Historical biogeography of Loranthaceae (Santalales): Diversification agrees with emergence of tropical forests and radiation of songbirds

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ABSTRACT

Coadaptation between mistletoes and birds captured the attention of Charles Darwin over 150 years ago, stimulating considerable scientific research. Here we used Loranthaceae, a speciose and ecologically important mistletoe family, to obtain new insights into the interrelationships among its hosts and dispersers. Phylogenetic analyses of Loranthaceae were based on a dataset of nuclear and chloroplast DNA sequences. Divergence time estimation, ancestral area reconstruction, and diversification rate analyses were employed to examine historical biogeography. The crown group of Loranthaceae was estimated to originate in Australasian Gondwana during the Paleocene to early Eocene (59 Ma, 95% HPD: 53–66 Ma), and rapidly diversified, converting from root parasitic to aerial parasitic trophic mode ca. 50 Ma during the Eocene climatic optimum. Subsequently, Loranthaceae were inferred to be widespread in Australasia and South America but absent in Africa. The African and European members were derived from Asiatic lineages. The burst of diversification of Loranthaceae occurred during a climatic optimum period that coincides with the dominance of tropical forests in the world. This also corresponds to the trophic mode conversion of Loranthaceae and rapid radiation of many bird families – important agents for long-distance dispersal in the Cenozoic.

1. Introduction

"In the case of the mistletoe, which draws its nourishment from certain trees, which has seeds which must be transported by certain birds… It is therefore, of the highest importance to gain a clear insight into the means of modification and coadaptation."

Darwin (1859)

Loranthaceae, the largest family of Santalales with 76 genera and more than 1000 species (Nickrent, 1997 onwards), are mainly distributed in tropical and subtropical regions of the Americas, Africa, Asia and Australia, with a few species extending to the temperate zones in Europe and East Asia (Vidal-Russell and Nickrent, 2008a). Although most genera of Loranthaceae are aerial parasites, three are root parasitic (Kuijt, 1969, 2015). The aerial parasitic members of the family

produce viscous seeds that first attach to host branches and then germinate to form haustorial connections to the host's vascular system (Kuijt, 1969). This distinct heterotrophic mode, which was observed and studied by Darwin (1859), evolved five times independently in Santalales: in the families Amphorogynaceae, Loranthaceae, Misodendraceae, Santalaceae and Viscaceae, each of which includes plants commonly called "mistletoes" (Nickrent et al., 2010).

Relationships within Loranthaceae have been explored in several molecular phylogenetic investigations (Wilson and Calvin, 2006; Vidal-Russell and Nickrent, 2008a,b), and in the latter the timing of the evolution of the mistletoe habit was examined using 39 representative members of Santalales. A tribal and subtribal classification for Loranthaceae was proposed by Nickrent et al. (2010) based on both molecular and morphological evidence. Base chromosome numbers

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correlate well with the defined tribes within the family (Vidal-Russell and Nickrent, 2008a), where x = 8 and 9 are derived numbers, possibly originating via aneuploid reductions from the plesiomorphic condition x = 12.

Based on the current disjunctive pantropical distribution pattern of the family, Barlow (1983, 1990) proposed that Loranthaceae once had a wide distribution in Gondwana during the Late Cretaceous. He inferred that four major evolutionary lines were then isolated by the fragmentation of the supercontinent including Afro-Indian, Indian-Indoasian, Australasian-Papuasian and South American lingeages, and that these lines evolved independently into present day taxa. In a biogeographical study sampling five-DNA regions and 36 genera, Vidal-Russell and Nickrent (2007) inferred that Loranthaceae originated and spread in Gondwana (including present day land-masses of Australia, New Zealand, South America and New Guinea) 75–85 million years ago (Ma) during the Late Cretaceous, which was long after the separation of Africa and India from Gondwana (before the Late Cretaceous; McLoughlin, 2001). This hypothesis indicated that Loranthaceae were absent from Africa and India in the Late Cretaceous. Grímsson et al. (2017a) conducted a molecular phylogenetic analysis of 60 Loranthaceae taxa, primarily using sequences generated by Vidal-Russell and Nickrent (2008a,b) and Su et al. (2015). The topology of their maximum likelihood (ML) analysis recovered many previously documented relationships but also showed several anomalous positions such as those of *Aetanthus*, *Atkinsonia*, and *Lepeostegeres*. In a second paper, Grímsson et al. (2017b) conducted ML analyses of plastid and nuclear genes for ca. 100 taxa. While significant incongruence between their plastid and nuclear data was not found, the data were not concatenated to construct a total evidence tree. The relationships recovered differed little from those reported in Su et al. (2015). A reduced taxon dataset (42 taxa), was used to produce a dated phylogeny, with the root set as *Tupeia antarctica* (a stem parasite) based on pollen evidence. This analysis estimated the crown group of the family arose in the Eocene, ca. 50 Ma, however, outgroups outside Loranthaceae were not included, and ancestral area reconstruction and diversification analyses to explain the historical biogeography of Loranthaceae were not conducted.

Here we conducted phylogenetic and biogeographical analyses using both nuclear and chloroplast DNA regions based on intensive taxon sampling (including 62 of the 76 genera in Loranthaceae). Our major aims are to reconstruct the biogeographical history of Loranthaceae reconciled with present day distributions, fossil data, and geological information, as well as to investigate the diversification dynamics of Loranthaceae and explore the correlation with its hosts and dispersal vectors (pollinators and seed dispersers).

2. Materials and methods

2.1. Sampling, DNA extraction, amplification and sequencing

We sampled 89 species in 62 of the 76 genera in Loranthaceae including the previous unsampled genus *Elytranthe*. Additionally, sixteen species of Misodendraceae, Schoepfiaceae, Santalaceae and Aptandraceae were selected as outgroups based on previous molecular phylogenetic studies (Vidal-Russell and Nickrent, 2008a; Su et al., 2015). Nuclear small-subunit ribosomal DNA (SSU rDNA), large-subunit ribosomal DNA (LSU rDNA), and three chloroplast DNA regions (*rbc*L, *mat*K and *trn*L-F) were used for analyses. Voucher information and GenBank accession numbers are listed in Table S1 (Appendix).

Genomic DNA was extracted from silica gel dried tissues or herbarium material using the CTAB procedure (Doyle and Doyle, 1987). Polymerase chain reactions and sequencing were performed using the primers designed by Vidal-Russell and Nickrent (2008a,b) and Taberlet et al. (1991). The sequences were aligned either in SeAl (Rambaut, 2007) or in Geneious v.8.0.5 (Kearse et al., 2012). Some portions from the *trn*L-F region were excluded from the final analyses because poor alignment cast uncertainty upon site homology.

2.2. Phylogenetic analyses

Phylogenetic analyses were initially conducted for individual DNA regions using the maximum likelihood (ML) method with a rapid bootstrap analysis in RAxML v.8.2.8 (Stamatakis, 2006; Stamatakis et al., 2008). Individual analyses detected no well-supported topological conflicts (i.e., incongruences among individual DNA regions with BS < 70%; Hillis and Bull, 1993). We thus conducted further phylogenetic analyses for the combined dataset of five DNA regions using both ML and Bayesian inference (BI) methods. The ML trees were generated with the GTR + I + G substitution model applying 1000 bootstrap replicates. The best-fitting models for the combined datasets were determined by the Akaike information criterion (AIC) as implemented in jModelTest v.2.1.6 (Darriba et al., 2012). The Bayesian analysis was performed in MrBayes v.3.1.2 (Ronquist and Huelsenbeck, 2003) on the CIPRES Science Gateway Portal (Miller et al., 2010) based on the same models as in the ML analysis. The Markov chain Monte Carlo (MCMC) algorithm was run for 10,000,000 generations with a total of four chains, starting from a random tree, and trees were sampled every 1000 generations. The program Tracer v.1.6 (Rambaut et al., 2014) was used to check that effective sample sizes (ESSs) were attained for all relevant parameters assessed (> 200). With the first 25% of sampled generations discarded as burn-in, the 50% majority-rule consensus tree and Bayesian posterior probabilities (PP) were obtained using the remaining trees.

