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ORIGINAL ARTICLE

Vicariance or long-distance dispersal: historical biogeography of the pantropical subfamily Chrysophylloideae (Sapotaceae)

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ABSTRACT

Aim Continental disjunctions in pantropical taxa have been explained by vicariance or long-distance dispersal. The relative importance of these explanations in shaping current distributions may vary, depending on historical backgrounds or biological characteristics of particular taxa. We aimed to determine the geographical origin of the pantropical subfamily Chrysophylloideae (Sapotaceae) and the roles vicariance and dispersal have played in shaping its modern distribution.

Location Tropical areas of Africa, Australasia and South America.

Methods We utilized a recently published, comprehensive data set including 66 species and nine molecular markers. Bayesian phylogenetic trees were generated and dated using five fossils and the penalized likelihood approach. Distributional ranges of nodes were estimated using maximum likelihood and parsimony analyses. In both biogeographical and molecular dating analyses, phylogenetic and branch length uncertainty was taken into account by averaging the results over 2000 trees extracted from the Bayesian stationary sample.

Results Our results indicate that the earliest diversification of Chrysophylloideae was in the Campanian of Africa *c.* 73–83 Ma. A narrow time interval for colonization from Africa to the Neotropics (one to three dispersals) and Australasia (a single migration) indicates a relatively rapid radiation of this subfamily in the latest Cretaceous to the earliest Palaeocene (*c.* 62–72 Ma). A single dispersal event from the Neotropics back to Africa during the Neogene was inferred. Long-distance dispersal between Australia and New Caledonia occurred at least four times, and between Africa and Madagascar on multiple occasions.

Main conclusions Long-distance dispersal has been the dominant mechanism for range expansion in the subfamily Chrysophylloideae. Vicariance could explain South American–Australian disjunction via Antarctica, but not the exchanges between Africa and South America and between New Caledonia and Australia, or the presence of the subfamily in Madagascar. We find low support for the hypothesis that the North Atlantic land bridge facilitated range expansions at the Palaeocene/Eocene boundary.

Keywords
Africa, Australasia, land bridges, Late Cretaceous, long-distance dispersal, molecular dating, Neotropics, Sapotaceae, Tertiary, vicariance.

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INTRODUCTION

Pantropical distributions have interested biogeographers for centuries. How is it possible that groups of organisms adapted to tropical conditions have acquired disjunct distributions on landmasses that are so widely separated as Africa, Asia and South America?

Two processes have been invoked to explain transoceanic distributions: long-distance dispersal and vicariance. Darwin (1859) and Carlquist (1974, 1981, 1996) recognized long-distance dispersal as an important process in the colonization of oceanic islands. With the acceptance of plate tectonics, common distributions for many groups were presumed to stem from the same geohistorical processes (Raven & Axelrod, 1974). The assumption of an underlying geological sequence of events fuelled the birth of vicariance biogeography (Nelson & Platnick, 1981; Humphries & Parenti, 1986). Vicariance biogeography has dominated historical biogeography for decades, in part due to the claim that hypotheses of dispersal were not falsifiable, that is, any distribution can be explained by dispersal. However, recent advances in molecular techniques, phylogenetic inference and divergence-time estimation have indicated that long-distance dispersal has played a more significant role in shaping modern distributions, resulting in a major shift in our view of historical biogeography (de Queiroz, 2005; Michalak *et al.*, 2010; Renner *et al.*, 2010). Even iconic examples of vicariance such as the plant genera *Araucaria* and *Nothofagus* have been demonstrated to disperse over long distances (Setoguchi *et al.*, 1998; Swenson *et al.*, 2001; Cook & Crisp, 2005).

Distributions across all main tropical areas are found in a number of vascular plant families for which dated phylogenies have been produced, including Annonaceae (Richardson *et al.*, 2004; Erkens *et al.*, 2009), Burseraceae (Weeks *et al.*, 2005), Campanulaceae (Antonelli, 2009), Ebenaceae (Duangjai *et al.*, 2009), Malpighiaceae (Davis *et al.*, 2002), Melastomataceae (Renner *et al.*, 2001), Meliaceae (Muellner *et al.*, 2006), Moraceae (Zerega *et al.*, 2005) and Rubiaceae (Antonelli *et al.*, 2009). These studies demonstrate that the timing of the diversification of those families is incongruent with the break-up sequence of Gondwana (McLoughlin, 2001). It has also been proposed that Annonaceae, Burseraceae, Malpighiaceae, Melastomataceae, Meliaceae, Moraceae and Rubiaceae migrated along the North Atlantic land bridge (NALB; McKenna, 1983; Tiffney, 1985), also called the Thulean Bridge (reviewed by Sanmartín *et al.*, 2001). This relatively short-lived connection could have been established across southern Greenland at latitudes of 45–50° N at the boundary of the Late Palaeocene/Early Eocene, some 55 million years ago (Ma) (Raven & Axelrod, 1974; Tiffney, 1985; Morley, 2000, 2003). The existence of the NALB coincides with the Late Palaeocene Thermal Maximum (LPTM, 55 Ma) and the Early Eocene Climatic Optimum (EECO, 52 Ma), both events found within a period of global warming of sea surface temperatures from 8 to 12 °C between 58 and 52 Ma (Zachos *et al.*, 2001). The position of tectonic plates and climatic conditions were the prerequisite for the formation of boreotropical forests at high latitudes, allowing the exchange of lineages between Europe and North America. There is copious evidence in the fossil record for the existence of tropical elements in high-latitude floras at the time of the EECO (e.g. the London clay flora; Reid & Chandler, 1933). The EECO period was followed by the break-up of the NALB at about 50 Ma, and a decrease in palaeo-temperatures to pre-LPTM levels by 45 Ma. This decline in temperature resulted in contraction of boreotropical vegetation to lower latitudes, which in turn caused phylogenetic splits (effectively vicariance events), for instance in Annonaceae (Erkens *et al.*, 2009), Meliaceae (Muellner *et al.*, 2006) and Rubiaceae (Antonelli *et al.*, 2009).

