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Authors

Ranasinghe, Subhani W.
Nishii, Kanae
Möller, Michael
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Biogeographic history of the pantropical family Gesneriaceae with a focus on the Indian plate and diversification through the Old World

Subhani W. Ranasinghe[1] (iD), Kanae Nishii[2,3] (iD),
Michael Möller[2*] (iD), Hannah J. Atkins[2*] (iD), John L. Clark[4] (iD),
Mathieu Perret[5] (iD), Abdulrokhman Kartonegoro[6] (iD), Lian-Ming Gao[7,8] (iD),
David J. Middleton[2,9] (iD) and Richard I. Milne[10] (iD)

[1] National Herbarium, Department of National Botanic Gardens, Peradeniya, Sri Lanka;

[2] Royal Botanic Garden, Edinburgh, Scotland, UK;

[3] Kanagawa University, Kanagawa, Japan;

[4] Marie Selby Botanical Gardens, 1534 Mound Street, Sarasota, Florida, USA;

[5] Conservatoire et Jardin botaniques de Genève & Department of Plant Sciences, University of Geneva, Switzerland;

[6] Research Center for Biosystematics and Evolution, National Research and Innovation Agency (BRIN), Indonesia;

[7] CAS Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Science, Kunming 650201, China;

[8] Lijiang Forest Biodiversity National Observation and Research Station, Kunming Institute of Botany, Chinese Academy of Sciences, Lijiang 674100, Yunnan, China;

[9] Singapore Botanic Gardens, National Parks Board, 1 Cluny Road, Singapore 259569;

[10] Institute of Molecular Plant Sciences, School of Biological Sciences, University of Edinburgh, Edinburgh, UK.
*Correspondence: Hannah J. Atkins, hatkins@rbge.org.uk and Michael Möller, mmoeller@rbge.org.uk

Abstract

The Gesneriaceae consists of around 150 genera and c. 3750 species with a predominantly tropical and subtropical distribution across all continents. Although previous studies have proposed an American origin of Gesneriaceae, the biogeographic history of this pantropical plant family is still unclear, particularly in the Old World. To address this, we assembled the most comprehensively sampled matrix of Gesneriaceae with 143 Gesneriaceae genera and 355 species, including key samples from Sri Lanka analysed here for the first time. We generated molecular phylogenies based on four plastid gene regions (*ndh*F, *mat*K, *rps*16 and *trn*L-F), obtained fossil-calibrated trees, and reconstructed ancestral areas and dispersal routes using Bayesian methods. Our results confirm the origin for the family in the Early Palaeocene (67. Ma) in the region of present-day Central America & Andean South America, and that diversity in the Old World originated from a long-distance dispersal event from South America around 59 Ma, most likely to the Indian plate, which was an island at the time. This lineage then dispersed to Malesia and later East Asia, which would ultimately become a major centre of diversity and source of many dispersals to other regions. Our results thus highlight the Indian plate as a likely key player in the early diversification of Old World Gesneriaceae, even though it is now more diverse

Highlights

- The Gesneriaceae originated in the region of modern-day Central America and Andean South America during the early Palaeocene.

- Gesneriaceae arrival into the Old World probably occurred through a long-distance dispersal event from the Americas around 60 Ma.

- There is plausible evidence that the Indian plate was a key locus in the diversification and distribution of the Old World Didymocarpoideae.

- The Gesnerioideae subfamily diversified in the Late Eocene, after the Didymocarpoideae in the Early Eocene.

- This study underlines the importance of rare, stochastic events in shaping diversity.

elsewhere, and hence offer novel insights into this plant family's dispersal routes and areas of diversification in the Old World.

Introduction

Vicariance and long-distance dispersal (LDD) are the two processes by which global biotic disjunctions can be explained, but these hypotheses can be difficult to distinguish for any particular disjunction. However time-calibrated phylogenies, especially when supported by near-complete taxon sampling, can address this question by determining the time and direction of movement between landmasses (e.g., Renner 2004a,b, Givnish et al. 2004, Sytsma et al. 2004, Buerki et al. 2011, Olmstead 2013, Baker and Couvreur 2013a,b, Perret et al. 2013, Armstrong et al. 2014, Dupin et al. 2016, Luebert et al. 2017, Wu et al. 2018, Schneider et al. 2022). For pantropical plant groups, LDD is considered important but the role of island chains as potential stepping stones, and the precise routes employed, are still debated (e.g., Schneider et al. 2022, Zhao et al. 2022).

The Indian plate, the land portion of which comprises the Indian subcontinent, was part of the Gondwanan supercontinent 150 million years ago (Ma) (Jokat et al. 2003), before separating from Africa 130-110 Ma (Morley 2003, Lomolino et al. 2017), then Madagascar and the Seychelles 99-66 Ma (Ashton and Gunatilleke 1987, Plummer et al. 1998, Lomolino et al. 2017), and then drifting northwards and colliding with Eurasia 55-42 Ma (Ashton and Gunatilleke 1987, Briggs 2003). Dramatic climatic shifts during its northward journey resulted in the loss of many endemic plant lineages (Morley 1998, 2000, 2003), but the region might have played a key role in the diversification of species-rich plant families in Asia, such as Dipterocarpaceae and Zingiberaceae (e.g., Karanth 2006, Ashokan et al., 2022) as the recipient of long-distance dispersals (e.g., Zhao et al. 2022); the site of rapid *in situ* radiations (e.g., Surveswaran et al. 2021) and as 'a biogeographical raft' (Zhao et al. 2022). Certainly, biotic exchanges following collision with Eurasia would have had profound effects on the composition of the flora of that region (e.g., Mani 1974, Conti et al. 2002, Karanth 2006, Sen et al. 2019), but most biogeographic studies involving the Indian plate have focused on animals, with plants examined only rarely (e.g., Sen et al. 2019, Zhao et al. 2022).

The Gesneriaceae is a pantropical family of around 150 genera and c. 3,750 species (GRC 2022) (Fig. 1). It comprises herbs, shrubs and occasionally small trees and shows exceptional morphological diversity across the family with highly diversified flowers adapted to a wide range of pollinators (Weber 2004, Roalson and Roberts 2016). The fruits are either fleshy with seeds
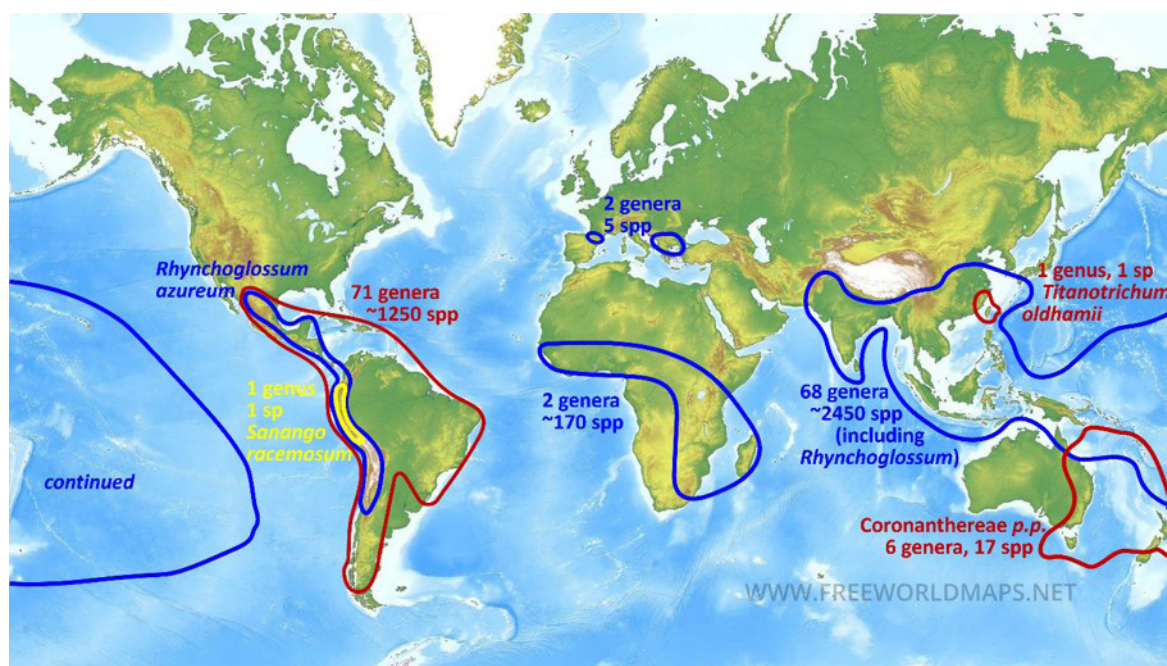

Figure 1. Distribution and approximate taxa numbers of Gesneriaceae worldwide. Didymocarpoideae subfamily in blue; Gesnerioideae subfamily in red; Sanangoideae subfamily in yellow (base map modified from: http://www.freeworldmaps.net).

most likely dispersed by animals, or dry and dehiscent capsules with seeds dispersed by gravity, wind, or rain (Weber 2004). Molecular dating indicates stem ages for the family between 58 and 76 Ma (Perret et al. 2013, Petrova et al. 2015, Roalson and Roberts 2016, Fonseca 2021), much younger than the break-up of Gondwana 180-160 Ma (Jokat et al. 2003), and hence rejecting Burtt's (1998) proposal that a Cretaceous Gondwanan origin could explain the modern distribution of the family. Instead, an origin in the temperate Andes and Amazonian rainforests during the late Palaeocene period, followed by diversification within South America and then migration of two major lineages through Antarctica to Asia and Australasia, was proposed (Perret et al. 2013, Roalson and Roberts 2016).