2.3. Divergence time estimation

We estimated the lineage divergence times of Loranthaceae using the uncorrelated lognormal Bayesian method in BEAST v.1.8.0 (Drummond et al., 2012). The datasets were partitioned based on five DNA regions using the "unlink substitution model" option, and to each partition a substitution model from the results of jModelTest v.2.1.6 (Darriba et al., 2012) was applied. All dating runs relied on a Yule process tree prior. A lognormal distribution was used for the five calibration points (Deng et al., 2014). We conducted two separate MCMC runs of 150,000,000 generations with samples taken every 15,000 generations. Tracer v.1.6 (Rambaut et al., 2014) was used to check if ESSs for all relevant parameters were well above 200 and that stationarity had been reached. A maximum credibility tree was then built by TreeAnnotator v.1.8.0 (Rambaut and Drummond, 2010) with the initial 25% of trees discarded as burn-in. The final result was visualized in Figtree v.1.4.0 (Rambaut, 2009).

Most fossils recognized as Santalales are represented by pollen grains of Cretaceous and Tertiary age (Vidal-Russell and Nickrent, 2008b). We gave two fossil calibrations for the outgroups of Loranthaceae. The crown age of the tribe Anacoloseae of Aptandraceae was constrained to 70 Ma (95% HPD: 66.0–72.1 Ma) based on the fossil of *Anacolosidites* recorded since the Maastrichtian (Malécot and Lobreau-Callen, 2005). The fossil pollen of *Misodendrum* (as *Compositoipollenites*) was recorded from middle Eocene (ca. 45 Ma) (Zamaloa and Fernández, 2016). Hence the crown age of Misodendraceae was constrained to 45 Ma (95% HPD: 41.2–48.6 Ma). The stem age of Loranthaceae was constrained to 70 Ma (95% HPD: 69.4–72.6 Ma) based on the fossil of *Cranwellia* (Mildenhall, 1980; Macphail et al., 2012). The crown node of the tribe Lorantheae was constrained to 42.8 Ma (95% HPD: 37.8–47.8 Ma) according to the fossil pollen Changchang MT identified as *Taxillus*, *Scurrula* and *Amyema* (Grímsson et al., 2017b). The crown node of the tribe Elytrantheae was constrained to 39.6 Ma (95% HPD: 38–41.2 Ma) according to the fossil pollen Profen MT3 (Grímsson et al., 2017b). The assignment of each fossil to a particular node and the age calibrations are discussed in detail in Text S1 (Appendix).

2.4. Ancestral area reconstruction

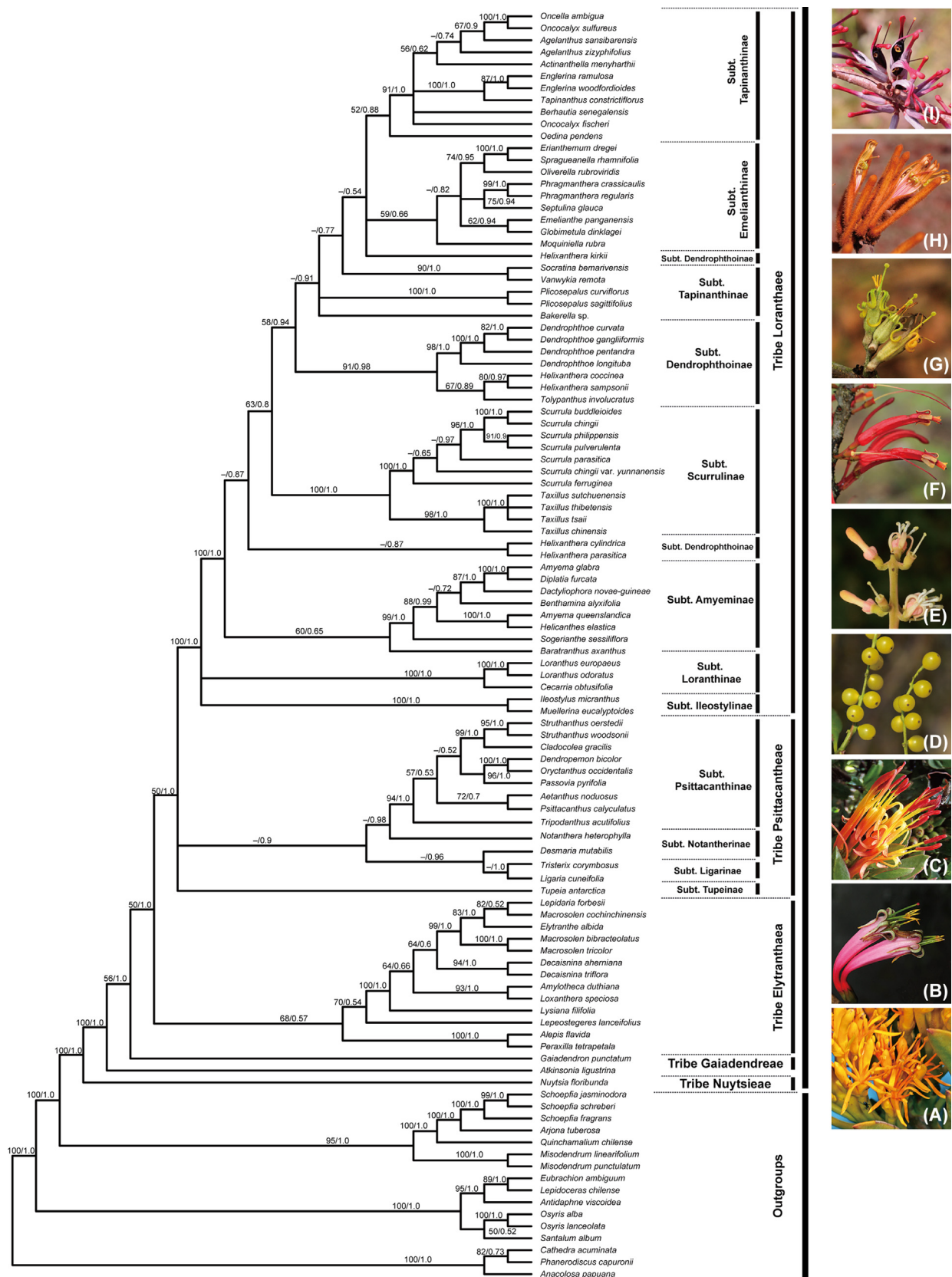We performed the ancestral area reconstruction using two methods:

Fig. 1. Majority rule consensus tree of Loranthaceae based on Bayesian inference of the combined datasets of five DNA regions (LSU rDNA, SSU rDNA, *mat*K, *rbc*L and *trn*L-F). ML bootstrap values and posterior probabilities (PP) of the BI analysis are presented above the branches. "–" indicates the support values less than 50%. The circumscription of tribes and subtribes follows the classification of Nickrent et al. (2010). **(A)**. *Nuytsia floribunda*; **(B)**.*Elytranthe albida*; **(C)**. *Tristerix longebracteatus*; **(D)**.*Loranthus tanakae*; **(E)**. *Helixanthera parasitica*; **(F)**.*Taxillus delavayi*; **(G)**. *Dendrophthoe pentandra*; **(H)**.*Phragmanthera regularis*; **(I)**. *Englerina woodfordioides*. Photo credits: R. L. Barrett (A, C), B.Liu (B, D-I).

(1) BioGeoBEARS (Matzke, 2013) implemented in R (R Core Team, 2016), and (2) a Bayesian approach to dispersal-vicariance analysis (Bayes-DIVA; Nylander et al., 2008) implemented in RASP v.3.2 (Yu et al., 2011) using datasets from the BEAST analysis.

The BioGeoBEARS method implements three likelihood-based models: Dispersal-Extinction-Cladogenesis (DEC; Ree and Smith, 2008), the likelihood version of dispersal–vicariance (DIVA; Ronquist, 1997; herein DIVALIKE), and the likelihood version of BayArea model (Landis et al., 2013; herein BAYAREALIKE). In each model, an additional "*j*" parameter (founder event/jump speciation) was added, which allows descendant lineages to have a different area from the direct ancestor (Matzke, 2013; Vasconcelos et al., 2017). Thus, a total of six models resulted. Additionally the number and type of biogeographical events were estimated by biogeographical stochastic mapping (BSM) implemented in 'BioGeoBEARS' (Matzke, 2015) under the best-fit biogeographical model (see Section 3). The biogeographical events were divided under the models including within-area speciation, vicariance and dispersal events (range expansions and founder events) (Dupin et al., 2017). Event frequencies were estimated from the mean and standard deviation of event counts from 100 BSMs.

The Bayes-DIVA method can minimize phylogenetic uncertainty by utilizing the posterior distribution of trees resulting from BEAST and generate credibility support values for alternative phylogenetic relationships (Nylander et al., 2008; Yu et al., 2011). For the Bayes-DIVA analysis, we loaded 10,000 trees from the BEAST analysis and computed a condensed tree as the final representative tree with the first 2500 trees discarded as burn-in.