Hallam (1994) and Morley (2000, 2003) have also suggested the possibility that some groups may have migrated via a southern route through Antarctica. Dated phylogenies of Myrtaceae (Sytsma *et al.*, 2004) and Proteaceae (Barker *et al.*, 2007) are consistent with migration from Australia through Antarctica to South America. There is some evidence of Myrtaceae fossils in the Late Cretaceous and Early Tertiary of Antarctica (Poole *et al.*, 2003). Dated phylogenetic evidence for whether megathermal (frost-intolerant) lineages could have taken this route is currently lacking. If this route were taken, we would expect vicariance events to date to the LPTM/EECO. These events could be a result of the opening of Antarctica to megathermal lineages from South America and Australia and subsequent restoration of the climatic barrier for these lineages shortly after the LPTM/EECO. Vicariance could also have resulted from the break-up of South America, Antarctica and Australia, which occurred *c.* 30–35 Ma (McLoughlin, 2001), although the likelihood of megathermal lineages persisting at these latitudes at that time seems low.

Sapotaceae are an important component of rain forests in all tropical regions. The family exhibits much morphological variation, ranging from shrubs and medium understorey trees to giant canopy trees. The family is divided into the three subfamilies Chrysophylloideae, Sapotoideae and Sarcospermatoideae, together comprising 58 genera and approximately 1250 species (Pennington, 1991; Govaerts *et al.*, 2001; Anderberg & Swenson, 2003; Swenson & Anderberg, 2005; Swenson *et al.*, 2007a). Sarcospermatoideae comprises *Sarcosperma* and possibly *Eberhardtia* (Smedmark *et al.*, 2006), two small genera restricted to South and East Asia. These are sisters to the large subfamilies Chrysophylloideae and Sapotoideae, both with *c.* 600 species each and with pantropical distributions. Relationships within Sapotoideae remain poorly understood, but within the subfamily the genus *Sideroxylon* is strongly supported as monophyletic, and relationships within this genus are reasonably well resolved (Smedmark & Anderberg, 2007). Based on a molecular dating analysis, Smedmark & Anderberg suggested that members of the *Sideroxylon* lineage entered the New World from Europe via the NALB early in the Eocene. Their results concur with the observation of fossil pollen of Sapotaceae from the Eocene present in both North America and Europe from these latitudes (Morley, 2000). Chrysophylloideae could also have migrated between Africa

and South America via this land connection. Evidence in favour of this is the presence of representatives of Chrysophylloideae in high latitude floras of Europe and North America during the Early Eocene (e.g. Reid & Chandler, 1933; Frederiksen, 1980; Graham, 1985; Gennett, 1996).

Swenson *et al.* (2008a) demonstrated that the main lineages in Chrysophylloideae are more or less restricted to large geographical areas such as Africa, Australasia and South America. However, no biogeographical or molecular dating analyses have been conducted for the subfamily so far. The purpose of this study is to estimate divergence times and ancestral areas of Chrysophylloideae in order to determine its biogeographical history. Primarily, we aimed to determine whether the current distribution was affected by the break-up of Gondwana, migration along the land bridges during the LPTM–EECO period, long-distance dispersal, or a combination of these. We also wished to determine whether the worldwide colonization of Chrysophylloideae exhibits a similar history to the genus *Sideroxylon* (Sapotoideae).

MATERIALS AND METHODS

Molecular data and phylogeny

This study is based on the molecular data set (including 66 species and nine molecular markers) published by Swenson *et al.* (2008a). Phylogenetic relationships were fully assessed and discussed in that study from combined analysis of molecular and morphological characters. In the current study, we performed an additional Bayesian analysis to generate a sample of trees for ancestral age reconstructions and dating analyses following the same settings as described by Swenson *et al.* (2008a), but with morphological characters excluded because they were shown to be highly homoplasious. The stationary (post burn-in) phase was determined based on the average standard deviation of split frequencies (Huelsenbeck & Ronquist, 2001). The post-burn-in trees were used to reconstruct a majority-rule consensus tree (Fig. 1). From the stationary phase of our Bayesian analysis, 2000 trees were selected at a set interval (each 1000th tree) and used for optimization of ancestral areas and the ages of nodes.

Calibration of nodes

To time calibrate the tree, we used several fossils of Sapotaceae (Table 1; Fig. 1). *Sapotaceoidaepollenites rotundus* is a microfossil from Australia assigned to Sapotaceae (Harris, 1972). Its affinity to extant genera was suggested to be with *Chrysophyllum* or *Pouteria*, where *Pouteria sensu* Pennington (1991) included *Beccariella*, *Planchonella*, *Sersalisia* and *Van-royena*. Therefore this fossil could belong to the ancestral lineage of both the Australasian clade H and *Chrysophyllum sensu* Pennington (1991). According to our phylogenetic reconstruction, it therefore could be used to constrain either the crown or the stem node of the clade combining clades C1 and D (Fig. 1, nodes Ia and Ib). The fossil taxon was first reported from the mainland and dated to the Middle Eocene (Harris, 1972). However, a Late Cretaceous record of *Sapotaceoidaepollenites rotundus*, *c.* 71 Ma, has been found in an offshore drillhole at Otway Basin (Stoian, 2002). This record may represent the earliest known fossil record of Chrysophylloideae (and Sapotaceae) from Australia. However, M. Harley (retired from RBG Kew, pers. comm., 2009) does not exclude the possibility that this fossil can be associated with Mimusopeae, which is in the subfamily Sapotoideae (Swenson & Anderberg, 2005).

Another microfossil, *Psilatricolporites maculosus*, is known from a sequence of sediments from the Palaeocene/Eocene transition (*c.* 55 Ma) in the Maracaibo Basin of western Venezuela (Lorente, 1986; cited by Rull, 2000), and from the Early Eocene in Colombia (Jaramillo & Dilcher, 2001). These authors affiliate the fossil with *Chrysophyllum*, but V. Rull (CSIC-Institut Botànic de Barcelona, pers. comm., 2010) suggests that it cannot be reliably associated with either *Chrysophyllum* or *Pouteria*. The *Psilatricolporites* from Venezuela is the oldest reported dated representative of Chrysophylloideae from the New World. Since *Chrysophyllum* in the New World represents at least three lineages (Swenson *et al.*, 2008a), we constrained the minimum age of the crown and stem nodes of clade G (Fig. 1, nodes IIa and IIb) to 55 Ma. This approach will include all New World representatives of the genera that are currently known as *Chrysophyllum* or *Pouteria*. A macrofossil of Sapotaceae has also been reported recently from the Cerrejón Formation in Colombia (Wing *et al.*, 2009), which was dated to the Late Palaeocene (58 Ma). This fossil, however, cannot be reliably affiliated with any extant genus of Sapotaceae.