Stem age estimates for the core family (i.e. excluding *Sanango*, which is sometimes excluded from the family) range from 57.5 million years (Ma) (Perret et al. 2013) through 67.7 Ma (Fonseca et al. 2021) to 71.88 or 73.07 Ma (Petrova et al. 2015, Roalson and Roberts 2016). These differences might be due to sampling differences: Perret et al. (2013) sampled only three Old World Gesneriaceae genera, whereas the supermatrix approach of Roalson and Roberts (2016) resulted in a >90% proportion of missing data. Furthermore, because Gesneriaceae lacks usable fossil calibration points, two of these studies relied on secondary calibration points obtained from large scale studies investigating the age of angiosperms, but these disagreed strongly regarding the crown age for Lamiales, e.g., c. 65 Ma (Li et al. 2019), c. 85-88 Ma (Magallón et al. 2015, Smith and Brown 2018) versus c. 153 Ma (Janssens et al. 2020). Hence the dates obtained may be questionable, and sampling gaps, particularly from South Asia, mean that no-one has yet addressed Burtt's (1998) assertion that the 'Indian plate' must be the 'centre of attention' in understanding the evolution of Gesneriaceae in the Old World.

The current study aims to address these points through greatly increased taxon sampling at genus level (94% of Gesneriaceae genera) including regions such as Sri Lanka not previously sampled, and the use of the same four DNA regions across all sampled accessions. Moreover, more robust age estimates are obtained by including samples representing all 24 other Lamiales families (Fonseca 2021) permitting the use of primary fossil calibration points from across the order. Our goal was to generate a robust, well-supported and time-calibrated phylogeny, to reassess the age and biogeography of the family, and in particular examine the significance of the Indian plate and LDD in the family's spread across the Old World. This will enhance our understanding of the mechanisms and global events involved in shaping the present-day pantropical distribution of plant groups.

Materials & Methods

Sampling

Throughout this paper, the family Gesneriaceae is taken to include *Sanango* (subfamily Sanangoideae) unless stated otherwise, following Weber et al. (2013).

Ingroup sampling: Within Gesneriaceae, 356 accessions representing 353 species were examined, covering 142 of the 151 currently recognised genera (including *Sepikea*) and covering all recognised subfamilies, tribes and subtribes (Table S1). These comprised the only species from the monotypic subfamily Sanangoideae, 155 accessions of 156 species from 73 out of 78 genera of the mainly New World (NW) subfamily Gesnerioideae, and 200 accessions of 196 species from 68 out of 72 genera from the mainly Old World (OW) subfamily Didymocarpoideae. Thirty-seven species from 19 of the 24 Gesneriaceae genera known from India and Sri Lanka were included. Material could not be obtained from five NW and four OW genera, all but one of which are monotypic.

Outgroup sampling: 49 species were sampled from all 24 families of order Lamiales (according to Schäferhoff et al. 2010, Luna et al. 2019, Li et al. 2021), with one to four species per family depending on its size (Table S1). Two species from Solanales and one from Gentianales were included as outgroups and the latter used to root the phylogenetic trees (as per Li et al. 2019, 2021, Janssens et al. 2020) (Table S1). In total the phylogenetic analyses included 408 samples.

DNA extraction and phylogenetic analyses

DNA extraction: Most samples were field collected leaf material dried in silica gel, which was ground using a Tissuelyser II (Qiagen, Hilden, Germany). Total genomic DNA was then extracted following one of three methods depending on leaf quality: a modified CTAB method (Doyle and Doyle 1987), QIAxtractor (Qiagen), or DNeasy Plant Mini kit (Qiagen) following manufacturers' protocols. DNA quality was tested by electrophoresis.

Four plastid DNA regions were PCR amplified following Luna et al. (2019). These comprised two coding genes, *ndh*F (Olmstead and Reeves 1995) and *mat*K including the intron (Sang et al. 1997, Perret et al. 2013), and two non-coding regions, i.e., the *rps*16 intron (Oxelman et al. 1997) and the *trn*L-F intron / intergenic spacer region (Taberlet et al. 1991).

For *ndh*F and *mat*K, two overlapping PCR amplifications were required to obtain the full region (Table S2; e.g., Ranasinghe 2017, Luna et al. 2019). PCR amplification was carried out for all regions with the following temperature regime: one cycle at 94°C for 3 minutes, followed by 35 cycles at 94°C for 1 minute, 55°C for 1 minute, 72°C for 1.5 minutes, and finally one cycle at 72°C for 10 minutes. The PCR products were purified using ExoSap-IT (USB Corporation, Ohio, USA), and direct cycle sequenced using Big Dye (Applied Biosystems, Waltham, MA, USA) following the manufacturer's protocols at Edinburgh Genomics (the University of Edinburgh).

The electropherograms were analysed in Sequencer v.5.1 (Gene Codes Corporation, Ann Arbor, Michigan, USA). All newly acquired sequences were submitted to GenBank (Table S1). The sequences obtained in this study and those acquired from GenBank (Table S1) were aligned online using MAFFT v.7 (https://mafft.

cbrc.jp/alignment/server/) (Kuraku et al. 2013, Katoh et al. 2019) and optimised manually.

Combinability between the four regions was tested by visually assessing the individual gene trees for highly supported incongruences, following Nishii et al. (2015). The result confirmed that there was no incongruence due to technical issues (e.g. mix-ups or contamination) between the four data matrices (*p*-value = 0.32), and the phylogeny analyses were therefore performed on a concatenated matrix of the four plastid regions. Maximum parsimony (MP) was implemented on unordered and equally weighted characters in PAUP. A two-step heuristic tree search strategy was employed generating first 10,000 PAUPRat starting trees (Sikes and Lewis 2001), which were then optimised using tree bisection-reconnection (TBR), with MulTrees and Steepest Descent options on (Möller et al. 2011) in PAUP. Branch support values were obtained from 10,000 random addition sequence bootstrap replicates with TBR on and MulTrees off (Möller et al. 2011).

Maximum likelihood (ML) analysis was carried out using the IQ-TREE online server (http://iqtree.cibiv.univie.ac.at) (Trifinopoulos et al. 2016), with the optimal substitution model set to be detected automatically for each sequence region; the models selected were GTR+F+G for *trn*L-F, and GTR+F+I+G for *mat*K, *ndh*F and *rps*16. The analysis was run with empirical state frequencies, and branch support obtained from 1,000 replicates of ultrafast bootstrapping with 1,000 iterations.

For Bayesian inference (BI) analyses, the best nucleotide substitution model for each marker was independently determined to be GTR+I+G using MrModelTest v.2 (Nylander 2004) choosing the AIC criterion (Akaike 1974). BI analyses were implemented in MrBayes v.3.2.7 (Ronquist and Huelsenbeck 2003, Ronquist et al. 2012). Two independent runs were executed with four Markov Chain Monte Carlo (MCMC) chains each, set to 10 million generations sampled every 500th generation with the heat set to 0.05, and with an enforced stop rule when the average standard deviation of split frequencies (ASDSF) reached 0.01. To further check that adequate convergence had occurred, the Potential Scale Reduction Factor (PSRF) was confirmed to be close to 1 (Gelman and Rubin 1992). The runs were further checked in Tracer v.1.7.1. (Rambaut et al. 2018), for effective sample size values for each parameter to have exceeded 200. At reaching the stop rule limit, 25% of the sampled trees were removed as burn-in and the remaining trees were used to generate a 50% majority rule consensus tree containing the clade support values as posterior probabilities (PP). The trees were visualized in FigTree v.1.4.4 (Rambaut 2006-2018).

Dating Analyses

To estimate divergence times, the four plastid DNA matrices were concatenated in BEAST v.1.10.4 (Suchard et al. 2018), using the substitution models determined above. We used an approach following Magallón et al. (2015) where the youngest points in the age range of each fossil were taken and placed at the earliest nodes, e.g., the crown nodes of families. The converse approach to use oldest fossil ages and their placement at the stem node might have resulted in older ages, but with greatly overlapping confidence intervals with our approach reported here (this study, youngest ages: 55.66-71.51 Ma; oldest ages: 54.64-73.58 Ma). The prior distributions for calibration points were set to lognormal for fossils, but normal for secondary calibration points (see below). A Birth-Death prior (Gernhard 2008) was chosen since many extinctions are likely to have occurred during the evolution of the family, particularly within tribe Epithemateae (e.g., Burtt 1977, Weber et al. 2013, Ritchie et al. 2017). The analysis was also run with Yule prior to determine the extent to which prior choice affected the outcome. We ran 27 independent MCMC runs, each of 100 million states and sampled every 1,000[th] generation. Convergence between these runs was checked in Tracer v.1.7.1, ensuring that the effective sample size was > 200 for each parameter. LogCombiner v.1.10.4 and TreeAnnotator v.1.10.4 were used to obtain the final combined metric tree, ages and confidence intervals. The consensus tree was visualized with FigTree v.1.4.4.

Calibration points: There is only one fossil known for Gesneriaceae, pollen of *Rhabdothamnus* from the Quaternary of New Zealand (Mildenhall 1980). However, it is of too young an age to be useful. Thus, we selected nine Lamiales fossils from outside Gesneriaceae that have been identified based on the presence of reliable reproductive structures such as seed and/or fruits (Table 1). Most of these are verified and described in detail in Martínez-Millán (2010) and Magallón et al. (2015). For all primary fossil calibration points, their minimum ages were chosen as the crown age for families, except for species-level fossils including the monotypic Paulowniaceae (Table 1).