Six biogeographical areas were defined based on the distribution of extant Loranthaceae and their relatives: A = Asia (including southern Japan, Korean Peninsula, mainland of East and South Asia, Indochina and Malesia, but excluding New Guinea); B = Australasia (including Australia, New Zealand, New Guinea and Pacific Islands); C = Africa (including the coastal area of the Arabian Peninsula and Sub-Saharan Africa); D = Americas (including Mexico, Central and South America); E = Europe (including western Asia and central and southern Europe); F = Madagascar. The Indian subcontinent (the mainland of South Asia) began rifting from Australia-Antarctica ca. 136 Ma (Gibbons et al., 2013), which was much earlier than the origin of the Loranthaceae, thus we did not define the Indian subcontinent as a separate biogeographical area. Loranthaceae in the New World are in two groups: the early-diverging genus *Gaiadendron* whose distribution is mostly in Andean South America but also extending northward to Central America, and Psittacantheae, whose greatest generic diversity is in Andean South America (*Desmaria*, *Ligaria*, *Tristerix*, *Notanthera*) with the distributions of some genera (*Struthanthus*, *Passovia*, *Psittacanthus*) extending northward into Mexico. Psittacantheae are endemic to the Americas and the tribe appears to be monophyletic. Thus, we did not create further biogeographical division. With denser taxon sampling (additional species within speciose genera), finer-scale biogeographical divisions will be required. Our paper has taken a broad overall perspective, thus investigating more detailed patterns may await future work.

2.5. Diversification rate analyses

The temporal variation in the diversification rates of Loranthaceae was visualized by lineage-through-time (LTT) plots using the R package APE v.3.4.1 (Paradis et al., 2004). The ultrametric trees obtained from the BEAST analyses were used to generate semilogarithmic LTT plots with the outgroups pruned. The confidence intervals were calculated based on 1000 trees randomly selected from the set of BEAST trees. We determined the time point at which incomplete taxon sampling would begin to have a significant effect on the LTT plot following Couvreur et al. (2011).

We further used TreePar v.3.3 in R (Stadler, 2011) to identify the locations of temporal shifts in diversification rates of Loranthaceae. TreePar analyses were carried out using a grid setting of 0.1 million

years with both the Yule and birth-death models. Rate shifts were recognized as significant when $p < 0.05$ using the likelihood ratio test.

3. Results

3.1. Phylogenetic relationships

We generated 123 sequences from the newly collected samples (mostly from China and East Africa) representing 31 species. These were combined with 323 sequences obtained from GenBank. Of the 525 cells (105 species for five DNA regions), 446 cells had sequence data, thus the matrix was 85% filled (Table S1). The combined dataset resulted in a matrix of 7175 characters and the detailed information of each DNA region is shown in Table S2. Phylogenetic trees from individual nuclear and chloroplast partitions resulted in lower resolution of relationships within Loranthaceae than the combined dataset. The topologies from ML and BI analyses of the combined dataset were highly congruent and we thus present the Bayesian tree with BS and PP values in Fig. 1. Comparisons between the nuclear and chloroplast phylogenetic results are presented in Fig. S1.

Nuytsia, the monotypic genus of tribe Nuytsieae was strongly supported as sister to the remaining Loranthaceae lineages (BS = 100% and PP = 1.0; Fig. 1). Following Nuytsieae, *Atkinsonia* and *Gaiadendron* occur in a grade (tribe Gaiadendreae) followed by tribes Elytrantheae, Psittacantheae and Lorantheae (Fig. 1). In this analysis, Elytrantheae (BS = 68% and PP = 0.57) and Lorantheae (BS = 100% and PP = 1.0) were supported as monophyletic, while Psittacantheae and Gaiadendreae were non-monophyletic. In the tribe Elytrantheae, *Alepis* plus *Peraxilla* and *Lepeostegeres* are successive sisters to a well supported clade that included the other taxa sampled from this tribe. *Elytranthe albida* and *Lepidaria forbesii* were nested within *Macrosolen* with high support value (BS = 99% and PP = 1.0). The relationships of the four subtribes of Psittacantheae were not well resolved (Fig. 1). In the largest tribe Lorantheae, Ileostylinae, Loranthinae, and a clade composed of the other five subtribes formed a tritomy, with each of the three clades receiving good support. The African subtribe Tapinanthinae was not monophyletic with Emelianthinae nested within it. *Septulina*, originally classified in Tapinanthinae, was placed within Emelianthinae, and *Oncocalyx* and *Agelanthus* are not monophyletic (Fig. 1). The African endemic species *Helixanthera kirkii* grouped with other African members, while two other clades from Asia clustered with species from Asia (*H. coccinea* and *H. sampsonii* in Dendrophthoinae; *H. parasitica* and *H. cylindrica* sister to the clade consisting of Scurrulinae plus Dendrophthoinae and the African subtribes).

3.2. Divergence times and diversification rates

The divergence time estimations for Loranthaceae are presented in Fig. 2A. The crown age of Loranthaceae was estimated to be 59.38 Ma (95% HPD: 52.58–65.59 Ma; node 1, Fig. 2A). Two genera of the tribe Gaiadendreae, *Atkinsonia* and *Gaiadendron*, diverged 51.3 Ma (95% HPD: 45.71–57.42 Ma; node 2, Fig. 2A) and 50.04 Ma (95% HPD: 44.61–55.9 Ma; node 3, Fig. 2A), respectively. The tribe Elytrantheae split from the ancestors of Psittacantheae plus Lorantheae ca. 48.05 Ma (95% HPD: 42.39–53.15 Ma; node 4, Fig. 2A). The tribes Psittacantheae and Lorantheae split 46.9 Ma (95% HPD: 41.36–51.95 Ma; node 6 in Fig. 2A), and began to diversify 44.33 Ma (95% HPD: 36.84–51.1 Ma; node 7, Fig. 2A) and 41.95 Ma (95% HPD: 37.5–46.31 Ma; node 8, Fig. 2A), respectively.

The LTT curves plotted as a function of time showed that speciation within Loranthaceae rapidly increased since the beginning of the Eocene (Fig. 2B). TreePar analyses rejected the null hypothesis of a constant diversification rate for Loranthaceae under a birth-death process with $\chi^2 = 14.16$ and $p = 0.02$. Moreover, this method detected one significant shift in the diversification rate as well as a dramatic increase in the number of Loranthaceae lineages at 50.2 Ma.
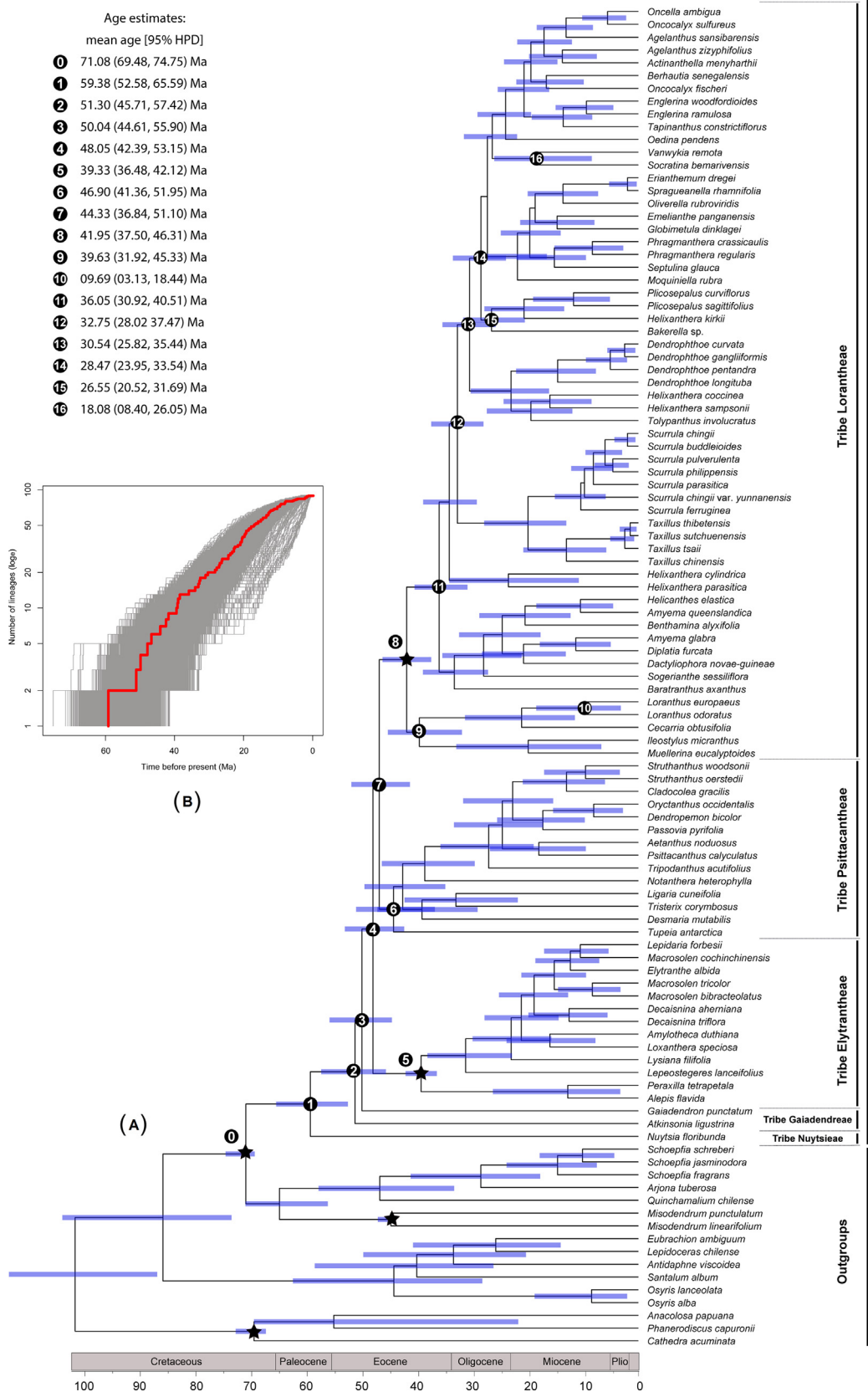
Fig. 2. (A) Maximum clade credibility tree inferred from BEAST based on the combined datasets of five DNA regions. The bars around node ages indicate 95% highest posterior density intervals. Node constraints are indicated with stars. Nodes of interests were marked as 0–16. (B) Lineages through time (LTT) plots for Loranthaceae inferred from R-APE package.