A leaf fragment of *Pouterlabatia lanceolata* was reported from the Rio Turbio formation in Santa Cruz, Argentina, representing deposits from the middle Eocene, *c.* 45 Ma (Hunicken, 1955). We assigned this record as the minimum age of the node of a clade of two species: a species of *Pouteria* and a species of *Chromolucuma* (node III). This clade includes *P. gardneriana*, or *Labatia lanceolata*, an old synonym to which the fossil name refers (Govaerts *et al.*, 2001). Therefore we believe that this species may be one of the closest extant species to the fossil taxon. Node III (Fig. 1) should represent the stem node of the inferred clade of the fossil and extant species.

Fossil pollen of *Psilastephanocolporites malacanthoides* was reported from upper Eocene sediments in Nigeria and assigned to *Malacantha* (Jan du Chêne *et al.*, 1978). *Malacantha* is a genus united with *Pouteria* by Pennington (1991), but it will most probably be resurrected when the circumscription of the group is clearer (Swenson *et al.*, 2008a). The stem node of *Pouteria alnifolia* (= *Malacantha alnifolia*) (Fig. 1, node IV) is used as a 35 Ma minimal constraint for the age of the clade of some African members of the subfamily (Fig. 1, clade E).

A leaf impression from Landslip Hill (New Zealand) has been associated with *Pouteria costata* (Campbell, 2002), the only extant species of Sapotaceae in New Zealand (Govaerts *et al.*, 2001). The association is based on the secondary venation and overall leaf shape. The Landslip Hill strata can be dated to the Oligocene/Miocene transition (Lindqvist,

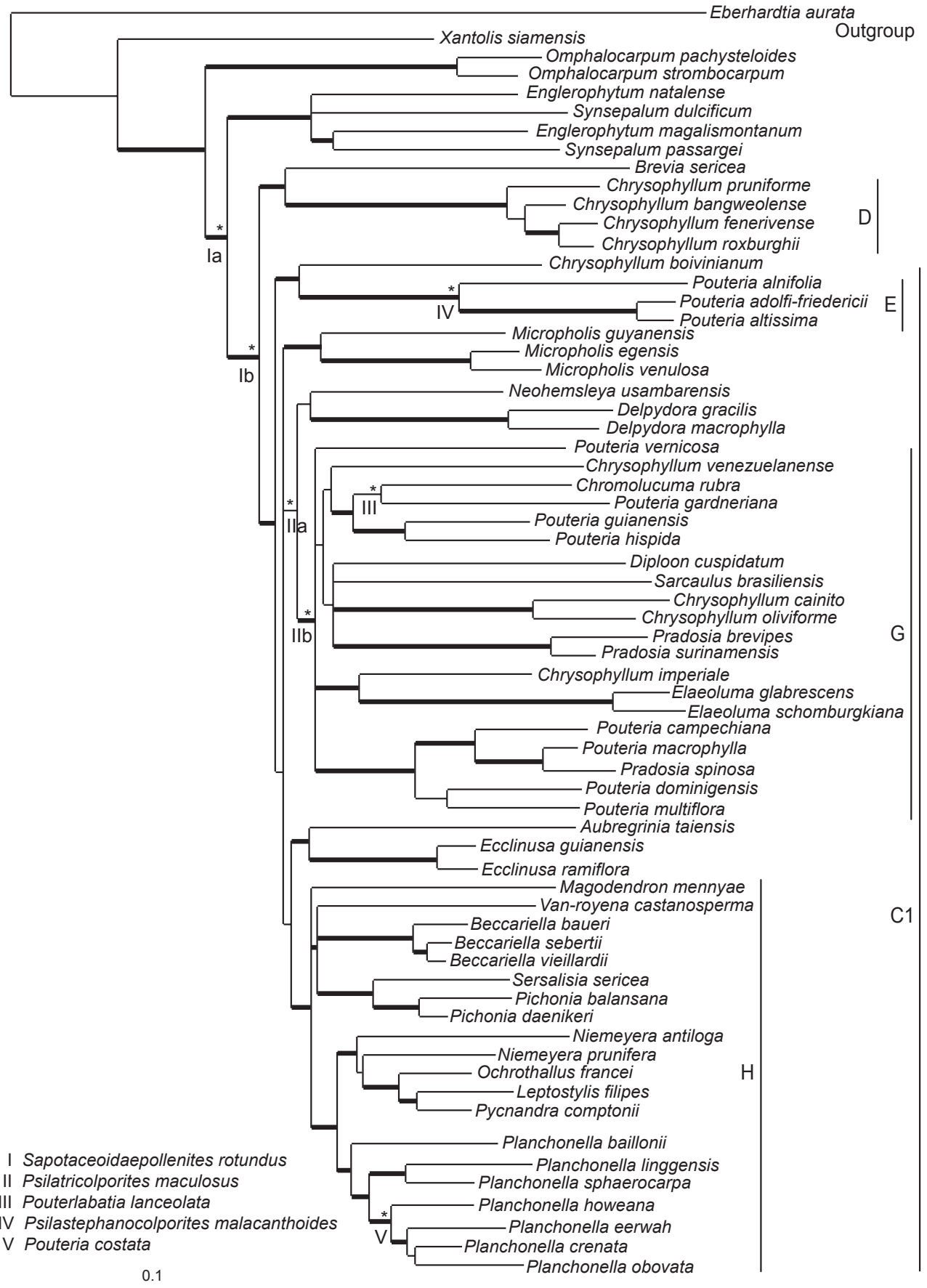

Table 1 Fossils used for calibration and divergence-time estimates of the crown node of Chrysophylloideae (Sapotaceae) following the method of Bremer *et al.* (2004).