The stem age of Lamiales forms an important secondary calibration point for dating Gesneriaceae diversification. However, previous age estimates for Lamiales from angiosperm-wide phylogenies range from 88 Ma (Magallón et al. 2015, Smith and Brown 2018) to 153 Ma (Janssens et al. 2020), due perhaps to differences in taxon sampling, marker usage, algorithms employed, and especially the number, quality, and placement of fossil calibration points (see Li et al. 2019). To account for this uncertainty, we selected an age distribution peaking at 88 Ma with a long tail up to 140 Ma, so as to not exclude older ages in the prior distribution.

Age estimates for Gesneriaceae likewise ranged from ~43 Ma (Zanne et al. 2014) to 103 Ma (Janssens et al. 2009), but in comprehensive studies with > 80 Gesneriaceae species, the crown age only ranged between 57.5 Ma (Perret et al. 2013) and 73.07 Ma (Roalson and Roberts 2016). Petrova et al. (2015) obtained a somewhat median age with 71.88 Ma and we chose this estimate as the crown age of Gesneriaceae (including *Sanango*) in this study, as it included a balanced OW / NW sampling and near complete data matrices.

Table 1. Details of fossil and secondary calibration points used in the present study.

Node	Age (Ma)	Set node	Prior	Position	Age set	SD	References
1	33.9-28.1	*Acanthus*	Ln	Stem	28.1	1	Reid and Chandler 1926, Hooker et al. 2009, Seldon 2014
2	50.0-49.0	Bignoniaceae*	Ln	Crown	49.5	1	Wehr and Hopkins 1994, Pigg and Wehr 2002
3	47.8-38.0	Byblidaceae	Ln	Crown	38.0	1	Conran and Christophel 2004
4	33.9-28.1	*Catalpa*	Ln	Stem	28.1	1	Reid and Chandler 1926
5	47.8-38.0	*Fraxinus**	Ln	Stem	38.0	1	Call and Dilcher 1992
6	33.9-28.1	Lamiaceae	Ln	Crown	28.1	1	Reid and Chandler 1926; see also Hooker et al. 2009
7	15.97-11.6	Paulowniaceae	Ln	Stem	11.6	1	Butzmann and Fischer 1997, Manchester et al 2009, Fischer and Butzmann 2006
8	5.33-2.58	Pedaliaceae	Ln	Crown	2.58	1	Tralau 1964, 1965, Martínez-Millán 2010
9	23.03-5.33	Plantaginaceae	Ln	Crown	5.3	1	Łańcucka-Środoniowa 1977
10(S)	71.88	Gesneriaceae	Normal	Crown	71.88	5	Petrova et al. 2015
11(S)	88.25	Lamiales	Normal	Stem	88.25	20	Magallón and Sanderson 2005; see also Bremer et al. 2004

Calibration points marked "(S)" are secondary. Gesneriaceae (point 10(S)) includes *Sanango*. Fossils marked with an asterisk were excluded following cross-validation analysis.

For cross-validation we used the approach of Near and Sanderson (2004), where the trees were calibrated on each individual fossil in turn, and the sum of the squared (SS) differences at the other calibration points calculated, from which the average squared deviations (*s*) for all fossils was obtained. The fossil with the largest deviation was removed, and *s* recalculated for the remaining fossils, and this was repeated until only two fossils remained. After plotting the *s* values, the fossils with the most impact on reducing *s* were identified and excluded. Only the remaining fossils were then used as fossil calibration points in the final dating analysis.

Biogeographic analyses

For ancestral area reconstructions (AAR), the metric MCC BEAST tree was used in BioGeoBEARS v.1.1.1 (Matzke 2013a) in R v.4.1.2 (R Core Team 2021) run in RStudio v.2021.09.1 (RStudio Team 2021). Prior to AAR, the tree was cropped to remove all outgroup taxa except Calceolariaceae, the sister family to Gesneriaceae, to avoid interference of the states at the root on the estimates of the ingroup, and the tree was trimmed to one sample per taxon at species level (= 359 samples) (Matzke 2014).

To obtain a clearer pattern for the Indian plate and surrounding areas, the Asia-Pacific area was subdivided into five regions: the 'Indian plate' (I),

'East Asia' (N), 'Australia & Pacific' (P), 'Sunda Shelf & Philippines' (S), and 'Wallacea & New Guinea' (W) (Fig. 2). These areas were selected to elucidate potential migration routes and are those frequently used in Asian biogeographic studies, reflecting as they do both tectonic history of the region and previously understood biogeographic patterns (see Raes and van Welzen 2009 and references therein). Within Malesia, there have been many differing studies on the biogeographic regions (see van Welzen et al. 2011), often resulting in several biogeographic regions, but to avoid nearing computational limits due to the presence in multiple areas of widespread species (Matzke 2016), such as *Rhynchoglossum obliquum* and *Rhynchotechum parviflorum*, we have chosen to divide Malesia into just two regions based on Wallace's Line. To these we added four regions corresponding roughly to other continents, i.e. 'South America' (A), 'Central America & West Indies' (C), 'Europe' (E), and 'Africa & Madagascar' (F) (Fig. 2, Table 2). The Indian plate comprised Sri Lanka, Bangladesh, and India except the northeastern part (Lomolino et al. 2017, Sen et al. 2019). The East Asian region included China, Taiwan, Japan, continental Southeast Asia and the Himalayas (Sen et al. 2019), plus Northeast India, whose Gesneriaceae species more closely resemble those of the neighbouring East Asian regions than they do other Indian species (Sinha and Datta 2016,
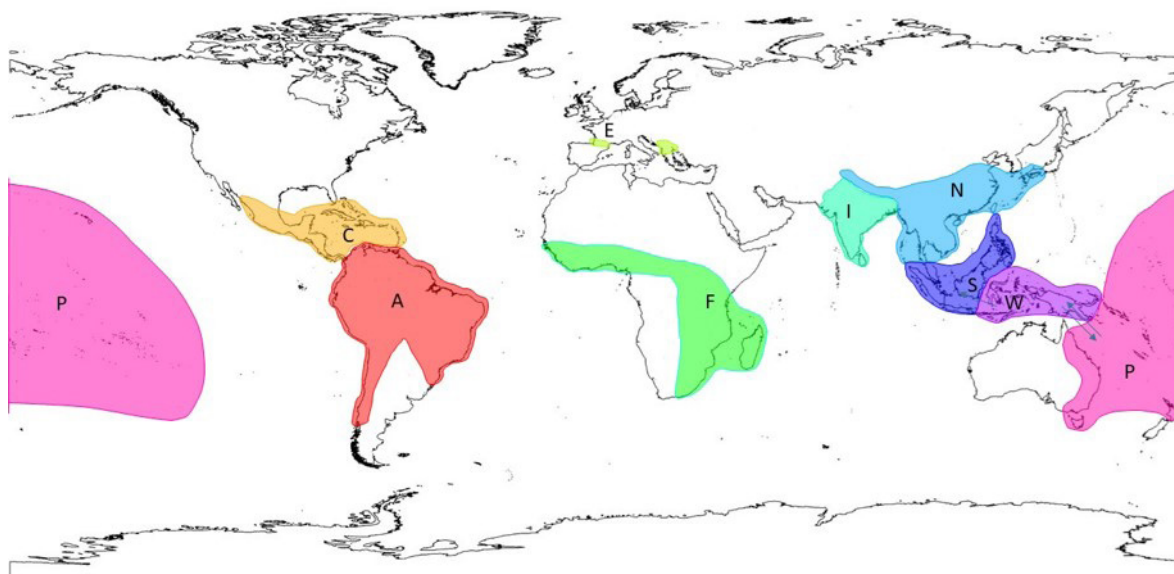
Figure 2. Defined geographic regions used for AAR of Gesneriaceae. A – South America; C – Central America & West Indies; I – Indian plate; E – Europe; F – Africa & Madagascar; N – East Asia; P – Australia & Pacific; S – Sunda Shelf & Philippines; W – Wallacea & New Guinea (base map modified from https://www.theworldofmaps.com/sites/theworldofmaps.com/files/WGS84_1.jpg).

Table 2. Geographic regions defined for the ancestral area reconstruction in BioGeoBEARS in the current study.

Code	Region
A	South America.
C	Central America (Panama through to Mexico), & West Indies (Caribbean islands).
E	Europe (Pyrenees, Balkans, Greece).
F	Africa & Madagascar (South Africa, East & West Africa, Madagascar and Comoro islands).
I	Indian plate (Indian subcontinent including Bangladesh, Sri Lanka).
N	East Asia (Northeast India, Nicobar & Andaman Islands, Nepal, Bhutan, China, Japan, Taiwan, Cambodia, Laos, Myanmar, Thailand & Vietnam).
S	Sunda Shelf & Philippines (including Java, Bali, Sumatra, Borneo, Peninsular Malaysia).
W	Wallacea & New Guinea (including Sulawesi, Maluku and the Lesser Sunda Islands (excl. Bali)).
P	Australia & Pacific (Australia, New Zealand, Pacific islands).

