitales as the sole calibration point. This study inferred an age of 78 ± 8 Ma SE for the divergence of *Hedycarya* and *Peumus*, the only two Monimiaceae included. This fits surprisingly well with the fossil-documented minimal age of Monimiaceae of 83 Ma (see Introduction and Materials and Methods). An analysis using penalized likelihood on a matrix of 983 non-gapped chloroplast and nuclear nucleotide positions for 34 species of Monimiaceae with a minimal/maximal calibration range (Renner, 2005b), as opposed to the 53 species, 2593 nucleotides and two calibration points used here (albeit with the *rbc*L data highly incomplete; Appendix S1), also obtained similar divergence times. The confidence intervals on the inferred divergence times, however, are large (Table 1).

Does the break-up of Gondwana fit with divergences in the Monimiaceae?

As documented by leaf and wood fossils, Monimiaceae date back at least to the Upper Cretaceous (see Materials and Methods). Given the family's distinct pollen (in some genera), it is surprising that there are no pollen fossils; a comparison of Lower Cretaceous pollen of *Inaperturopollenites crisopolensis* from central Africa with *Hedycarya* (Muller, 1981) is obsolete in the light of more recent findings (J. Doyle, University of California, Davis, December 2008). On the other hand, there may be even earlier Cretaceous reproductive structures that represent Monimiaceae. Thus Dettmann *et al.* (2009) described a late Albian (*c.* 100 Ma) flower that may represent Monimiaceae, although the fossil also has affinities with another Laurales family, the Gomortegaceae. The oldest unambiguous Monimiaceae fossils, however, come from Antarctica and Africa, in both cases *c.* 83 Myr old, that is, old enough for the family to have been around during later stages of the break-up of East Gondwana at 120–40 Ma (see Introduction).

In the light of the molecular phylogeny, chronogram and biogeographical reconstruction (Figs 2–4), however, the break-up of West Gondwana is rejected as having played a role in the history of Monimiaceae, because no sister-group relationship matches the required *c.* 100 Myr time window (even with the 95% CIs; Fig. 3). The only split that overlaps with a phase of the break-up of Gondwana is that between the Chilean *Peumus* and the Australian *Palmeria* clade (Figs 2–4). Based on the molecular clock, this split occurred 57 (37–75) Ma, which would allow for Antarctica as a migration corridor between Australia and South America. Eocene palaeo-temperatures near Seymour Island, off the north-eastern side of the Antarctic Peninsula (where Monimiaceae wood fossils have been found; Poole & Gottwald, 2001), indicate a 10 °C cooling from the early Eocene, when mean temperatures were *c.* 15 °C, through the end of the Eocene (minimum *c.* 5 °C; Ivany *et al.*, 2008). Much of this cooling took place between 52 and 41 Ma. The Antarctic coastline and the Trans-Antarctic Mountains, however, supported *Nothofagus* forests well into the mid-Miocene (15–13 Ma; Truswell, 1989). Land contact between Antarctica and Australia was maintained up to *c.* 40 Ma (Li & Powell, 2001).

Another possibly Gondwanan lineage is *Hortonia* (Figs 2–4), dated to 71 (57–84) Ma and today comprising one species on Sri Lanka (see Materials and Methods for possible 83-Myr-old *Hortonia* woods). Within *Hortonia*, two species have been distinguished, *H. angustifolia* (Thw.) Trim., a river bank shrub in the perhumid south-west, and *H. floribunda* Wight ex Arn. from upper montane forest, also in the south-west; morphological distinctions between them are unclear (P. Ashton, Harvard University, personal communication, January 2010). Axelrod (1971) suggested northward rafting of *Hortonia* on the Deccan plate (India/Sri Lanka, Madagascar, the Seychelles). The Deccan plate separated from Antarctica 130–124 Ma (Gaina *et al.*, 2007), and by 83 Ma, the distance between India and Antarctica was at least 2100 km (Ali & Aitchison, 2009). Thus if *Hortonia*, here dated to 71 (57–84) Ma, dispersed from Antarctica to Sri Lanka, it would have had to cross a vast distance of ocean. Other suspected ancient endemics on Sri Lanka are the Crypteroniaceae *Axinandra zeylanica* (Conti *et al.*, 2004), the dipterocarp *Stemonoporus* and the Dilleniaceae *Schumacheria*. The Sri Lankan warm temperate and perhumid climates resemble those of Peninsular Malaysia and Sumatra, and are thus very different from those of the Indian mainland, perhaps facilitating the survival of tropical-adapted lineages (P. Ashton, Harvard University, personal communication, January 2010).