Node	Taxon	Fossil	Affiliation to extant taxon	Geological period	Estimated age of fossil (Ma)	Locality	Age of crown node 1 (Ma)	λ
I	*Sapotaceoidaepollenites rotundus*	Pollen	Sapotaceae	Campanian	71	Australia	91.0	2.5×10^1
II	*Psilatricolporites maculosus*	Pollen	*Chrysophyllum*	Palaeocene/Eocene	55	Venezuela	89.5	2.5×10^1
III	*Pouterlabatia lanceolata*	Leaf imprint	*Pouteria gardneriana*	Middle Eocene	45	Argentina	101.2	6.3×10^1
IV	*Psilastephanocolporites malacanthoides*	Pollen	*Pouteria alnifolia*	Late Eocene	35	Nigeria	83.6	3.2×10^3
V	*Pouteria costata*	Leaf imprint	*Planchonella costata*	Oligocene/Miocene	23	New Zealand	93.3	1.6×10^2

These fossils were also used as minimum age constraints in dating analyses where the mean estimate of the total age of crown node was used. Labelling of nodes is as in Fig. 1. λ = smoothing parameter used in r8s for each penalized likelihood estimate (see Materials and Methods). The mean total age of crown node 1 is 91.7 Ma (standard deviation = 6.4 Ma).

1990). It has also been demonstrated that *P. costata* belongs to the same clade as *Planchonella eerwah* from Australia, *P. crenata* from New Caledonia, *P. howeana* from Lord Howe Island, and the widespread taxon *P. obovata* (Swenson *et al.*, 2007a,b). The relationships amongst these species are unresolved, so we constrained the minimum age of the crown node of this clade (Fig. 1, node V) to the Oligocene/Miocene transition (23 Ma).

Molecular dating analysis

Divergence times were estimated using the penalized likelihood (PL) method of Sanderson (2002) using the software r8s version 1.70 (Sanderson, 2004). We applied the Truncated Newton algorithm with bound constraints, which can handle age constraints and uses gradients for better convergence of rates. The outgroup taxon (*Eberhardtia aurata*) was pruned prior to analysis. Cross-validation was undertaken on the Bayesian majority-rule consensus tree to select an optimal smoothing value that was used in subsequent PL analyses, where confidence intervals on parameters (mutation rate/divergence time) were estimated. We used the sample of 2000 trees representing a posterior probability distribution in the Bayesian analysis. Each tree was dated independently, and means and confidence intervals were calculated using TreeAnnotator (Drummond & Rambaut, 2006).

The mean age of crown nodes is frequently difficult to estimate, and age variation often stems from multiple sources (Sanderson & Doyle, 2001). The same situation has been shown to apply for Sapotaceae (Smedmark & Anderberg, 2007). Bremer *et al.* (2004) recommended using the mean value from several reference fossils to reduce the variability in molecular dating estimates. Following this method, we used each of the available calibration points as fixed age constraints. We also accounted for uncertainty in the placement of calibration points to either stem or crown nodes (Magallón, 2004; Renner, 2005; Ho & Phillips, 2009). In our analyses, this uncertainty applied to the cases of *Sapotaceoidaepollenites rotundus* and *Psilatricolporites maculosus* (nodes Ia, Ib, IIa and IIb; Fig. 1). Since we would like to avoid adding unjustified weight to the fossils with uncertain positions in further estimations of the mean age of the crown node of the subfamily, we selected in each of two uncertain cases only one placement. The selection was performed using the approach of Near *et al.* (2005). We fixed the ages of the two fossils with two alternative placement positions in PL analyses, and calculated the difference between the molecular and fossil estimates for all other fossil-dated nodes in the phylogeny (Near *et al.*, 2005). The placements of fossils with a lower value of the sum of squared deviations (nodes Ia and IIb) were included in further analyses, where ages of each of the five fossils were used as a fixed age constraint to estimate the age of the crown node of Chrysophylloideae (node 1). This provided us with five age estimates for the crown node of Chrysophylloideae, including *Xantolis*. Cross-validation to select an optimal smoothing value was performed separately for each of these analyses. The mean of the five values obtained was subsequently used as a fixed age constraint for the crown node of the whole subfamily, while the other nodes, specified by fossils and phylogenies, were constrained as minimum ages. We note that the fossil records used for calibration of molecular rates in our phylogenetic reconstruction are evenly distributed through time and space (Table 1). In addition to the increased precision of age estimates from multiple fossil records, this should also reduce a possible bias associated with under-representation of particular areas and geological periods in the fossil record.

Figure 1 Bayesian 50% majority-rule consensus shown as a phylogram of the subfamily Chrysophylloideae (Sapotaceae) using seven chloroplast and two nuclear DNA markers from Swenson *et al.* (2008a). Branches shown as thick black lines indicate posterior probabilities ≥0.95. The scale bar indicates the amount of nucleotide change per site. Asterisks refer to nodes; roman numerals to fossils used as minimum age constraints for the calibration of molecular rates in the dating analyses (Table 1). Letters refer to clades *sensu* Swenson *et al.* (2008a): D and E being restricted to Africa, G to South America, H to Australasia, and we add clade C1 here as discussed in the text.

Ancestral area reconstructions

We defined six main areas of distribution of Chrysophylloideae: Africa, Australia (including New Guinea), Madagascar, New Caledonia, South America and Southeast Asia (including Sundaland). The ranges of almost all species of our sample are restricted to one of these areas, except for three species. *Chrysophyllum roxburghii* is widespread, ranging from Madagascar in the west to Australia in the east; *Planchonella linggensis* grows in Australia, New Caledonia and neighbouring islands; and *Planchonella obovata* is also widespread, ranging from Australia in the south to China in the north and the Seychelles in the west (Govaerts *et al.*, 2001).

Fitch optimization, implemented in the software Mesquite version 2.7 (Maddison & Maddison, 2009), was used to infer the distribution of internal (ancestral) nodes in the phylogeny. This is a maximum-parsimony method capable of handling widespread terminal taxa. To evaluate the robustness of our results under different optimization methods, we also ran a maximum-likelihood (ML) analysis using the Markov *k*-state one-parameter model implemented in Mesquite. Contrary to parsimony, ML methods take into account branch length (or time). The drawback, however, is that ML optimizations in Mesquite cannot handle multiple terminal states (widespread species) and only one area can be selected for each of the three widespread species in our sample. Triono *et al.* (2007) demonstrated that multiple samples of *Planchonella obovata* from much of its range are monophyletic, which also is true for *P. linggensis* (Swenson *et al.*, 2007a,b). Therefore we chose to assign the state according to where the particular sample came from: New Caledonia for *P. linggensis*, Southeast Asia for *P. obovata* and Madagascar for *C. roxburghii*.