Möller et al. 2017). East Asia also included the Nicobar & Andaman Islands whose closeness to Myanmar and Thailand lead to floristic similarities, though they also have some Malesian elements (Balakrishnan and Ellis 1996). The combination of Australia with the Pacific islands followed Roalson and Roberts (2016), and formed the largest area, containing six NW and two OW Gesneriaceae genera (Fig. 1). Calceolariaceae is a South American family, other than two New Zealand species that occupy derived positions within the family (Andersson 2006, Nylinder et al. 2012, Roalson and Roberts 2016), so the outgroup was coded as South American.

Three models of AAR were explored: DEC (dispersal-extinction cladogenesis; Ree and Smith 2008), DIVA (dispersal-vicariance analysis; Ronquist 1997) and BayArea (Bayesian inference of historical biogeography for discrete areas; Landis et al. 2013). Because the latter two models were implemented in a maximum likelihood framework, they are referred to as DIVA-like and BayArea-like (Matzke 2013b). The factor 'j' was included to allow founder event jumps which may be an important process in the biogeographical history of the family (Matzke 2014, 2022) in order to obtain probability distributions for the most likely ancestral areas for lineages. We followed Roalson and Roberts (2016) in exploring whether adding the parameter subset sympatry ('s') would improve the BayArea-like model fit, as it only allows exact range-copying sympatry, and a number of species had wide geographic ranges. Likelihood ratio tests were applied to find the best fitting model to generate the output of the biogeographical events and most probable ancestral areas of distribution (Matzke 2013a). We performed 500 simulations of biogeographical stochastic mapping (BSM) in BioGeoBEARS (Matzke

2016, Dupin et al. 2016) on the best model to obtain the number of biogeographic events, e.g., anagenesis (range switch and range expansion dispersal), and cladogenesis (i.e., narrow sympatry, subset sympatry, vicariance, and founder events), that may be involved in the shaping of the present-day distribution of the species.

Results

Phylogeny analysis

A total of 553 sequences were downloaded from GenBank and 993 sequences were newly generated here (Table S1). Across the four plastid DNA regions, 86 sequences (5.3%) were missing. The concatenated matrix was 8,573 characters long, of which 7,236 were included for analyses after the exclusion of poor 5' and 3' ends of the matrices and the removal of a hypervariable region in *rps*16. The final matrix contained 2,912 (40.3%) constant, 1,087 (15%) autapomorphic, and 3,237 (44.7%) parsimony informative sites (Table S2). The MP analysis of the concatenated dataset resulted in 115,583 most parsimonious trees of 22,434 steps length (Fig. S1), with a CI of 0.3441 and a high RI of 0.8087. This large number of possible trees was largely generated by unresolved nodes near the tips of the tree (Fig. S2), whereas deeper relationships relevant to biogeography tended to be fully resolved and well-supported. The BI analysis had a convergence diagnostic of 0.009988 ASDSF reached after 3.8 million generations, and a PSRF between 0.999 and 1.067 with an average of 1.002 (Table S3). The ML tree had a best log-likelihood of -142,097.933.

The MP majority rule consensus tree, and the ML and BI trees were mainly congruent wherever the branches were highly supported (Figs S1-S5). The outgroup family relationships were basically as resolved as in Luna et al. (2019) and Li et al. (2021), with Plocospermataceae (MPBS: 100%; MLBS: 100%; BIPP: 1) splitting off first in Lamiales, followed by a clade comprising Carlemanniaceae plus Oleaceae (MPBS: 100%; MLBS: 100%; BIPP: 1), and then Tetrachondraceae (MPBS: 100%; MLBS: 100%; BIPP: 1). The 18 families that comprise the core Lamiales (Hilu et al. 2003) formed a large clade identical or highly similar to that in Luna et al. (2019); this clade was sister to a clade in which *Peltanthera floribunda* (Peltantheraceae) was sister (MPBS: 85%; MLBS: 100%; BIPP: 1) to Calceolariaceae plus Gesneriaceae. The relationship between the latter two families was highly supported (MPBS: 91%; MLBS: 100%; BIPP: 1). Within Gesneriaceae, the monophyly of both Gesnerioideae and Didymocarpoideae had maximum support in all analyses, as did their sister relationship to one another, with *Sanango racemosum* (Sanangoideae) branching off first in the family.

All tribes and subtribes (leaving aside four monotypic ones) in Gesneriaceae were monophyletic with high to maximum support ((70-)93-100%/1PP), except subtribes Besleriinae, Didissandrinae and Leptoboeinae (Fig. 3, Table S4). Subtribe Anetanthinae was nested within subtribe Besleriinae, whereas the

two genera classified in subtribe Didissandrinae, *Didissandra* and *Tribounia* fell in different parts of the tribe Trichosporeae clade, and *Championia* (placed in subtribe Leptoboeinae by Weber et al. 2013) fell outside the clade of this subtribe with high branch support (MPBS: 79%/100%; MLBS: 99%/100%; BIPP: 1/1) (Fig. 3, Figs S1-S5, Table S4). The relationships between subtribes and tribes received mostly maximum branch support across all analyses.

Divergence time estimates

The cross-validation analysis revealed that the SS values were highest for the fossils of *Fraxinus* and Bignoniaceae (Fig. S6), and their removal resulted in the strongest drops in the '*s*' values (Fig. S7), and they were removed for the final dating analysis. It is noteworthy that these two fossils were not verified or included by Martínez-Millán (2010) or Magallón et al. (2015). The use of Yule prior gave very similar results to the birth-death prior in our BEAST analyses, so only the latter is reported here.

The BEAST analysis estimated the family Gesneriaceae to have diverged from Calceolariaceae 66.84 Ma (HPD: 58.4-75.48 Ma) and begun diversifying 63.48 Ma (HPD: 55.66-71.51 Ma) (Fig. 3, Fig. S8, Table 3). Within Gesneriaceae, the major subfamilies Didymocarpoideae and Gesnerioideae diverged 59.46 Ma (HPD: 51.56-67.68 Ma), but these subfamilies began to diversify at greatly different times, respectively 55.96 Ma (HPD: 48.27-63.95 Ma), and 38.6 Ma (HPD: 28.45-52.01 Ma).

The divergence of the East Asian *Titanotrichum* lineage from its NW relatives in Gesnerioideae was calculated as an early Oligocene event, 33.36 Ma (HPD: 22.97-45.79 Ma). Two other intercontinental disjunctions, each between a species pair, were estimated to be recent events in the late Miocene: the NW-distributed *Rhynchoglossum azureum* diverged from the Sri Lankan *R. gardneri* 5.94 Ma (HPD: 2.32-10.79 Ma), whereas the African *Epithema tenue* diverged from the South and Southeast Asian *E. ceylanicum* 7.62 Ma (HPD: 3.41-12.66 Ma).

Among the Indian taxa examined, the age (i.e. time since divergence from its closest sampled relative) of *Jerdonia indica* was estimated to be 51.55 Ma (HPD: 43.93-59.61 Ma), and that of *Championia reticulata* as 46.78 Ma (HPD: 39.32-54.48 Ma). Thus, both represent ancient lineages of early Eocene origin (Fig. 3, Fig. S8). The ages of other species recorded on the Indian plate ranged from 1.84 Ma (*Lysionotus serratus*; HPD: 0.51-3.9 Ma), to 18.95 Ma (*Corallodiscus lanuginosus*; HPD: 8.57-31.12 Ma), in the Quaternary and Miocene epochs respectively (Fig. 3, Fig. S8).

Ancestral area reconstruction

In all three models tested in the BioGeoBEARS analysis, the addition of 'j' to allow consideration of founder events, significantly improved the likelihood values (Figs S9-S11, Table 4) although the results were very similar under all models. Adding parameter '*s*', for subset sympatry, to the BAYAREAlike+j (LnL=-579.8) model further significantly lowered the likelihood
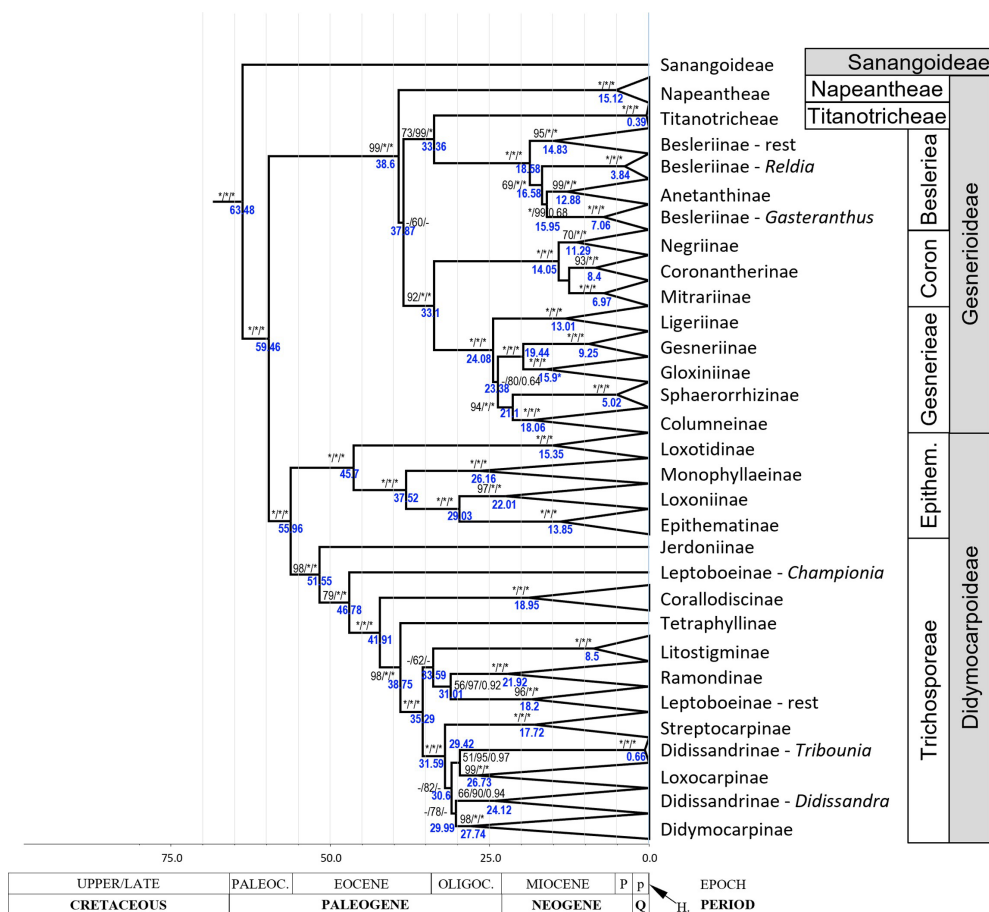
Figure 3. Simplified BEAST time-calibrated chronogram to subtribal level of Gesneriaceae samples included in the analysis of 408 samples, with ages shown below the branches (in blue), and superimposed above branches MPBS, MLBS, and BIPP support values. * indicates maximum support, - indicates support values <50% (BS) or <0.5 (PP); PALEOC. – Palaeocene; OLIGOC. – Oligocene; P – Pliocene; p – Pleistocene; Q – Quaternary. To the right subfamily (shaded grey boxes) and tribes (open boxes) are indicated: Epithem. – Epithemateae; Coron. – Coronanthereae.