Table 1

Comparison of the fit of different models of biogeographical range evolution and model specific estimates for different parameters (d = dispersal, e = extinction, j = weight of jump dispersal (founder speciation)).

Model	Parameter no	LnL	d	e	j	AIC	AIC weight
DEC	2	−125.37	3.00×10^{-3}	5.51×10^{-2}	0	255.93	0.612
DEC + j	3	−124.96	3.40×10^{-3}	1.20×10^{-1}	0.00317	254.74	0.397
DIVALIKE	2	−143.57	2.00×10^{-3}	1.20×10^{-4}	0	291.1	1
DIVALIKE + j	3	−130.37	9.00×10^{-4}	1.00×10^{-8}	0.019	266.7	5×10^{-5}
BAYAREALIKE	2	−157.18	8.00×10^{-4}	1.46×10^{-2}	0	318.4	1
BAYAREALIKE + j	3	−125.32	4.00×10^{-4}	1.00×10^{-8}	0.0244	256.6	0

Loranthaceae began to diversify at a low rate with r_1 = 0.0033 species per million years (Myr^{-1}), but increased to 0.0909 species Myr^{-1} at 50.2 Ma. While the Yule process of the TreePar analysis generated a younger result (24.7 Ma) for the shift in diversification rate (r_1 = 0.095 and r_2 = 0.129), this was not considered significant (p = 0.08). Thus the following discussion is based on the results under the birth-death process.

3.3. Ancestral area reconstruction

Ancestral area reconstruction in BioGeoBEARS and Bayes-DIVA yielded highly congruent results. However, the results from BioGeoBEARS show higher resolution for more nodes than Bayes-DIVA. Among the six models, the results indicate higher log likelihood values for three parameters in comparison to two parameters (Table 1), thus indicating jump speciation (i.e., dispersal between non-adjacent areas) as an important pattern in range variation of Loranthaceae. Moreover, the BioGeoBEARS analyses showed DEC + j was the best-fit biogeographical model. Thus, we only present the reconstruction of BioGeoBEARS under the DEC + j model (Fig. 3). The result of ancestral area reconstructions from Bayes-DIVA is showed in Fig. S2. The number of nodes in Figs. 2A and 3 are consistent, and a summary of the divergence age estimations and ancestral area reconstruction is presented in Table 2. Our biogeographical stochastic mapping (BSM) results under the best-fit biogeographical model DEC + j revealed that most biogeographical events comprise within-area speciation (64%) and dispersals (34%), with very few (2%) vicariant events (Table S3).

The stem group of Loranthaceae was estimated to diverge from its closest relatives in Australasia (area B) and America (area D) (node 0, Fig. 3), and subsequently diversified in Australasia during the Paleocene (node 1, Fig. 3). *Atkinsonia* and *Gaiadendron* originated during the early Eocene in Australasia (nodes 2 and 3, Fig. 3). The aerial-parasitic members diverged from the ancestor of Elytrantheae in Australasia (node 4, Fig. 3), and more than one dispersal event between Australasia and Asia were suggested during the diversification of this tribe. The crown group of Psittacantheae diverged in Australasia following a split into *Tupeia* (New Zealand) and the New World lineage (node 7, Fig. 3). The largest group of Loranthaceae, tribe Lorantheae, diverged in Australasia and diversified in the Old World (node 6, Fig. 3). The most recent common ancestor of each of the extant subtribes of Lorantheae was estimated to diversify in Australasia and Asia during the middle Eocene (node 8, Fig. 3). The subtribes Ileostylinae and Loranthinae diverged in Australasia (node 9, Fig. 3), while Amyeminae and Scurrulinae originated in Asia (nodes 11 and 12, Fig. 3). The African lineage (Emelianthinae plus Tapinanthinae) split from the ancestor of Dendrophthoinae in Asia during the Oligocene (node 13, Fig. 3), and diversified independently in Africa (node 14, Fig. 3). Moreover, the African members dispersed to Madagascar twice (nodes 15 and 16, Fig. 3), and the latest major dispersal within Loranthaceae was the migration from Asia to Europe during the Miocene (node 10, Fig. 3).

4. Discussion

4.1. Phylogenetic relationships

The phylogenetic results reported here are an advancement over previous analyses (Wilson and Calvin, 2006; Vidal-Russell and Nickrent, 2008a; Su et al., 2015; Grímsson et al., 2017a,b) in terms of taxon and gene sampling. The overall tree topology is congruent with those obtained in earlier studies, and as before, some clades received strong support, such as the tribe Lorantheae, whereas others did not, including low support along the "backbone" of the tree. However, the topology within Loranthaceae and positions of some genera (e.g. *Tupeia*) are incongruous with those from Grímsson et al. (2017a), these probably due to differences in taxon sampling, gene sampling, alignment, and outgroup selection.

In tribe Elytrantheae, the samples of *Elytranthe* and *Lepidaria* were shown to be on a clade with three species of *Macrosolen* with strong support (BS = 99% and PP = 1.0) (Fig. 1). These three genera were considered closely related by Danser (1936) who placed them in subtribe Elytranthinae, but transferred various species between the genera. Indeed Barlow (1997) considered treating *Elytranthe* and *Macrosolen* as congeneric. Various characters vary between species in these three genera, such as whether the inflorescence axis is elongated or flat and the degree to which floral bracts enlarge and form an involucre. Thus relationships in this group are at present unclear and further molecular work with greater taxon sampling is required to sort out generic boundaries.

Helixanthera, a member of Dendrophthoinae, has been resolved as non-monophyletic by previous studies (Vidal-Russell and Nickrent, 2008a; Su et al., 2015). Our phylogenetic analysis recognizes three clades that differ in their biogeographical distributions. The African endemic species *Helixanthera kirkii* groups with the African members of Lorantheae (part of Tapinanthinae), while two other clades from Asia cluster with the Asian members (Dendrophthoinae and sister to Scurrulinae) (Fig. 1), suggesting that the African members of *Helixanthera* should be recognized as a separate genus. Our study also indicates that subtribe Tapinanthinae is not monophyletic and *Septulina* is nested within Emelianthinae (Fig. 1). The two subtribes are endemic to Africa, and they share the same chromosome number (x = 9), as well as indeterminate inflorescences (Kuijt, 1981; Vidal-Russell and Nickrent, 2008a; Nickrent et al., 2010). Additionally, our results show that two African genera, *Oncocalyx* and *Agelanthus,* are not monophyletic (Fig. 1). Further studies should be conducted to resolve the phylogenetic relationship between Tapinanthinae and Emelianthinae and test the monophyly of the African genera.