Transoceanic long-distance dispersal

The geographical origins of the Sri Lankan *Hortonia* and the African *Xymalos* cannot be inferred with certainty (Fig. 4). In alternative, equally likely trees (not shown), *Xymalos* places as sister to the Madagascan *Tambourissa* clade, and if additional data were to support this position, then arrival from Madagascar would be likely. *Xymalos monospora* today occurs in montane forests in East Africa, West Cameroon and on Bioko, an island connected to Africa during the most recent glacial

period, 10,000 years ago (Lee *et al.*, 1994). Most of the remaining clades also are confined to distinct biogeographical regions. Clade I, comprising *Mollinedia*, *Hennecartia*, *Macropeplus* and *Macrotorus*, is endemic in South America; clade II, comprising *Tambourissa*, *Decarydendron* and *Ephippiandra*, is restricted to Madagascar and the Mascarenes; clade III, *Hedycarya*, *Kibariopsis* and *Leviera*, is restricted to New Zealand, New Caledonia and Australia (with one species ranging from Queensland to Tasmania); and clades IV and V, *Wilkiea/Kairoa/Kibara* and *Steganthera* and allies, are restricted to New Guinea and tropical Australia.

The Australian/New Guinean genus *Palmeria* and the Mascarene genus *Monimia* are inferred to have diverged 32 (16–48) Ma. However, the Mascarenes, where *Monimia* today has three species (Lorence, 1985), have been available for colonization by terrestrial organisms only for the past 8–15 Myr (Thébaud *et al.*, 2009); Mauritius is *c.* 8.4 Myr old and Réunion is only *c.* 3.6 Myr old. Source regions could have been the Malesian region or Madagascar, which (together with mainland Africa) is the source of most of the flora of the Mascarenes (Cadet, 1977). Since *Monimia* does not occur on Madagascar today, however, the second scenario requires assuming extinction of the lineage there. Dispersal from the Malesian region therefore is a simpler explanation, and such trans-Indian ocean dispersal has also been invoked to explain other relatively young range disjunctions (inferred from molecular clocks). Examples are *Hernandia mascarenensis* and its Malesian sister clade, which diverged from each other during the Upper Miocene (Michalak *et al.*, 2010), and nine other plant groups with sister clades in Australasia and Madagascar (Li *et al.*, 2009). These floristic connections were perhaps aided by the repeated existence of sizeable islands in the Indian Ocean during the past 30 Ma (Warren *et al.*, 2010). By whatever route *Monimia* reached Réunion and Mauritius, its presence there provides a striking example of an island lineage being older than the islands on which it occurs. Similar cases are known from Arecaceae (*Hyophorbe* in the Mascarenes; Cuenca *et al.*, 2008), Araceae (*Helicodiceros muscivorus* on Mediterranean Islands; Mansion *et al.*, 2008), and Cucurbitaceae (*Dendrosicyos socotranus* on Socotra; Schaefer *et al.*, 2009). The example of *Hillebrandia sandwicensis* on Hawaii (Clement *et al.*, 2004) was based on an incorrect fossil assignment (Renner, 2005a).

The inferred ages of the six species of *Tambourissa* sequenced for this study (Fig. 3, clade I) fit with published age estimates for Mayotte, Mauritius and Réunion (above), and are in line with results from other dated plant clades occurring in the Western Indian Ocean basin (e.g. Malcomber, 2002; Bone *et al.*, in press). However, *Tambourissa* has at least 50 species on the Mascarenes, Comoros and Madagascar (Lorence, 1985), more of which would need to be included to test whether dispersal has followed the island-age progression rule (leading to within-island speciation and monophyletic island clades). The relatively basal positions of *Decarydendron*, a Madagascan genus of four species (one of them included here), and *Ephippiandra*, a likewise purely Madagascan genus of seven species (one

included), may fit this rule. It also appears that Rodrigues, the smallest of the Mascarene Islands and located 560 km east of Mauritius in the middle of the Indian Ocean, may once have harboured *Tambourissa* (Strahm, 1989).