value (BAYAREAlike+s+j: LnL=-515.0). There was virtually no difference in *P*-values between AIC and AIC$_c$. The automatically generated ΔAIC and ΔAIC$_c$ values were all >7 compared to the best model, and therefore the BAYAREAlike+s+j model is the most likely scenario (cf. Burnham et al., 2011), and is described here. Briefly, according to this model, South America (A) (0.62) is the ancestral area for the family and South America (A) and Central America & West Indies (C) (0.93-0.99) for most of the NW lineages and clades (Fig. 4). The Indian plate (0.42) emerged as the most likely ancestral area for the Didymocarpoideae (and hence all OW species except *Titanotrichum* and some Australia/Pacific lineages). From here, lineages spread to East Asia, and from there to the Sunda Shelf & Philippines, Wallacea & New Guinea and the Australia & Pacific islands (Fig. 4).

In the NW, the BSM analysis indicated that South America (A) was the main source area producing almost 11 dispersal events (17.2% of all dispersal events starting within the NW). Dispersal from South America (A) into Central America (C) occurred 6.9 times, while 2.5 dispersal events were inferred from South America to Australia & Pacific (P) (in Coronanthereae), and 0.79 events to

East Asia (N) (*Titanotrichum*). Central America (C) was an important source area with 2.21 dispersal events to South America (Fig. 5, Figs S12, S13, Table 5, S5, S6).

In the OW, East Asia (N) was the most important source area with 29.1 events (46.7% of OW dispersal events). Most dispersals were from East Asia (N) to the Sunda Shelf & Philippines (S) (12.95 events), and to the Indian plate (I) (8.77 events). Europe & and Africa (F) were not the source of any dispersal events, but each was the destination of a single dispersal event from East Asia (N), concerning respectively subtribe Ramondinae (0.99) and subtribe Streptocarpinae (*Streptocarpus*) and *Epithema tenue* (1.26). The second most prolific source area in the OW was the Sunda Shelf & Philippines (S) with 11.3 events (18.2%), with 1.34 dispersals to the Indian plate (I) (*Rhynchotechum permolle*), 2.76 events to East Asia (N), and 5.77 to Wallacea & New Guinea (W). The Indian plate (I) was the source area for 3.1 dispersal events (5%), with 1.22 dispersals to East Asia (N), and one event to either South America (A, 0.54) or Central America (C, 0.47) (*Rhynchoglossum azureum*). Wallacea & New Guinea (W) and Australia & Pacific (P) were the source areas for just over 2 dispersal events each (Fig. 5, Tables 5, S5, S6).

Table 3. Divergence time estimates (in million years) of major nodes of Gesneriaceae (stem, crown) and HPD confidence interval obtained in the present study and comparable previous studies.

Node	this study	Fonseca (2021)	Roalson & Roberts (2016)	Petrova et al. (2015)	Perret et al. (2013)
Gesneriaceae (incl. *Sanango*) stem	66.84 (58.40-75.48)	-	76.03 (54.17-82.14)	77.79 (69.80-86.98)	63.56 (58.31-71.72)
Run with oldest fossil ages stem	79.48 (55.18-77.80)				
Gesneriaceae (incl. *Sanango*) crown	63.48 (55.66-71.51)	-	73.07 (51.93-81.27)	71.88 (67.72-82.08)	57.50 (45.10-68.10)
Run with oldest fossil ages stem	75.63 (54.64-73.58)				
Core Gesneriaceae (excl. *Sanango*) stem	63.48 (55.66-71.51)	67.70	73.07 (51.93-81.27)	71.88 (67.72-82.08)	57.50 (45.10-68.10)
Core Gesneriaceae (excl. *Sanango*) crown	59.46 (51.56-67.68)	61.51	69.66 (48.20-77.06)	65.52 (54.97-76.00)	44.70 (37.10-60.50)
Subfam. Sanangoideae	63.48	-			
Subfam. Gesnerioideae stem	59.46 (51.56-67.68)	61.51	69.66 (48.20-77.06)	65.52 (54.97-76.00)	44.70 (37.10-60.50)
Subfam. Gesnerioideae crown	38.60 (28.45-52.01)	53.52	46.85 (40.30-66.20)	41.90 (25.56-60.69)	36.20 (32.30-48.70)
Tribe Titanotricheae	33.36 (22.97-45.79)	-			
Tribe Beslerieae stem/crown	33.36 (22.97-45.79) / 18.58 (12.92-24.94)	50.26 / 32.07			
Subtribe Anetanthinae stem/crown	15.95 (10.91-22.02) / 12.88 (7.95-18.52)	[29.94 / 26.58]			
Subtribe Besleriinae (not monophyletic)	[33.36 (22.97-45.79) / 18.58 (12.92-24.94)]	n.m.			
Tribe Coronanthereae stem/crown	33.10 (24.32-44.72) / 14.05 (8.97-20.96)	48.69 / 33.91			
Subtribe Coronantherinae stem/crown	12.44 (7.66-18.54) / 8.40 (3.81-14.21)	26.7 / 20.20			
Subtribe Mitrariinae stem/crown	12.44 (7.66-18.54) / 8.40 (3.81-14.21)	n.m.			
Subtribe Negriinae stem/crown	14.05 (8.97-20.96) / 11.29 (5.17-17.93)	n.m.			
Tribe Gesnerieae stem/crown	33.10 (24.32-44.72) / 24.08 (18.65-30.39)	53.52 / 35.16			
Subtribe Columneinae stem/crown	21.10 (16.27-26.75) / 18.06 (14.05-22.85)	32.87 / 27.10			
Subtribe Gesneriinae stem/crown	19.44 (14.82-24.87) / 9.25 (5.13-14.41)	28.51 / 22.63			
Subtribe Gloxiniinae stem/crown	19.44 (14.82-24.87) / 15.9 (12.15-20.07)	28.51 / 22.56			
Subtribe Ligeriinae stem/crown	24.08 (18.65-30.39) / 13.01 (7.39-20.33)	35.16 / 23.00			
Subtribe Sphaerorrhizinae stem/crown	21.10 (16.27-26.75) / 5.02 (1.14-12.32)	32.87 / 6.47			
Subfam. Didymocarpoideae stem	59.46 (51.56-67.68)	61.51	69.66 (48.20-77.06)	65.52 (54.97-76.00)	44.70 (37.10-60.50)
Subfam. Didymocarpoideae crown	55.96 (48.27-63.95)	59.42	67.41 (46.61-75.03)	61.17 (50.62-71.47)	42.42 (28.28-53.35)
Tribe Epithemateae stem/crown	55.96 (48.27-63.95) / 45.70 (36.54-54.47)	59.42 / 51.56			
Subtribe Epithematinae stem/crown	29.03 (20.74-38.40) / 13.85 (8.43-20.26)	47.16 / 24.78			
Subtribe Loxoniinae stem/crown	29.03 (20.74-38.40) / 22.01 (12.31-31.86)	-			
Subtribe Loxotidinae stem/crown	45.70 (36.54-54.47) / 15.35 (7.91-25.66)	51.56 / 27.73			
Subtribe Monophyllaeinae stem/crown	37.52 (28.48-46.31) / 26.16 (17.69-35.66)	47.16 / 37.07			
Tribe Trichosporeae stem/crown	55.96 (48.27-63.95) / 51.55 (43.93-59.61)	59.42 / 48.48			
Subtribe Jerdoniinae stem	51.55 (43.93-59.61)	-			
Subtribe Corallodiscinae stem/crown	41.91 (34.97-49.15) / 18.95 (8.57-31.12)	48.48 / 21.44			
Subtribe Tetraphyllinae stem	38.75 (32.36-45.74)	-			
Subtribe Leptoboeinae stem/crown	31.01 (22.69-38.83) / 18.20 (11.78-25.90)	39.97 / 25.17			
Subtribe Ramondinae stem/crown	31.01 (22.69-38.83) / 21.92 (12.04-31.88)	39.97 / 34.38			
Subtribe Litostigminae stem/crown	33.59 (26.44-40.74) / 8.50 (2.91-17.36)	-			
Subtribe Streptocarpinae stem/crown	31.59 (26.07-37.41) / 17.72 (11.46-24.61)	38.5 / 27.56			
Subtribe Didissandrinae (not monoph.)	29.42 (24.3-35.2) / 0.66 (0.07-1.92) & 29.99 (24.6-35.49) / 24.12 (7.15-33.09)				
Subtribe Loxocarpinae stem/crown	29.42 (24.30-35.20) / 26.73 (21.88-32.23)	37.04 / 32.85			

n.m. – not measured/provided

Table 4. Results of BioGeoBEARS biogeographical model testing for Gesneriaceae under AIC and AIC_c selection. Model parameters: (d) anagenetic dispersal, (e) extinction, (j) jump dispersal or founder events, (s) subset sympatry. The best fit model is highlighted in grey.