Recently, Grímsson et al. (2017a) reported an extensive survey of pollen types in Loranthaceae, but also conducted a re-analysis of the Su et al. (2015) molecular data (no new data generated). Their conclusions and recommendations are addressed in the context of the data presented here. One criticism was that there was insufficient phylogenetic signal to support the classification of Loranthaceae presented in Nickrent et al. (2010). Indeed, several nodes along the "backbone" of the Loranthaceae tree consistently have low support (Vidal-Russell and Nickrent, 2008a; Su et al., 2015), however, the Nickrent et al. (2010)
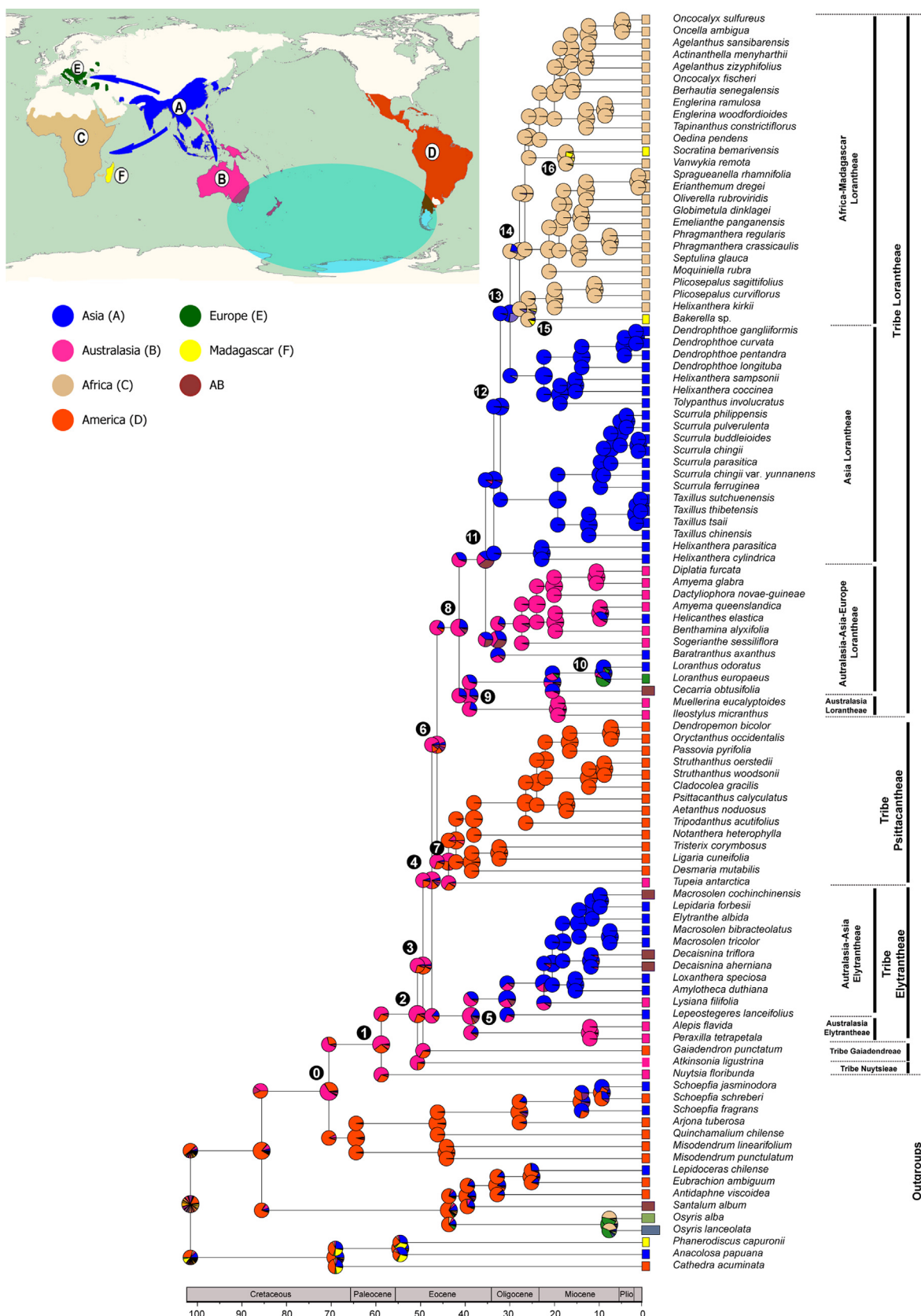
Fig. 3. Ancestral area reconstruction of Loranthaceae by BioGeoBEARS (j = 0.00317, LnL = −124.96). Geologic time scale is shown at the bottom. Area abbreviations are as follows: A = Asia (including southern Japan, Korean Peninsula, mainland of East and South Asia, Indochina and Malesia, but excluding New Guinea); B = Australasia (including Australia, New Zealand, New Guinea and Pacific Islands); C = Africa (including the coastal area of the Arabian Peninsula and Sub-Saharan Africa); D = Americas (including Mexico, Central and South America); E = Europe (including western Asia and central and southern Europe); F = Madagascar.

Table 2
Summary of supported clades, divergence age estimation (Ma) by BEAST and ancestral area reconstructions by Bayes-DIVA. Node numbers refer to Figs. 2A and 3. Area abbreviations are as follows: A = Asia (including southern Japan, Korean Peninsula, mainland of East and South Asia, Indochina and Malesia, but excluding New Guinea); B = Australasia (including Australia, New Zealand, New Guinea and Pacific Islands); C = Africa (including the coastal area of the Arabian Peninsula and Sub-Saharan Africa); D = Americas (including Mexico, Central and South America); E = Europe (including western Asia and central and southern Europe); F = Madagascar.

Node	Bayesian PP	Age estimates mean (95% HPD) [Ma]	BioGeoBEARS (DEC + *j*)	Bayes-DIVA (maximum probability)
0	1.0	71.08 (69.48, 74.75)	BD	B (67.11)
				D (20.03)
1	1.0	59.38 (52.58, 65.59)	B	B (94.64)
2	1.0	51.30 (45.71, 57.42)	B	B (97.22)
3	1.0	50.04 (44.61, 55.90)	B	B (86.93)
4	1.0	48.05 (42.39, 53.15)	B	B (75.52)
5	< 0.90	39.33 (36.48, 42.12)	B	B (65)
				AB (30.75)
6	1.0	46.90 (41.36, 51.95)	B	B (60.19)
				AB (34.76)
7	< 0.90	44.33 (36.84, 51.10)	B	B (87.99)
8	1.0	41.95 (37.50, 46.31)	B	AB (56.8)
				B (28.21)
9	< 0.90	39.63 (31.92, 45.33)	B	AB (61.57)
				B (30.73)
10	1.0	09.69 (03.13, 18.44)	A	A (85.56)
11	1.0	36.05 (30.92, 40.51)	A	A (52.47)
				AB (38.16)
12	< 0.90	32.75 (28.02, 37.47)	A	A (99.02)
13	0.94	30.54 (25.82, 35.44)	A	A (96.21)
14	0.91	28.47 (23.95, 33.54)	C	C (82.97)
15	< 0.90	26.55 (20.52, 31.69)	C	C (86.79)
16	1.0	18.08 (08.40, 26.05)	C	C (97.23)

classification took into account not only the molecular tree topology but also base chromosome number and morphology. Parts of that classification, as shown by the data presented herein, require modification. Issues associated with missing data still exist, although the present matrix is 85% filled, an improvement over Su et al. (2015). Low support for backbone relationships was seen in the present study and will likely only improve when additional informative genes can be added across all taxa.

Another criticism by Grímsson et al. (2017a) involved the position of *Nuytsia* as sister to the family which they claim was an artefact of missing data and ingroup-outgroup long-branch attraction. The present study has *Nuytsia* strongly supported as sister to Loranthaceae but this cannot be artefactual stemming from an "extremely divergent outgroup". Unlike Su et al. (2015) where the holoparasites in Mystropetalaceae and Balanophoraceae were included, Aptandraceae, Santalaceae, Misodendraceae and Schoepfiaceae were used in this study. Moreover, no extreme branch length heterogeneity was detected. The three chloroplast genes all show strong support for *Nuytsia* as sister to Loranthaceae whereas this relationship is not seen in the more conservative nuclear ribosomal genes (Fig. S1).