Divergence-time estimates (Fig. 3) and the biogeographical ancestral area reconstruction (Fig. 4) for the *Hedycarya* clade imply long-distance dispersal from Australia to New Zealand and New Caledonia. With our sampling of only four of the 12 species of *Hedycarya*, one of the seven *Levieria* (occurring from Queensland to Sulawesi), plus the monotypic *Kibariopsis*, it is not yet possible to test the mutual monophyly of these genera. The *Wilkiea* and *Steganthera* clades are inferred to have begun diversification in the Miocene or Pliocene, but species sampling here again is insufficient to infer the detailed history of these clades in New Guinea and tropical Australia.

The most unexpected biogeographical finding of this study is probably the young age of the Neotropical *Hennecartia–Mollinedia* clade (Fig. 3; Table 1). The tree topology, chronogram and biogeographical reconstruction (Figs 2–4), taken together, indicate that the ancestor of the *Mollinedia* clade arrived from Australasia by long-distance dispersal. The ability of Monimiaceae to disperse across salt water is attested by their occurrence on islands of the Bismarck Archipelago, all the way east to New Ireland Province (Philipson, 1986), and also by the trans-Indian Ocean dispersal discussed above. If the ancestor of the Neotropical clade indeed dispersed across the Pacific to the coast of South America, the established populations then would have had to spread across the still low Andes into Argentina, Paraguay and Brazil (Fig. 1). Palaeoelevation reconstructions indicate that the Chilean Altiplano had reached only half its current elevation by the Late Miocene (Gregory-Wodzicki, 2000; Garzione *et al.*, 2008). Relevant in this context is that *Hennecartia*, the first-diverging lineage in the *Mollinedia* clade (Figs 2 and 3), has the most southern and most temperate range, occurring between latitudes 22 and 32° S (Santos & Peixoto, 2001; Gonzalez, 2007). This may point to an ancestral habitat of the *Mollinedia* clade in the Southern Cone of South America. Sister group disjunctions spanning the southern Pacific are known for at least 20 other angiosperm genera or tribes (van Steenis, 1962; Heads, 2003), and there is evidence for a specific New Caledonia–Melanesia–tropical South America track (Heads, 2006, 2009).

To return to the main questions posed at the outset of this study: our findings suggest that the phylogeny and current ranges of Monimiaceae may indeed contain signatures of the break-up of Gondwana as hypothesized by Raven & Axelrod (1974; also Lorence, 1985). However, these authors knew only of the African fossils, not the Antarctic ones (Birkenmajer & Zastawniak, 1989; Poole & Gottwald, 2001), and they therefore invoked the break-up of West Gondwana (America/Africa) as explaining some of the Monimiaceae ranges. This view was also influenced by the then prevailing circumscription of the family, which still included the Neotropical/African Siparunaceae and the Neotropical/Australasian Atherospermataceae, families now known not to be close to Monimiaceae (Renner, 1999, 2005b; Renner *et al.*, 2000). Our results reject West

Gondwana as playing a role, but the inferred divergence time of Chilean *Peumus* and Australian *Palmeria* is sufficiently old for dispersal (overland or across narrow seas) between South America, Antarctica and Australia.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Appendix S1 Species names and authorities, herbarium vouchers, geographical provenience and GenBank accession numbers for the material included in this study.

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BIOSKETCHES

Susanne S. Renner is a professor of biology at the University of Munich and director of the herbarium and botanical garden. This study on Monimiaceae is part of a broader focus on the biogeography of the basal angiosperm clade Laurales.

Joeri S. Strijk is currently a PhD student in the laboratory of Christophe Thébaud at the University of Toulouse, where he is working on the evolution of the plant lineages of Madagascar and the Mascarenes.

Dominique Strasberg is a botanist at the University of La Réunion. His research focuses on biogeography and conservation.

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