AIC Model	LnL	numparams	d	e	j	s	AIC	ΔAIC	model weight	P
DEC	-590.8	2	0.0028	6.2×10^{-05}	0	1.00	1186	150	8.2×10^{-33}	8.8×10^{-09}
DEC+J	-574.3	3	0.0023	1.0×10^{-12}	0.0049	1.00	1155	119	4.6×10^{-26}	
DIVALIKE	-628.2	2	0.0036	1.0×10^{-12}	0	0	1260	224	4.8×10^{-49}	3.8×10^{-10}
DIVALIKE+J	-608.6	3	0.0026	1.0×10^{-12}	0.0064	0	1223	187	5.7×10^{-41}	
BAYAREALIKE	-799.8	2	0.010	0.010	0	0	1604	568	1.4×10^{-123}	1.1×10^{-97}
[BAYAREALIKE+J0	-579.8	3	0.0007	0.022	0.0048	0	1166	130	1.9×10^{-28}]	
BAYAREALIKE+J	-579.8	3	0.0007	0.022	0.0048	0	1166	130	1.9×10^{-28}	4.8×10^{-30}
BAYAREALIKE+s+J	-515.0	4	0.0008	1.0×10^{-07}	0.0091	0.51	1036	0	1	

AIC_c Model	LnL	numparams	d	e	j	s	AIC_c	$ΔAIC_c$	model weight	P
DEC	-590.8	2	0.0028	6.2×10^{-05}	0	1.00	1186	148	8.6×10^{-33}	8.8×10^{-09}
DEC+J	-574.3	3	0.0023	1.0×10^{-12}	0.0049	1.00	1155	117	4.7×10^{-26}	
DIVALIKE	-628.2	2	0.0036	1.0×10^{-12}	0	0	1260	222	5.0×10^{-49}	3.8×10^{-10}
DIVALIKE+J	-608.6	3	0.0026	1.0×10^{-12}	0.0064	0	1223	185	5.8×10^{-41}	
BAYAREALIKE	-799.8	2	0.010	0.010	0	0	1604	566	1.5×10^{-123}	1.1×10^{-97}
[BAYAREALIKE+J0	-579.8	3	0.0007	0.022	0.0048	0	1166	128	1.9×10^{-28}]	
BAYAREALIKE+J	-579.8	3	0.0007	0.022	0.0048	0	1166	128	1.9×10^{-28}	4.8×10^{-30}
BAYAREALIKE+s+J	-515.0	4	0.0008	1.0×10^{-07}	0.0091	0.51	1038	0	1	

Table 5. Results of the biogeographic stochastic modelling (BSM) of Gesneriaceae for all dispersal events from the BAYAREAlike+s+j model in BioGeoBEARS. Numbers shown are means with SD in parentheses.

From: \ To:	A South America	C Central America	E Europe	F Africa	I Indian plate	N East Asia	S Sunda & Philippines	W Wallacea & New Guin.	P Australia & Pacific
A South America	0 (0)	6.92 (1.81)	0 (0)	0 (0)	0.38 (0.49)	0.79 (0.67)	0.094 (0.29)	0 (0)	2.49 (1.02)
C Central America	2.21 (1.13)	0 (0)	0 (0)	0 (0)	0.12 (0.32)	0.57 (0.58)	0.056 (0.23)	0 (0)	0.38 (0.49)
E Europe	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.004 (0.063)	0 (0)	0 (0)	0 (0)
F Africa	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.004 (0.063)	0.006 (0.077)	0 (0)	0 (0)
I Indian plate	0.54 (0.51)	0.47 (0.5)	0.01 (0.1)	0.092 (0.29)	0 (0)	1.22 (0.85)	0.38 (0.53)	0.37 (0.5)	0 (0)
N East Asia	0.006 (0.1)	0.004 (0.063)	0.99 (0.11)	1.26 (0.6)	8.77 (1.38)	0 (0)	12.95 (2.08)	4.87 (1.22)	0.20 (0.4)
S Sunda & Phili.	0 (0)	0 (0)	0.002 (0.045)	0.65 (0.6)	1.34 (0.96)	2.76 (1.6)	0 (0)	5.77 (1.42)	0.80 (0.67)
W Wallacea & NG	0 (0)	0 (0)	0 (0)	0.02 (0.41)	0.28 (0.52)	1.03 (0.83)	0 (0)	1.00 (0.69)
P Austr. & Pac.	1.15 (0.75)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.006 (0.1)	1.00 (0.69)	0 (0)

Discussion

We conducted the most comprehensive genus-level phylogenetic, dating, and biogeographic analysis to date of the family Gesneriaceae, with more sampled genera than previous work on the family (142 out of 151 genera) and a balanced inclusion of NW and OW samples. The completeness of the data matrix was very high with only ~5% missing data. For the trees generated, the branch support values were mostly 100% BS and/or 1 PP, providing the basis for a stable and strongly supported phylogenetic hypothesis with very little incongruence between the MP, ML and BI analyses (Figs S1-S5) providing a solid foundation for our studies. Our topologies here based on chloroplast data largely agree with the trees obtained by Ogutcen et al. (2021) based on the phylogenomic analysis of 418 single-copy nuclear genes. Topological differences with this study mainly concern the more weakly supported relationships among subtribes, indicating that phylogenomic approaches targeting a large number of nuclear genes might be needed to fully resolve and stabilise phylogenetic relationships in Gesneriaceae. However, topological differences between the current study and Ogutcen et al. (2021) do not involve the key biogeographic events detected here, providing more confidence in our broad scale biogeographic analysis.