Grímsson et al. (2017a) suggested that instead of *Nuytsia*, the New Zealand endemic *Tupeia antarctica* is sister to the family and this conclusion was based mainly upon its spheroidal pollen (Type A) that is essentially unique in Loranthaceae. Problems associated with this concept are as follows. *Tupeia* is a stem parasite, thus its placement as sister to the family would require the evolution of stem parasitism, its loss in *Nuytsia*, *Atkinsonia* and *Gaiadendron*, and then re-appearance in the clade leading to Elytrantheae. The only way to avoid this unparsimonious scenario would be to propose that the ancestor of *Tupeia* was in fact a root parasite and that this lineage (in the absence of cladogenesis) achieved its present aerial parasitism mode independent of the remainder of the family. To place *Tupeia* as sister to Loranthaceae increases the 5-gene tree length (in maximum parsimony) by 45 steps, an increase of 6%. Finally, while pollen morphology may track phylogeny in some cases, in others its divergence has little correlation with phylogenetic tree topology. Indeed even within Loranthaceae, *Phthirusa hutchinsonii* shares the Type A pollen type, yet Grímsson et al. (2017a)

do not propose relocating this taxon from Psittacantheae. Moreover, the genus *Oryctanthus* (Psittacantheae) has Type D pollen that differs dramatically from Types B and C seen in most Loranthaceae. It seems clear that autapomorphic and sometimes convergent pollen types occur in Loranthaceae (and other Santalales), thus such micromorphological features should not be granted overwhelming phylogenetic significance.

4.2. Historical biogeography of Loranthaceae

4.2.1. Origin and early diversification on Gondwana

The divergence times of Loranthaceae from this study are congruent with results from Magallón et al. (2015) and Grímsson et al. (2017b) (Table S4). The biogeographical analyses and divergence time estimations suggest that the stem group of Loranthaceae originated in Australasia ca. 71 Ma during the Maastrichtian (Late Cretaceous; node 0, Figs. 2A and 3; Table 2), and its crown age dates to 59.38 Ma (95% HPD: 52.58–65.59 Ma; node 1, Figs. 2A and 3; Table 2). The Gondwana supercontinent was formed by fusion of several cratons in the Southern Hemisphere during the Cambrian period, and began to break up since the Early Jurassic (McLoughlin, 2001; Lomolino et al., 2010). During the early evolution of Loranthaceae in the Late Cretaceous, Australasia and Antarctica remained connected, and Antarctica and South America were very close or even contiguous (Barlow, 1983, 1990; McLoughlin, 2001; Vidal-Russell and Nickrent, 2007; Lomolino et al., 2010; Nickrent, 2011). Thus, the ancestors of Loranthaceae might have spread between Australasia and South America via Antarctica by birds or small arborial marsupials (Amico and Aizen, 2000). These ancestors were also likely widespread in these areas in the Late Cretaceous and early Cenozoic, during which time the climate of Gondwana was much warmer than today (Zachos et al., 2001; Lomolino et al., 2010).

The result from BSM (Table S3) indicated that within-area speciation is the most frequent type of biogeographical event in Loranthaceae. Within-area speciation events were considered preponderant in most of the large clades of Loranthaceae that are endemic to single areas as defined in our study. Additionally, we found that dispersal without "range contractions" was the principal driver of range evolution which

occurred about eighteen times more often than vicariance. Dupin et al. (2017) suggested that dispersal events seem to be the most common factor for the distribution of plants, whereas, vicariant events are important factors for range evolution in many animals. Thus dispersal events between both proximal and distant regions appear to have been frequent in the historical biogeography of Loranthaceae, and may have been facilitated by colonization or domination of Loranthaceae host plants in tropical forests.

According to our molecular dating, aerial parasites might have arisen from root parasites while South America, Antarctica and Australia were still contiguous, 48.05–50.04 Ma in the early Eocene. *Nuytsia*, *Atkinsonia* and *Gaiadendron* are the only root-parasitic genera that survive today, and they represent the earliest lineages of Loranthaceae. These genera were estimated to originate 59.38 Ma, 51.3 Ma and 50.04 Ma, respectively (nodes 1, 2 and 3; Figs. 2A and 3). Following the breakup of southern Gondwana, two lineages of root parasites (*Nuytsia* and *Atkinsonia*) remained in Australia. The present day American endemic members, *Gaiadendron* and Psittacantheae, originated in Australasia, and spread to southern South America via Antarctica 50.04 Ma and 44.33 Ma (nodes 3 and 7; Figs. 2A and 3), respectively.

4.2.2. Long-distance dispersal of Loranthaceae to North America, Greenland and Europe from Late Cretaceous to middle Eocene

Numerous studies report pollen of Loranthaceae from North America (USA and Canada), Greenland and Europe during the Eocene (Krutzsch, 1959; Englehardt, 1964; Jarzen, 1973, 1977; Elsik, 1974; Elsik and Dilcher, 1974; Frederiksen, 1980; Taylor, 1987; Oschkinis and Gregor, 1992; Dilcher and Lott, 2005; Gregor, 2005; Hottenrott et al., 2010; Gregor and Oschkinis, 2013; Manchester et al., 2015; Grímsson et al., 2017b). Although Grímsson et al. (2017b) discussed the locations and ages of these pollen records, they provided no explanation for the appearance of these fossils. Our results indicate that the ancestor of Loranthaceae and the root-parasitic genera originated since the Late Cretaceous to early Eocene under warm and moist climates. Moreover, the burst of diversification of Loranthaceae occurred during a climatic optimum (ca. 50 Ma; see below). Furthermore, birds, the most important factor for dispersal of Loranthaceae, underwent a great diversification since 50 Ma (Jetz et al., 2012; Claramunt and Cracraft, 2015). The latter authors indicated that birds spread from South America to North America then to Europe via Greenland during the late Paleocene to middle Eocene. Such migrations may have been pivotal in providing long distance dispersal and thus wide distribution of ancestral Loranthaceae.

Taylor (1989) examined *Gothanipollis* pollen from Eocene deposits in Tennessee USA and concluded they are most similar to large-flowered neotropical taxa (e.g. *Psittacanthus*, *Aetanthus*). Similar identifications were reached when examining pollen from Cretaceous deposits in Alabama (Jarzen, 1978) and Oligocene deposits in Puerto Rico (Graham and Jarzen, 1969). These studies indicate that North American Loranthaceae were derived from South American ancestors. Skelton et al. (2003) and West et al. (2015) suggested that the climate during the early Eocene was warm, and forests extended through North America to present day Alaska. Dispersal from South America to North America can be explained by islands that emerged after the proto Antilles collided with the Bahamas plate during Ypresian (ca. 50 Ma) (Graham, 2003; Morley, 2003; Pennington and Dick, 2004). Cuenca et al. (2008) and Baker and Couvreur (2013) suggested the connection between North America and South America during the end of the Cretaceous to early Eocene based on dispersal route of Arecaceae (palm family). The North Atlantic land bridges across the north end of the Atlantic Ocean linking northern Canada to Europe via Greenland have been viewed as a principal and most plausible route for the intercontinental spread of thermophilic boreotropical flora between the Old and the New Worlds from the early Eocene until the late Miocene (Tiffney, 1985a,b; Wen, 1999; Tiffney and Manchester, 2001; Liu et al., 2015). Thus, the North

American Loranthaceae that were originally derived from South American relatives likely spread to Europe via this route, which is in agreement with Taylor (1990) who said "the pollen may be from an ancestral plexus which reached from South America to North America to Europe, possibly along the Tethys seaway to southeast Asia. Regional extinction may explain the current disjunct distribution".

The major extant lineages of Loranthaceae differentiated in Australasia and South America between 30 and 44 Ma, but during this time the ancestor of Loranthaceae that occurred in North America, Greenland and Europe became extinct, which coincides with the major cooling event in the late Eocene to early Oligocene (Zachos et al., 2001, 2008). Other "neotropical elements" that became extinct in North America in the Oligocene are discussed by Leopold and MacGinitie (1972). Thus, at present no species of Loranthaceae occur in North America north of Mexico or in Greenland and only one (*Loranthus europaeus*) occurs in Europe (see below).