To take phylogenetic uncertainty into account, ancestral state optimizations were performed independently on 2000 chronograms. Ancestral states for each node of the reference tree were computed by counting all trees with a certain state (for parsimony) and by averaging the relative likelihoods (for ML) of the same node across the entire tree sample.

RESULTS

The phylogenetic relationships and posterior probabilities from the present analysis of exclusively molecular characters corroborate those reported by Swenson *et al.* (2008a) (Fig. 1). We label the clades so that they concur with those of Swenson *et al.* (2008a), with the addition of clade C1, which we discuss here. Figure 2 shows the dated 50% majority-rule consensus tree of the Bayesian analysis (a chronogram), with branch lengths representing mean values as estimated for the dating analysis. Mean age and confidence intervals of the crown node of Chrysophylloideae and several well supported nodes are reported in Tables 1 and 2. The age variation of the crown node was relatively low (SD = 6.4 Ma), indicating good convergence of molecular rates for the longest branches in the tree. This result suggests that, assuming fossils are correctly placed, the age estimates are robust and do not change significantly if some fossils (for example, the two fossils with uncertain taxonomic affinity) are excluded from analyses.

Ancestral areas were inferred with confidence (relative likelihood for the ancestral area 0.95 or higher) for most nodes in the tree, and the results from the parsimony optimization are shown in Fig. 2. Results were robust, regardless of the optimization method used (parsimony or ML) for all clades except the root (node 1) and nodes 7 and 10 (Table 2). For the latter nodes, both methods yielded Australia or New Caledonia as ancestral areas but disagreed concerning the directionality of dispersals. In parsimony, Australia was inferred to act as a source area from where repeated dispersal events took place to New Caledonia, whereas in ML the opposite scenario was inferred (Table 2).

The crown node of the subfamily (node 1) represents the split between the Southeast Asian genus *Xantolis* and the remaining species. The ancestral area of this node cannot be determined with confidence, since this requires a more thorough analysis of the entire family. The age of the node is estimated as 79–105 Ma, indicating that *Xantolis* and Chrysophylloideae diverged in the mid-Cretaceous or somewhat later.

The age and ancestral area of the earliest diversification in Chrysophylloideae (excluding *Xantolis*, node 2) is in the Campanian of Africa, between 73 and 83 Ma. This split was followed by several diversifications in the same continent. Node 3 represents the strongly supported crown node of clade C1. Descendants of the inferred ancestor of this clade subsequently diverged and colonized Australia, Madagascar, New Caledonia and South America. Node 4 is estimated to 54–68 Ma and represents diversification between African clade E and Madagascan *Chrysophyllum boivinianum*. Node 5 is the crown node of the large Neotropical clade G and has strong Bayesian support (posterior probability (PP) = 0.99). Its age was estimated to 54–64 Ma. At node 6, another disjunction is

Figure 2 Dated phylogenetic tree (chronogram) of Chrysophylloideae (Sapotaceae) obtained from penalized likelihood analysis (Sanderson, 2002, 2004); clades in capital letters are labelled as in Fig. 1. The influence of topological and branch-length uncertainties on age estimates is indicated as 95% confidence limits (blue bars) around means for crown nodes of all strongly supported clades. Pie charts report the relative likelihoods of ancestral areas (following the legend) for internal nodes of the same clades, estimated by parsimony optimization. The numbered nodes represent crown nodes of important colonization events, discussed in the text and Table 2. Larger pie charts indicate the first diversifications within Africa, South America and Australia. The palaeomap indicates hypothesized migration routes. The time-scale follows that of Walker & Geissman (2009); the palaeomap (adapted from Scotese, 2001) shows the positions of the continents *c.* 65 Ma. Abbreviations: K/T = Cretaceous–Tertiary (Cenozoic) transition (dotted line); LPTM = Late Palaeocene Thermal Maximum (grey bar); Palaeoc. = Palaeocene; PL/P = Pliocene/Pleistocene.