Divergence time of Gesneriaceae

Our conservative dating approach attaching the youngest possible age of each fossil to a stem node (following Magallón et al. 2015), revealed an origin for Gesneriaceae around the Cretaceous-Palaeogene boundary (67.23 Ma), with diversification beginning soon afterwards (63.87 Ma). The two main clades in Gesneriaceae had very different diversification patterns, with the mainly OW Didymocarpoideae diversifying much earlier in the Early Eocene (56.29 Ma), whereas the extant members of the mainly NW Gesnerioideae did not begin to diversify until the late Eocene (39.34 Ma). These differences were in line
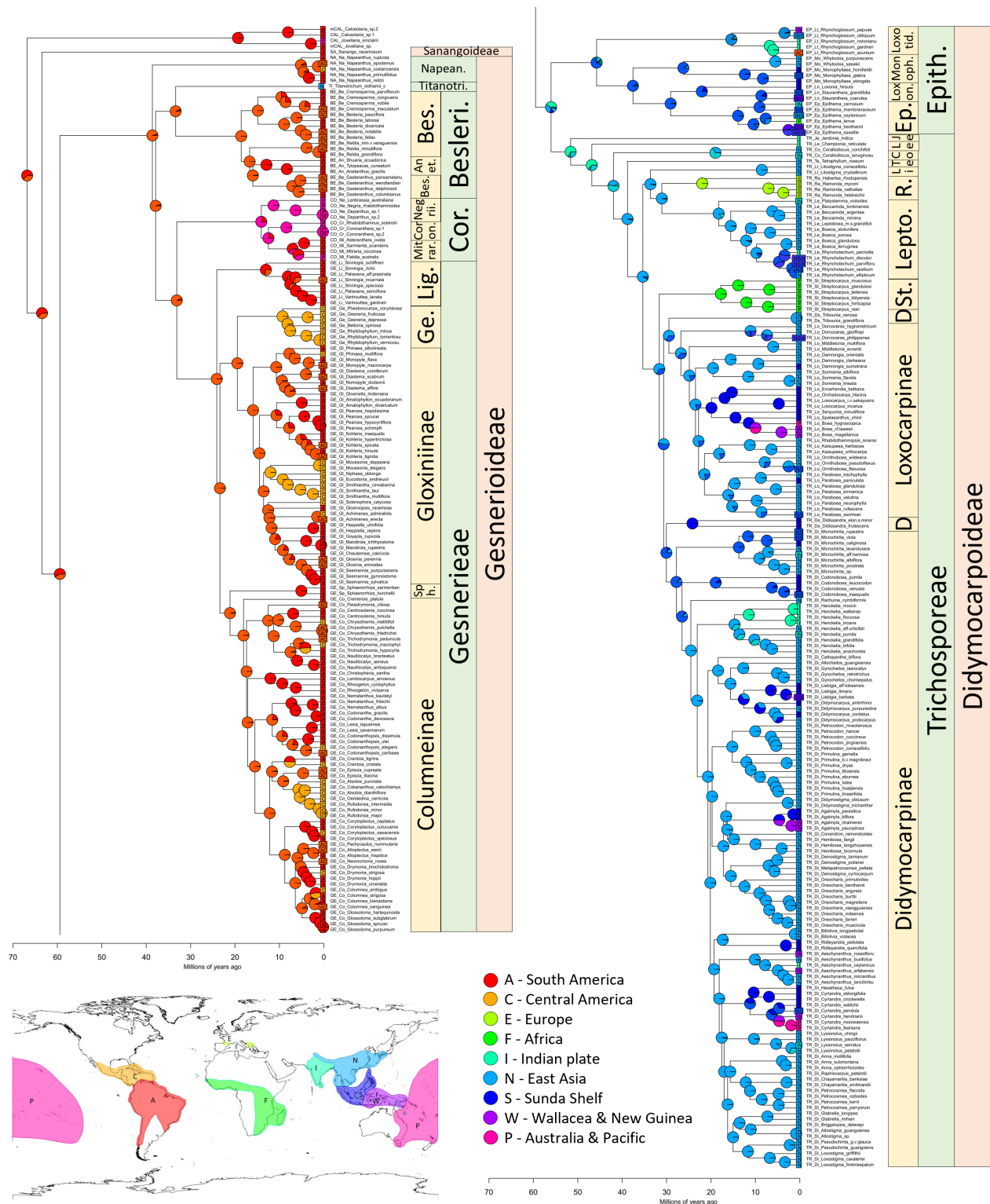
Figure 4. Ancestral range estimation for the family Gesneriaceae based on the BEAST ultrametric tree, and the best fitting model determined by BioGeoBEARS (BayArea-like+s+j). Areas are colour-coded as indicated in the insets. Pie graphs at each node indicate the probability of presence in a given area (or combined areas). Subfamilies (pale pink), tribes (light green) and subtribes (pale yellow) are indicated. Abbreviations used: **Tribes**: Besleri. = Beslerieae, Cor. = Coronanthereae, Epith. = Epithemateae, Napean. = Napeantheae, Titanotri. = Titanotricheae. **Subtribes**: Anet. = Anetanthinae, Bes. = Besleriinae, Coron. = Coronantherinae, Co. = Corallodiscinae, D. = Didissandrinae, Ep. = Epithematinae, Ge. = Gesneriinae, Je. = Jerdoniinae, Le./Lepto. = Leptoboeinae, Lig. = Ligeriinae, Li. = Litostigminae, Loxon. = Loxoniinae, Loxotid. = Loxotidinae, Mitrar. = Mitrariiinae, Monoph. = Monophyllaeinae, Negrii. = Negriinae, R. = Ramondinae, Sph. = Sphaerorrhizinae, St. = Streptocarpinae, Te. = Tetraphyllinae.
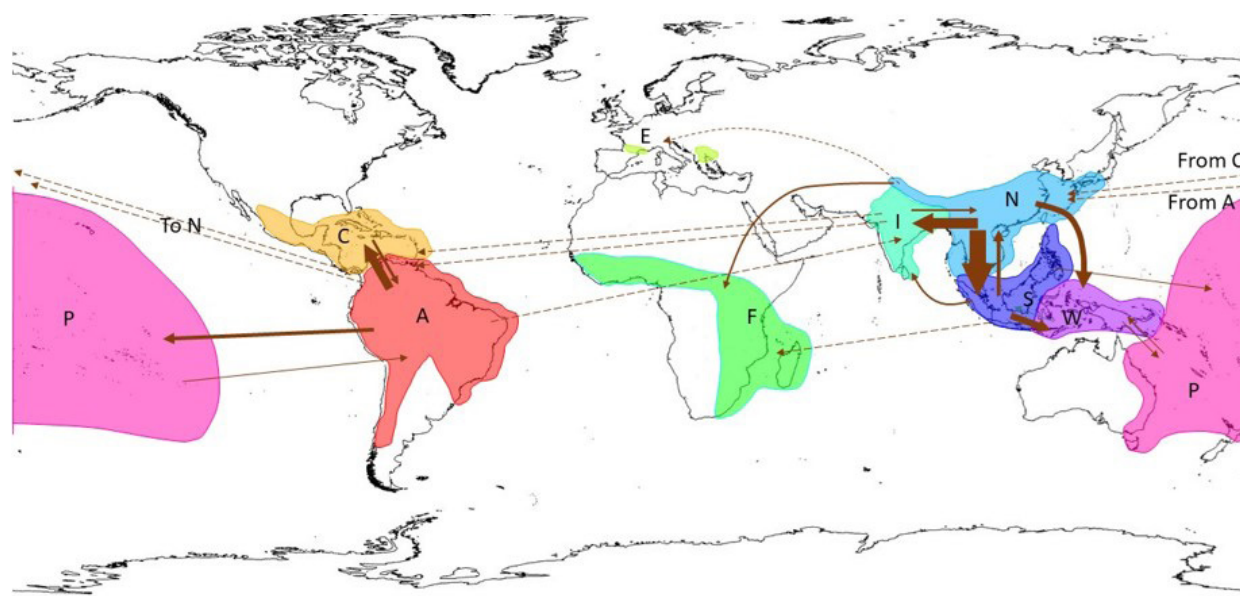
Figure 5. Graphical summary of the Biogeographical Stochastic Mapping (BSM) analysis of Gesneriaceae in BioGeoBEARS on the best-fitting model, BayArea-like+s+j, showing dispersal events (with a rate higher than 0.4) between geographic regions. The thickness of the lines is roughly proportional to the number of predicted dispersal events (founder events and range expansion). Events with counts below 1 are indicated by a dotted line. (base map modified from https://www.theworldofmaps.com/sites/theworldofmaps.com/files/WGS84_1.jpg).

with earlier studies (e.g., Roalson and Roberts 2016, suppl. fig. 3; Fig. 3). In general, our age estimates were most similar to those of the order level analysis of Fonseca (2021), older than those of Perret et al. (2013), and younger than those of Petrova et al. (2015) and Roalson and Roberts (2016) (Fig. S14).

Transoceanic dispersal into the OW, and early diversification in South Asia

Our analysis indicates three early probable transoceanic dispersal events from the NW to the OW including Australasia. The earliest such dispersal event was the common ancestor of the Didymocarpoideae into the OW around 59.46 Ma, newly reported in the current study (Fig. 4, Figs S8, S15). The most likely arrival point (42% probability, Fig. 4) was the Indian plate (see detailed discussion below). This was followed by the ancestor of *Titanotrichum* which reached East Asia c. 33.36 Ma, whereas that of the Coronanthereae reached the Pacific c. 33.1 Ma (Figs 4, 5); both of these events were previously detected (Woo et al. 2011, Perret et al. 2013).

All three of these dispersal events to the OW require either an LDD event, or a long journey via intervening landmasses such as Africa, Antarctica and/or Australia, leaving no extant descendant along the way. LDD events are known to occur regularly through geological time (Higgins et al. 2003, Nathan 2006), with a minimum of 72 detected for Urticaceae alone (Wu et al. 2018); indeed, Gesneriaceae exhibits relatively few by comparison (Fig. 5), and the families are of comparable age. During the period when all

three Gesneriaceae dispersal events occurred, 60-30 Ma, Antarctica had an equable climate (Thorn and DeConto 2006), was connected to South America (Barker and Burrell 1977), and exchanged flora with it (e.g., Taylor 1991, Morley 2003, Sytsma et al. 2004, Knapp et al. 2005, Buerki et al. 2011). Hence it is perfectly plausible that one or more of the three dispersing lineages moved over land into Antarctica and then dispersed north from there, as has been proposed for the Coronanthereae (Perret et al., 2013).

The presence of *Titanotrichum* in Asia (Taiwan, Japan and China) and the absence of relatives in Malesia argues in favour of a direct LDD as hypothesised for the arrival of other disjunct plant groups in Taiwan, such as Lardizabalaceae (Wang et al. 2020), although the similar age of this event with the Coronanthereae could possibly suggest a co-migration overland through Antarctica. Overall, in all three cases, all of LDD direct from South America, LDD from Antarctica, or stepping stone dispersal via another route, are possible hypotheses to be explored in the future.

The role of the Indian plate

Key to the occurrence and diversification of the OW lineage in Asia is the location of the arrival point of the Didymocarpoideae common ancestor, around 59.46 Ma. The most likely arrival point (42% probability, Fig. 4, Fig. S11) was the Indian plate, followed by East Asia (29%) and Sunda Shelf & Philippines (11%); other scenarios from the analysis can be discounted because they require simultaneous arrival onto the Indian plate and another area with which it was not contiguous at the time. The two subclades into which

Didymocarpoideae then divided are strongly supported to be Indian plate (Trichosporeae) and Sunda Shelf & Philippines (Epithemateae) in origin (Fig. 4), and hence the analysis appears to be presenting three scenarios. In order of likelihood (Fig. 4), these are (i) (42%) Indian plate arrival followed by dispersal of Epithemateae to Sunda Shelf & Philippines, (ii) (29%) East Asia arrival and dispersal of Trichosporeae and Epithemateae to the Indian plate and Sunda Shelf & Philippines respectively, and (iii) (11%) Sunda Shelf & Philippines arrival followed by dispersal of Trichosporeae to the Indian plate. Scenarios (i) and (iii) are both consistent with Morley's (2003) suggestion of early Eocene floristic exchanges involving the Sunda Shelf, close to the equator. Scenario (ii) requires either extinction on the Asian mainland following the two dispersal events (unlikely given that several Didymocarpoideae lineages thrived and diversified there), or multiple successive dispersals to the Indian plate, which would be less parsimonious. Based on this, and the low (11%) probability for scenario (iii) from Fig. 4, an Indian plate arrival will be discussed here as the most probable scenario, with the necessary caveat that the other two cannot be ruled out. Moreover, because an Indian plate origin is strongly supported for Trichosporeae, which is far more species-diverse than Epithemateae and accounts for the great majority of OW species outside of Malesia, the Indian plate is strongly indicated here to have played a crucial role in the early history of OW Gesneriaceae, even if it was not the original arrival point.