4.2.3. Dispersal to Asia

The ancestral area reconstruction inferred that Loranthaceae dispersed from Australasia to Asia and back to Australasia several times (Figs. 3 and S2). The disjunction between Asia and Australasia is closely related to plate tectonics and climate, and dispersal by island-hopping birds has been commonly used to explain this disjunction pattern (Morley, 1998, 2003) because many island chains between Asia and Australasia appeared during the late Eocene to early Oligocene (Holloway and Hall, 1998; Meimberg et al., 2001; Morley, 2003; Clayton et al., 2009; Hall, 2012; Zahirovic et al., 2014). In the earliest dispersal period, Asia and Australasia were separated by a deep ocean because much of Sundaland was submerged (Hall, 2012). Some of the potential dispersers, e.g., fruit pigeons and large cuckoos, can travel at least several hundred kilometers (Higgins, 1999) and the large seeds were occasionally passed within 5.5 h (Wotton et al., 2008). Therefore, with distances of 500–1000 km between land areas at the time of the earliest dispersals from Australia to Asia, such events would have been at the upper limits of dispersal distances (Wotton et al., 2008; Cibois et al., 2013). All the dispersals between Australasia and Asia occurred since the late Eocene (less than 36.05 Ma, 95% HPD: 30.92–40.51 Ma; node 11; Fig. 2A). The taxa involved in these migrations evolved into the Australasian endemic genera (*Alepis*, *Peraxilla*, *Lysiana*, *Ileostylus*, *Muellerina*, *Sogerianthe*, *Dactyliophora*, *Diplatia* and *Benthamina*), Asian endemic genera (*Helicanthes*, *Baratranthus*, *Loxanthera*) or genera shared by both areas (*Lepeostegeres*, *Amylotheca*, *Decaisnina*, *Macrosolen* and *Cecarria*). Loranthaceae must have reached New Guinea and dispersed into Asia, where it differentiated into the *Amyema* complex in Malesia, while some other lineages in the tribes Elytrantheae and Lorantheae continued migration into Asia. In addition, the climate during this time was warm and moist in most of Southeast Asia (Zachos et al., 2001), which may have facilitated the migration of Loranthaceae through Southeast Asian islands to Australasia or back to Asia. Migration of the Australian mistletoe bird *Dicaeum* (Dicaeidae) (Reid, 1988) may have allowed more derived genera such as *Amyema*, *Amylotheca*, *Dactyliophora* and *Dendrophthoe* to migrate back into Australia, obscuring the historical distribution of these lineages.

Our analyses also included some samples collected from the Indian subcontinent (*Helicanthes elasticus* from India; *Loranthus odoratus* and *Scurrula pulverulenta* from Nepal, and *Tolypanthus involucratus* from Bhutan). The Indian subcontinent separated from Gondwana around 126–132 Ma (including India and Madagascar at that time) (McLoughlin, 2001; Morley, 2003; Lomolino et al., 2010), and the Indian Plate broke away from Madagascar and began drifting rapidly northward at ca. 100 Ma (Morley, 2003), and then collided with Eurasia at 43–50 Ma (McLoughlin, 2001; Morley, 2003; Zahirovic et al., 2014). Our results indicated that all the Indian samples diverged after 18.5 Ma: *Tolypanthus involucratus* ca. 19.41 Ma (95% HPD: 11.8–27.4 Ma), *Helicanthes elasticus* ca. 10.44 Ma (95% HPD: 4.25–18.43 Ma), *Loranthus odoratus* ca. 9.69 Ma (95% HPD: 3.13–18.44 Ma), and *Scurrula*

pulverulenta ca. 4.58 Ma (95% HPD: 1.69–7.89 Ma), much later than the collision between India and Eurasia. Thus the Indian members of Loranthaceae could only derive from Asian or Australasian ancestors, in contrast to earlier vicariance theories involving Africa (Fig. 3).

4.2.4. Migration to Africa, Madagascar and Europe

Africa was separated from Gondwana around 162 Ma (McLoughlin, 2001), long before Loranthaceae originated in Gondwana. Loranthaceae reached Africa during the early Oligocene (Fig. 3), thus Gondwanan vicariance is a very unlikely explanation for the Asia–Africa disjunction. The disjunction between Asia and Africa could be explained by three hypotheses: (1) migration via the Eocene boreotropical forests (Davis et al., 2002; Weeks et al., 2005; Muellner et al., 2006); (2) overland migration via land bridges (Zhou et al., 2012); and (3) transoceanic long-distance dispersal (Renner, 2004; Yuan et al., 2005; Clayton et al., 2009). The first hypothesis relied on the existence of extensive boreotropical forests from Europe across South Asia associated with the Eocene thermal maximum ca. 50–52 Ma (Zachos et al., 2001, 2008). During the optimum climatic period, most regions of northern Africa including areas now occupied by the Sahara were dominated by rainforests (Raven and Axelrod, 1974; Axelrod and Raven, 1978). These tropical forests could have extended much farther north than extant forests, enabling floristic exchanges between Africa and Asia in both directions (Wolfe, 1975; Morley, 2000). This hypothesis has been used to explain the disjunction between Asia and Africa in some angiosperm families (Davis et al., 2002, 2005; Weeks et al., 2005). However, the time of this expansion of boreotropical forests did not coincide with the Asian – African divergence time (Oligocene) within Loranthaceae. The second hypothesis (overland migration) suggested that floristic elements might have migrated between Asia and Africa around 20 Ma when the closure of the Tethys Sea established direct land connection between Africa and western Asia (Zohary, 1973; Raven and Axelrod, 1974; Lu et al., 2013). However, the disjunction between Asia and Africa within Loranthaceae occurred some time earlier than the closure of the Tethys Sea (30.54 Ma, 95% HPD: 25.82–35.44 Ma; node 13, Fig. 2A). The third hypothesis has been important in explaining plant intercontinental disjunctions (De Queiroz, 2005; Yuan et al., 2005; Clayton et al., 2009; Warren et al., 2010; Thiv et al., 2011; Nie et al., 2012). Long-distance dispersal has been used to explain the disjunction between Asia and Africa in several genera of angiosperms: *Adansonia* (Malvaceae) 2–15 Ma (Baum et al., 1998); *Osbeckia* (Melastomataceae) 7–16 Ma (Renner and Meyer, 2001; Renner, 2004); *Exacum* (Gentianaceae) < 35 Ma (Yuan et al., 2005); *Eurycoma*, *Brucea* and *Soulamea* (Simaroubaceae) during the Oligocene (Clayton et al., 2009); *Cayratia* (Vitaceae) < 66 Ma (Lu et al., 2013). Although Asia and Africa were not contiguous during the late Eocene to Oligocene, the distance between East Africa and West Asia was sufficiently close (Morley, 2003) to have allowed the migration of Loranthaceae from Asia to Africa by birds. Our results show that African Loranthaceae are the younger members of the family, having originated after 28.47 Ma (Fig. 3), i.e. the Chattian of the Oligocene. Global cooling began in the Rupelian of the Oligocene that triggered local extinctions of thermophilic plants or disruption of the boreotropical belt (Zachos et al., 2001, 2008; Wei et al., 2015). This cooling also shut off the migration between Asia and Africa which may explain why the two continents share few disjunct genera (exceptions include *Dendrophthoe*, *Taxillus*, and *Helixanthera,* but see below).

A hypothesis involving transoceanic long-distance dispersal should also be considered as an explanation of the disjunction of Loranthaceae between continental Africa and Madagascar. Our analyses indicated that the Madagascan Loranthaceae originated in Africa and dispersed to Madagascar at 26.55 Ma (95% HPD: 20.52–31.69 Ma; node 15, Figs. 2A and 3) and 18.08 Ma (95% HPD: 8.4–26.05 Ma; node 16, Figs. 2A and 3). Thus a long-distance dispersal was likely mediated by birds from Africa to Madagascar.

European *Loranthus* is phylogenetically most closely related to *L.*

odoratus from Asia, diverging from that species 9.69 Ma (95% HPD: 3.13–18.44 Ma) (Figs. 2A and 3). Moreover, that clade is sister to the Australasian *Cecarria*, diverging in the Eocene (39.63 Ma). These data suggest that members of the extant *Loranthus* clade originated in Australasia and migrated north into Asia and then westward into Europe, recolonizing areas where early lineages of Loranthaceae once existed but are now extinct. After a climatic optimum during the middle Miocene, the climate was drying and cooling especially in central Asia, northwestern China and Mongolia (Zachos et al., 2001, 2008; Miao et al., 2013; Wu et al., 2015). In particular, since the Miocene most areas of western and central Asia turned into deserts caused by the uplifting of the Himalayas (Favre et al., 2015). The distribution of *Loranthus europaeus* is scattered from central and southeastern Europe to western Asia. In Iran and Afghanistan one encounters *L. grewingkii* and in Nepal, *L. odoratus*. Six species occur in China, particularly in the subtropical zones. Thus, the distribution of the genus is continuous from Europe through the Himalayas to eastern Asia, finally coming close to the distribution of *Cecarria*, which is known from the Philippines.