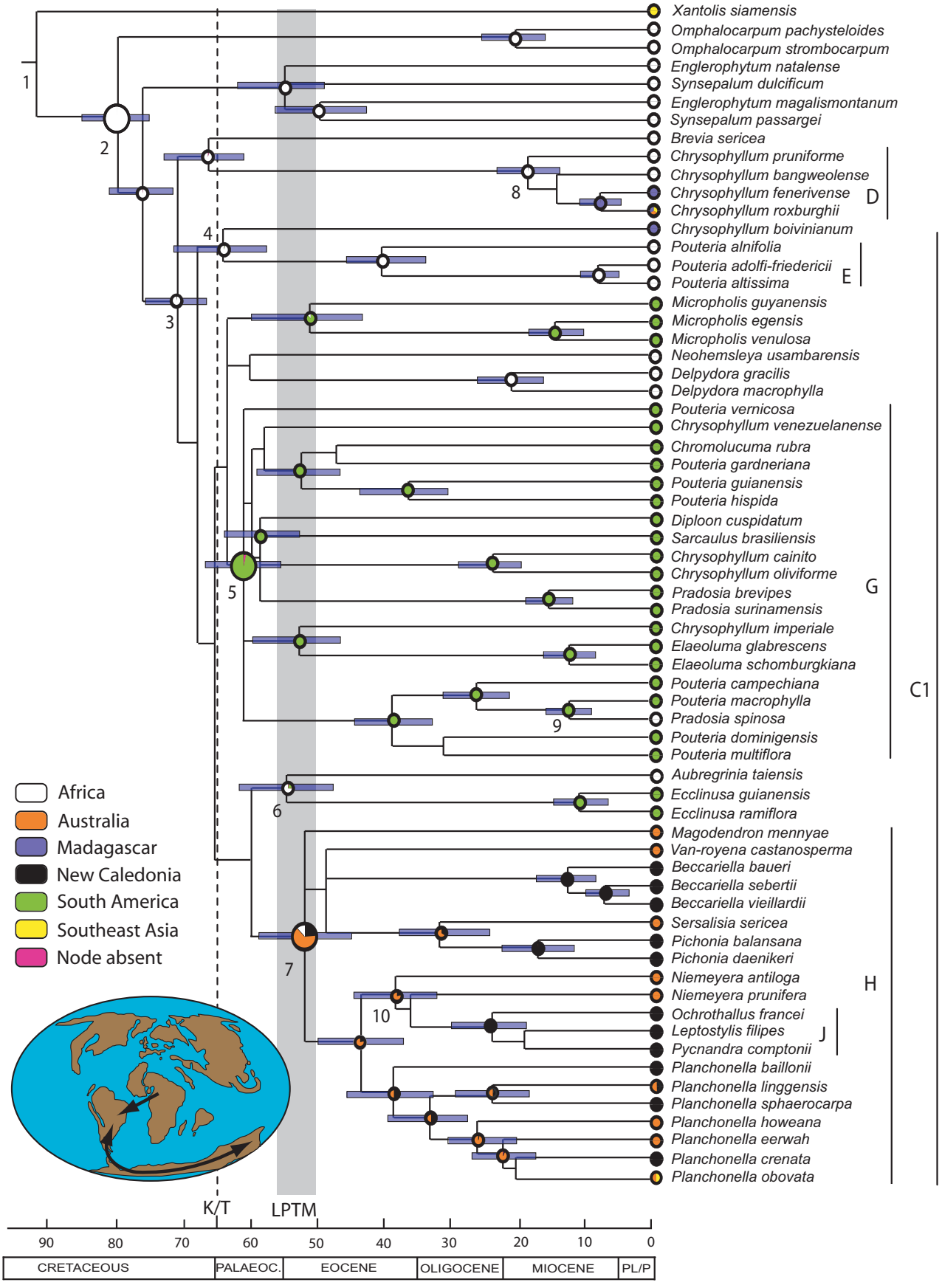

Table 2 Summary statistics of the ancestral area reconstruction using parsimony and maximum likelihood (ML) analyses and molecular dating analysis for key nodes in the Chrysophylloideae (Sapotaceae) phylogeny.

		Ancestral area: parsimony		Ancestral area: ML		Age estimates (Ma)		
Node	PP	I	II	I	II	Mean	Lower	Upper
1	–	Asia: 1.00	–	Africa: 0.67	Asia: 0.26	91.7	–	–
2	1.00	Africa: 1.00	–	Africa: 0.99	Asia: 0.01	77.8	72.9	82.7
3	1.00	Africa: 0.90	S. America: 0.01	Africa: 0.94	S. America: 0.06	66.5	61.4	71.6
4	0.96	Africa: 1.00	–	Africa: 0.93	S. America: 0.05	61.0	53.8	68.2
5	0.99	S. America: 1.00	–	S. America: 1.00	–	59.0	53.8	64.2
6	0.97	Africa: 0.71	S. America: 0.30	Africa: 0.73	S. America: 0.24	55.7	48.2	63.2
7	1.00	Australia: 0.65	New Caledonia: 0.17	New Caledonia: 0.83	Australia: 0.10	52.5	45.7	59.3
8	1.00	Africa: 1.00	–	Africa: 0.98	Madagascar: 0.02	18.8	13.8	23.8
9	1.00	S. America: 1.00	–	S. America: 0.99	Africa: 0.01	10.5	6.7	14.3
10	1.00	Australia: 0.79	New Caledonia: 0.21	New Caledonia: 0.90	Australia: 0.15	38.6	32.1	45.0

Both analyses were calculated on a sample of 2000 trees. Node numbers refer to Fig. 2 and their Bayesian posterior probabilities (PP). Results from the ancestral area reconstructions are reported for the first (I) and the second (II) most frequent areas. Widespread distributions are coded as such in parsimony and the values are calculated counting all trees with a state, whereas in ML widespread taxa are coded for a single area and values represent the averaged relative likelihood over the tree sample. Age estimates are derived from penalized likelihood analyses. 'Lower' and 'Upper' indicate 95% confidence limits around mean age estimates.

indicated between Africa and the New World, which occurred at 48 to 63 Ma. We cannot determine with confidence the age of the first appearance of Sapotaceae in Australia because of phylogenetic uncertainty in placement of the stem node of clade H. The age of the crown node of this clade (node 7) was estimated to 46–59 Ma, indicating the time when this lineage started to diversify into the *c.* 200 extant species.

Among the more derived clades, the ancestral area of clade D is Africa (node 8). The age of this node is estimated to 14–24 Ma, and should be the oldest possible age of the most recent common ancestor of lineages in this clade with descendants in Africa and Madagascar. The age of node 9 was found to be 7–14 Ma and indicates the time when the Neotropical species *Pouteria macrophylla* and the African species *Pradosia spinosa* last shared a common ancestor. Finally, node 10 is estimated to be 32–45 Ma, followed by 18–30 Ma for the crown node of clade J. This clade and its two sisters represent the split between *Niemeyera* in Australia and *Pycnandra sensu* Swenson & Munzinger (2009) in New Caledonia. The stem node of clade J (node 10) is the earliest point at which the oldest dispersal between landmasses could have occurred (the case of *Beccariella* is discussed further below). The age of the crown node of clade J indicates the time when the genus began to diversify on New Caledonia, and is the latest point when the oldest dispersal onto New Caledonia occurred.

DISCUSSION

Sapotaceae are in the order Ericales, an order of 22 families (APG III, 2009) that diversified rapidly in the Early Cretaceous (*c.* 120–100 Ma; Bremer *et al.*, 2004). In the dated phylogeny of Bremer *et al.* (2004), which utilized six well characterized fossils within Ericales, Sapotaceae are in an unresolved position among several other families that diversified at the boundary of the Early and Late Cretaceous. The stem node of the family is estimated to be 103 Ma, based on a single Sapotaceae sample, *Manilkara*, which is a member of the subfamily Sapotoideae (Swenson & Anderberg, 2005). Our age estimate of the crown node of Chrysophylloideae, the sister group to Sapotoideae, is 91.7 Ma (79–105 Ma), which is not inconsistent with the age estimate of Bremer *et al.* (2004) for the origin of the family.

Effect of Gondwanan vicariance on the biogeography of Chrysophylloideae

The likelihood estimates of age and ancestral area for the earliest evolutionary events in Chrysophylloideae suggest that the subfamily diverged in Africa during the Late Cretaceous, after its split from Asian *Xantolis*. Our estimate of the oldest split between the African and the Neotropical lineages is between 61 and 72 Ma (node 3, Table 2). At this time, opportunities for vicariance between Africa and South America had passed, for it was at least 30 million years (Myr) since the low latitude connection between these continents broke up around 105 Ma (McLoughlin, 2001). However, at the time of this phylogenetic split, short-distance overseas dispersal may have been possible via island chains of the Sierra Leone Rise and/or the Rio Grande Rise–Walvis Ridge. Doyle & Le Thomas (1997) and Richardson *et al.* (2004) suggested that this migration route may have been taken by Annonaceae.

At the time of the split between the Australasian lineage (clade H) and its most recent common ancestor with lineages from other landmasses (mid-Palaeocene, Fig. 2), Australia was still connected with South America via Antarctica at high latitudes (McLoughlin, 2001; Hall, 2009). Hence the only possible vicariance that could have been caused by break-up of Gondwana is between Australia, Antarctica and South America. Australia split from Antarctica *c.* 35 Ma and Antarctica split from South America *c.* 30–35 Ma (McLoughlin, 2001). Our age estimates for the split between South American and

Australasian lineages is *c.* 60–65 Ma (ages of the stem nodes of clades G and H), which pre-dates the continental break-up of these landmasses. However, this estimate is consistent with migration of a megathermal lineage between South America and Australasia via Antarctica (Fig. 2) during global climatic warming at the time of the LPTM and the EECO (Zachos *et al.*, 2001). Post-EECO global climatic cooling (from *c.* 52 Ma) could have restored the climatic barrier for megathermal lineages in Antarctica and prevented their further migration through this land bridge between eastern and western parts of Gondwanaland. This is, to our knowledge, the first inference from dated molecular phylogenies for possible migration of a megathermal angiosperm lineage via this route, although fossil evidence for the presence of Chrysophylloideae in the Early Tertiary of Antarctica would be needed to confirm this scenario.

Could a stepping-stone route, via the NALB (McKenna, 1983; Tiffney, 1985), explain the arrival of Chrysophylloideae in South America? If this scenario were true, splits between lineages now restricted to Africa and South America should coincide with the time frame of the LPTM/EECO. Our age estimates suggest that Chrysophylloideae were present in the Neotropical region by the mid-Palaeocene at the latest (*c.* 60 Ma) (Fig. 2). This estimation pre-dates the LPTM/EECO by *c.* 5 Myr, which is largely inconsistent with migration via the NALB. We should also take into consideration that our age estimates are based on minimum age constraints, provided by fossils. They may therefore be somewhat biased to younger age estimates. Hence our results suggest that the NALB played no significant role in facilitating the colonization of South America by Chrysophylloideae.

Long-distance dispersal

Representatives of Sapotaceae are found on the islands of Fiji, Hawaii, New Caledonia, New Guinea, the Solomon Islands, Tahiti and Vanuatu. Some of these are geologically young volcanic islands that are a considerable distance from any continental land mass. Propagules of Sapotaceae are therefore clearly capable of dispersing significant distances across oceans. Our inferred dates for splits between Africa and South America are too young to have been caused by Gondwanan break-up, and too old to have been caused by break-up resulting from disruption of the NALB or the boreotropics. Given these dates, there must have been long-distance transoceanic dispersal events from Africa to South America or Australasia across the Atlantic or Indian Oceans.

Yoder & Nowak (2006) reviewed a comprehensive sample of phylogenetic studies, and concluded that much of the present-day biota of Madagascar must be descended from Cenozoic dispersers. Sapotaceae are also diverse in Madagascar, with several endemic genera (Aubréville, 1974). Representatives of both subfamilies Chrysophylloideae and Sapotoideae are present, although the latter subfamily has more species than the former. According to this analysis, the oldest colonization event of Chrysophylloideae from Africa to Madagascar is at node 4, which is dated at 54–68 Ma. Our analyses also indicate that an African ancestor of *Chrysophyllum sensu* Pennington (1991) colonized the island in the Miocene (clade D, Fig. 2). Both of these splits occurred well after Madagascar rifted from Africa (McLoughlin, 2001). It is also evident that the genus *Sideroxylon* (Sapotoideae) arrived in Madagascar via long-distance dispersal in the Eocene, again long after the rifting from Africa (Smedmark & Anderberg, 2007). *Capurodendron* is a Madagascan genus of uncertain affinity. However, one of its species has been already placed as sister to African *Lecomtedoxa* according to Smedmark & Anderberg (2007). It is therefore most likely that this genus also dispersed to the island after its split from the African landmass. The most probable source area of both Chrysophylloideae and *Sideroxylon* is Africa; Madagascar has a negligible probability of being the ancestral area according to ML estimations in both our study and that of Smedmark & Anderberg (2007). We can therefore deduce that Sapotaceae colonized Madagascar through at least three separate long-distance dispersal events: *Capurodendron*, *Chrysophyllum* and *Sideroxylon*, a result that supports the predominant biogeographical pattern found by Yoder & Nowak (2006).

Pradosia is a genus of 24 species of mainly trees, but also geoxylic subshrubs. The genus is restricted to South America (Govaerts *et al.*, 2001), with one exception, *P. spinosa*, which was described from West Africa (Ewango & Breteler, 2001). Analyses of molecular data demonstrate that *P. spinosa* is not a member of *Pradosia*, but is instead nested within a South American lineage of *Pouteria* (Swenson *et al.*, 2008a; Fig. 2). Based on our estimates, the most recent ancestor of *Pradosia spinosa* and *Pouteria macrophylla* (node 9) is estimated to have an age of 7–14 Ma, and given this, there is no other explanation than a long-distance dispersal from South America to Africa in the Late Miocene. Several similar cases of transatlantic dispersal were summarized by Renner (2004), who also suggested possible mechanisms for these events.

Australasian Chrysophylloideae are monophyletic (clade H, PP 1.00) and the parsimony ancestral area analysis identifies Australia as the ancestral area of that clade (node 7, Table 2). However, under the ML approach, the same node is optimized to New Caledonia. Four points are worth noting in interpreting this result. As mentioned earlier, (1) only the parsimony optimization in Mesquite can handle widespread terminals, which is particularly critical for this clade as it contains two widespread species; (2) in both parsimony and ML, none of these optimizations is highly supported across the tree sample; (3) phylogenetic resolution at this node is low; and (4) our taxon sampling does not include species from all areas in the Sunda Shelf, nor those occurring in (or endemic to) the islands of Fiji, Hawaii, Solomon, Tahiti and Vanuatu. We therefore consider the ancestral area optimizations within clade H to be provisional.