4.3. Burst of Loranthaceae diversification in tropical forests and coadaptation with birds

Our LTT plots and TreePar analyses indicated that a burst of diversification occurred in Loranthaceae ca. 50 Ma during the early Eocene (Fig. 2B). This was after the separation of Australasia and South America from Gondwana, but while Australia and South America were still contiguous via Antarctica. Additionally, our dating results indicated that aerial parasitism arose ca. 48–50 Ma. Zachos et al. (2001, 2008) suggested that the global climate was optimal during the early Eocene ca. 50–52 Ma. The global cooling that followed later in the Eocene caused the replacement of tropical vegetation with temperate floras at high latitudes. By early and middle Eocene, Antarctica was dominated by *Nothofagus* forests (Poole et al., 2001; Contreras et al., 2013). Misodendraceae, a family in the clade sister to Loranthaceae, are exclusive aerial parasites of their *Nothofagus* hosts. It is most likely that ancestral Loranthaceae aerial parasites also used *Nothofagus* trees as hosts. Tribes Elytrantheae and Psittacantheae are the first divergent lineages and some present day members (*Alepis* + *Peraxilla*, and *Desmaria*) parasitize *Nothofagus*, thus it is possible that this host specificity could be viewed as a plesiomorphic character. More derived members of Loranthaceae parasitize the tree species of angiosperms which are commonly dominant members of tropical forests (Lavin et al., 2005; Wang et al., 2009; Xiang et al., 2014). The tropical forests include tropical rainforest, tropical seasonal rainforest and subtropical evergreen broad-leaved forests, and occupy most of tropical and subtropical regions in the world (Xiang et al., 2016). Tropical forests were present during the Paleocene/Eocene, however, at that time this biome was located at middle paleolatitudes where the climate was more favourable (Morley, 2000, 2003; Jablonski, 2004; Schuettpelz and Pryer, 2009; Couvreur et al., 2011). By late Eocene, tropical forest retreated to lower latitudes (Contreras et al., 2013). Schuettpelz and Pryer (2009) suggested that the increase in epiphytic fern diversification was synchronous with the Paleocene/Eocene thermal maximum, which is the same time frame as Loranthaceae diversification. The epiphytic ferns have a niche entirely dependent on the presence of a well-developed rainforest biome. Many (but not all) aerially parasitic Loranthaceae occur on hosts in modern tropical rainforests characterized by high biodiversity, high rainfall and equable temperature (Richards, 1996; Wang et al., 2012). Modern tropical forests are dominated by angiosperms in taxa such as Fabaceae (Lavin et al., 2005), Sapindales (Wang et al., 2009), Rubiaceae (Antonelli et al., 2009) and Fagaceae (Xiang et al., 2014) and many of these not only serve as hosts for Loranthaceae (Qiu and Gilbert, 2003) but also appear to have diverged or radiated near the time of diversification of Loranthaceae. Moreover, flowering plants seem to have attained a level of ecological prominence during

the early Cenozoic comparable to that of today (Crane and Herendeen, 2006) and a striking increase was found in within-flora seed size near the time frame of the diversification burst of Loranthaceae (Sims, 2010). Thus the presence and development of the tropical rainforest biome may be directly associated with the switch in trophic mode from root to aerial parasite in Loranthaceae during the Eocene. The competition for light may have provided the selective pressure that favored branch parasitism in the tree canopy where higher rates of photosynthesis could be achieved. This trophic mode conversion facilitated the rapid diversification of the family during the Cenozoic in the rainforest dominant regions of South America, Asia and Australasia.

The fruits in Loranthaceae are one-seeded berries (except for *Nuytsia*, which has a winged samara-like fruit) and their bright colors (orange, yellow, red or white) represent striking adaptations for bird dispersal (Amico et al., 2007; Vidal-Russell and Nickrent, 2008a). Some birds that feed on such fruits have specialized feeding behaviours and are therefore considered coevolved specialist frugivores (but for an alternate viewpoint see Watson and Rawsthorne, 2013). Nutrition is derived from the mucilaginous materials associated with the viscin that encloses the seed. After foraging, the seed is excreted in the bird droppings or the sticky seed is wiped onto a host branch. Thus birds play an important role in dispersing Loranthaceae, especially members of the order Passeriformes, suborder Tyranni and suborder Passeri (Vidal-Russell and Nickrent, 2008a), which are commonly called songbirds. Although birds originated in the Mesozoic era, their diversification began to accelerate during the Cenozoic era. Based on a complete dated phylogeny of all extant species of birds, Jetz et al. (2012) inferred that birds underwent a major increase in diversification rate since ca. 50 Ma, including both songbirds and other more recent lineages. Members of the suborder Passeri, specifically families Meliphagidae, Nectariniinae and Dicaeidae pollinate and disperse mistletoes in Australasia, Asia and Africa. In the Americas, the families Tyrannidae and Cotingidae of suborder Tyranni are responsible for dispersal whereas hummingbirds (order Apodiformes) effect pollination. Passeri and Tyranni diverged from each other on Gondwana around 76 Ma (Barker et al., 2004). The Passeri radiated in Australia around 34 Ma, and then dispersed northwards into Asia. On the other hand, the Tyranni reached South America before the openning of the Drake Passage 30–34 Ma (Livermore et al., 2005) and further dispersed into northern South America and Central America during the Miocene (Ericson et al., 2003). This event might have been coupled with diversification of South American Loranthaceae (tribe Psittacantheae), which aided their migration north and their colonization of the New World tropics. Therefore, dispersal and diversification of Loranthaceae were accompanied by the coadaptation with birds, in particular the songbirds that were important agents in long-distance dispersal during the Cenozoic. Species-specific dispersal agents can also facilitate range expansion and species persistence under changing environmental conditions (Kakishima et al., 2015).

As an adaptation to flight, the entera of birds are usually too short to carry seeds for very long distances, thus Loranthaceae could only be dispersed in a step-wise fashion. Moreover, most of the seeds of Loranthaceae do not show a long dormancy and must germinate on suitable host branches in a timely manner, otherwise they soon senesce (Xiao and Pu, 1989). Therefore, the most suitable dispersal route for Loranthaceae appear to be contiguous continents and relatively proximal island chains, or even over ocean within ca. 500 km, while intercontinental dispersal is less likely. As a result, there are relatively few disjunct genera of Loranthaceae between different continents as step-wise dispersals generally result in more or less continuous distributions. One apparent exception is *Helixanthera* that has species in Africa and Asia. Our results show, however, that this genus is polyphyletic with the African and Asian members belonging to different clades. Although *Taxillus* is mainly an Asian genus, one species (*T. wiensii* Polhill, not sampled here) occurs in coastal Kenya. Polhill and Wiens (1998) alluded to a possible relationship between *T. wiensii* and genera

segregated from *Taxillus* by Balle (1955), thus we propose that *T. wiensii* may not belong to *Taxillus* as it is more likely to be derived from an African lineage. *Decaisnina forsteriana* (Schult) Barlow has a wide distribution among remote Pacific islands (Barlow, 1972), thus demonstrating that some mistletoes have adaptations to long-distance dispersal. In Australia and New Zealand, mistletoes are pollinated and dispersed by honeyeaters (Meliphagidae – Yan, 1993; Ladley and Kelly, 1996; Bach and Kelly, 2004). These birds were among the first lineages to diverge among the Passeri, an event estimated to have happened during the Eocene (Barker et al., 2004). The interaction of this bird lineage with Loranthaceae probably began in that epoch thus aiding the diversification and dispersal of tribe Elytrantheae during the Oligocene. This idea was suggested for other plant families that are also pollinated by honeyeaters, for example diversification of the bird-pollinated subtribe Embothriinae of Proteaceae that are pollinated by Meliphagidae (Barker et al., 2007). It is possible that these birds (Meliphagidae) dispersed Loranthaceae from Australia to New Zealand ca. 32 Ma in early Oligocene (*Alepis* and *Peraxilla* lineages) as registered in the fossil record (Lee et al., 2012). A second dispersal event might have occurred 16 Ma in the ancestor of *Ileostylus*.

5. Conclusion

The Gondwanan mistletoe family Loranthaceae originated in Australasia in the Late Cretaceous and then spread to South America via Antarctica but was absent in Africa and India. During the late Eocene and Oligocene, some genera of tribes Elytrantheae and Lorantheae were dispersed by birds from Australasia to Asia and back to Australasia several times. The lineages distributed in Africa and Europe are younger members that migrated from Asia after the middle Oligocene. The rapid diversification of Loranthaceae coincides with the formation of tropical and subtropical forests since the Eocene that provided numerous suitable host trees. The switch in trophic mode from root to aerial parasite and the subsequent rapid diversification of Loranthaceae that took place at ca. 50 Ma coincides with the radiation of songbirds that became important dispersal agents for these mistletoes.

Acknowledgments

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.ympev.2018.03.010.

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