As discussed above, it is possible that the subfamily colonized Australia from South America via Antarctica. But what is the relationship between two main areas of Chrysophylloideae in the region, Australia and New Caledonia? In an

earlier study based on a molecular phylogeny and using a restricted sample from the region, Bartish *et al.* (2005) identified a sister relationship between taxa confined to Australia and New Caledonia. Due to the lack of fossil data, they used published substitution rates in ribosomal DNA to calculate pairwise values of genetic differentiation between taxa. They estimated that an Australian lineage (*Niemeyera*) diverged from a New Caledonian lineage (*Pycnandra sensu lato*; Swenson *et al.*, 2008b; Swenson & Munzinger, 2009) 32.4 Ma, and suggested that establishment in New Caledonia was the result of a dispersal event. Ladiges & Cantrill (2007) argued in favour of vicariance and persisting land until the Palaeocene/Eocene boundary (*c.* 55 Ma). However, arguments against a vicariance scenario include the fact that there is geological evidence that New Caledonia was submerged during the Palaeocene and Eocene, and emerged again at *c.* 37 Ma (McLoughlin, 2001; Pelletier, 2006; Schellart, 2007; Grandcolas *et al.*, 2008; Hall, 2009). When separating from Australia, the continental crust stretched, thinned and subsided, followed by a south-west-directed ophiolite obduction, meaning that proto-New Caledonia was overthrusted by the oceanic crust that formed what today is known as the ultramafic nappe, covering a third of New Caledonia. In addition, patterns of biotic exchange from Australia to New Caledonia, deduced as dispersal younger than 55 Ma, are present in *Araucaria* (Araucariaceae; Setoguchi *et al.*, 1998), diving beetles *Papuadytes* (Balke *et al.*, 2007), sandalwood *Santalum* (Santalaceae; Harbaugh & Baldwin, 2007), the orange subfamily Aurantioideae (Rutaceae; Pfeil & Crisp, 2008), and *Diospyros* (Ebenaceae; Duangjai *et al.*, 2009).

Our parsimony analysis lends support to the idea that lineages of clade H colonized New Caledonia several times (Fig. 2). According to our analysis, the three New Caledonian *Beccariella* species diverged from their nearest Australian ancestor around 50 Ma. However, internal transcribed spacer (ITS) sequence analyses (Swenson *et al.*, 2007a) and genetic distances between Australian and New Caledonian *Beccariella* species (I.V.B., unpublished) indicate that the clade of three *Beccariella* species in our sample (Fig. 2) diversified relatively recently from its Australian sister lineages. There is congruence between the published age estimate within the Australasian group based on ITS data only (Bartish *et al.*, 2005) and this study (ages of node 10, 32.4 and 38.6 Ma, respectively). The genetic distances (obtained from published ITS sequences) between two clades of *Beccariella* from New Caledonia and their sisters from Australia suggest divergence times of *c.* 8 and 5 Ma, respectively, for these two cases. Hence, as we have an approximation of the level of variation in age estimates in our data, it is safe to conclude that *Beccariella* colonized New Caledonia on two occasions, and both occur later than the colonization event by *Pycnandra*. Thus the oldest event of origin and diversification in New Caledonia occurred between 38 and 24 Ma (mean age estimates of the stem and the crown nodes of clade J). Even if the bottom limit of the 95% confidence range for the age of the stem node is used (Table 2), the most recent common ancestor of node 10 is not old enough to have had the chance of rafting from Australia onto New Caledonia. In other words, these areas had rifted apart to a considerable distance by the middle Eocene, and the presence of Sapotaceae in New Caledonia must be inferred as independent dispersal events, lending strong support to earlier studies (Bartish *et al.*, 2005; Swenson *et al.*, 2007a,b). In fact, our results support the idea that New Caledonia emerged again in the Late Eocene, as proposed by Grandcolas *et al.* (2008). However, if New Caledonia was submerged until the Late Eocene, it could not be the ancestral area of clade H, as ML reconstructions suggest (Table 2). Our age estimations therefore disagree with the ML reconstruction, but support the parsimony one indicating that Australia was the more likely ancestral area for nodes 7 and 10.

Comparative biogeography of Chrysophylloideae and *Sideroxylon*

One aim of this study was to compare the biogeographical histories of Chrysophylloideae and the genus *Sideroxylon* (Sapotoideae). According to Smedmark & Anderberg (2007), *Sideroxylon* most probably originated in Africa *c.* 68.4 Ma (51.2–95.0 Ma). However, the basal relationships of their tree were poorly resolved and the four lineages could be the result of rapid radiation in the Northern Hemisphere in the early Cenozoic. Nevertheless, one lineage is restricted to Africa and the Indian Ocean islands, and two are found in the New World, mostly Central America and the Caribbean. Although the 95% age confidence interval of the *Sideroxylon* node P in their analysis is relatively wide, the mean value of 68.4 Ma concurs with our mean estimated age of the radiation of Chrysophylloideae into South America and Australia (66.5 Ma, node 3, Table 2).

Unlike the earliest evolution of Chrysophylloideae and Sapotoideae in the Late Cretaceous, later Palaeogene diversifications of these two groups of Sapotaceae were in different regions of the Neotropics. In Chrysophylloideae, the most likely ancestral area of node 5 is South America (mean age 59 Ma, Table 2), an area in which it radiated and was probably colonized from Africa by long-distance dispersal in the Early Palaeocene (Fig. 2). In contrast, the most likely ancestral area of nodes J and O of *Sideroxylon* is Central America, and their mean ages are 51.4 and 53.2 Ma, respectively (Smedmark & Anderberg, 2007). As proposed, *Sideroxylon* migrated from the Old to the New World (presently North America) via the NALB, where it subsequently radiated in the Early Eocene, some 5–10 Myr later.

In summary, historical biogeographical reconstructions in two pantropical lineages of Sapotaceae indicate that the ancestors of these clades colonized the New World through two different mechanisms that shaped similar disjunct patterns between the Old and the New World: long-distance dispersal and possible migration to Australia via a southern route in Chrysophylloideae and migration via a northern route, the NALB, in *Sideroxylon*.

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