Massive volcanic eruptions occurred on the Indian plate around 65 Ma lasting almost a million years, forming the Deccan Plateau and pushing the present-day Western Ghats to over 1,000 m a.s.l. (e.g., Renne et al. 2015, Richards et al. 2015, Schulte et al. 2010). This region was isolated in the Indian Ocean between the African and Australian plates at this point (e.g., Morley 2003, fig. 4; Bernardes et al. 2021, fig. 1), and around 5,000 km south from the Asian mainland (Wheeler et al. 2017). Volcanic eruptions, and crossing the equator during the northward rafting, might have led to biotic extinctions, and suppressed biodiversity on the plate (Lowery and Fraass 2019, Morley 2000, Rutschmann et al. 2004). Hence, the stem Didymocarpoideae might have arrived into a region undergoing significant biotic turnover, which created both opportunities for establishment and challenges for survival.

The first two diverging lineages of Trichosporeae are both monotypic Indian plate genera: the South Indian *Jerdonia*, and the now Sri Lankan *Championia*. These diverged respectively 51.55 and 46.78 Ma (Fig. 3), implying a long presence and high levels of extinctions of early Trichosporeae on the Indian plate. This might explain that these two relict lineages have greatly differing and unusual habits, with *Jerdonia* being a rosette perennial herb in South India with strongly zygomorphic flowers and unique capsules, whereas *Championia* in Sri Lanka is a caulescent shrubby plant with actinomorphic flowers (Gardner 1846, Wight 1848); they hence offer few clues as to the habit

of the Trichosporeae common ancestor. The Indian plate is known for its importance as a repository (e.g., Morley 2003, Karanth 2006), possibly reflecting relative stability in its southern part following the upheavals of extreme volcanism, progressive latitude change, and collision with Asia.

The Indian plate collided with the Eurasian plate (65-(55-50)-40) Ma (Wambulwa et al. 2021, and references therein), and this is consistent with fossil evidence of terrestrial faunal exchanges between the Indian and Asian plates around 54 Ma (Clementz et al. 2011). However, the first node that is likely to have been present in East Asia was the third divergence event within Trichosporeae, which was the divergence of *Corallodiscus* (comprising the monogeneric subtribe Corallodiscinae), from all other species, 41.91 Ma. Therefore, Trichosporeae might have taken longer than some other groups to migrate away from the Indian plate. The broad distribution of *Corallodiscus* includes parts of the Indian plate as well as much of China (Kamble et al. 2006, Rout et al. 2008). Since the Indian *Corallodiscus* sample did not represent a basal lineage in the genus phylogeny (Zhou et al. 2017), the *Corallodiscus* divergence event might have been the first to have occurred outside the Indian plate. By this time the Himalayan orogeny would have been underway, presenting suitably diverse habitats for biological diversification, potentially promoting the generation of new lineages which might have been better adapted to colonising regions further east (Wambulwa et al. 2021, and references therein).

From around 40 Ma onwards, the Indian plate gained further Gesneriaceae species almost entirely by dispersals from elsewhere. Chief among these were ~10 back dispersals from East Asia between the early Miocene and early Pleistocene (18.2 to 1.84 Ma) (Figs 3-6, Table 4). This involved at least eight genera including some species with wide distribution ranges (e.g., *Epithema ceylanicum*, *Rhynchoglossum obliquum* and *Rhynchotechum parviflorum*). We coded the Indian plate to exclude Northeast India because of geological uncertainties in this region and its similar flora to adjacent areas in East Asia. Had we included this region within the Indian plate, additional back-dispersals to the region would have been indicated, because most of the 20 Gesneriaceae genera in Northeast India have ranges extending eastwards into East Asia (Sinha and Datta 2016). One, presumably long distance, back-dispersal from the Indian plate to South America was inferred, involving *Rhynchoglossum azureum* (sister to the Sri Lankan *R. gardneri*) in the early Pliocene (5.94 Ma) underlining the role of the Indian plate in diversification of the family.

Diversification through the Old World: East Asia as a centre of diversity

Trichosporeae is the largest tribe in Gesneriaceae with around 2,400 species (Weber et al. 2020), and has several centres of diversity in Asia (Tan et al. 2020). From around 40 Ma onwards, most diversification in Trichosporeae occurred in East Asia, with many interchanges with neighbouring regions (Figs 3-6).
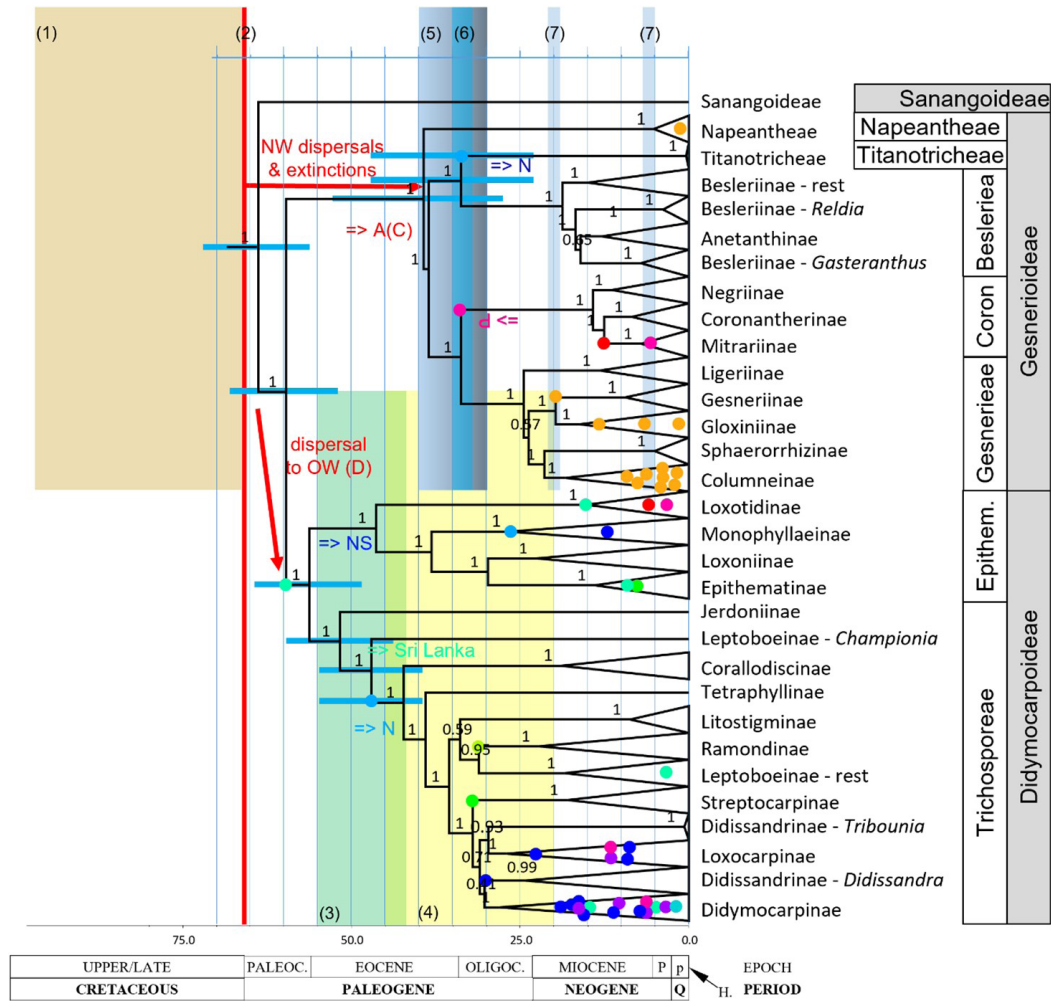
Figure 6. Simplified BEAST time-calibrated chronogram to subtribal level of Gesneriaceae samples included in the analysis of 408 samples, annotated with key dispersal events as coloured dots indicated by the BGB analysis. Each dot represents the destination of a separate dispersal event. ● 'Indian plate' (I), ● 'East Asia' (N), ● 'Australia & Pacific' (P), ● 'Sunda Shelf & Philippines' (S), and ● 'Wallacea & New Guinea' (W), ● 'South America' (A), ● 'Central America & West Indies' (C), ● 'Europe' (E), and ● 'Africa & Madagascar' (F). Colour code of dots as in Fig. 2. Posterior probabilities are given along the branches. Shaded HPD bars are given only for nodes linked to major geological events: (1) Orogenic origin of the Andes (Taylor 1991, Morley 2003); (2) Asteroid impact 66 Ma creating the Chicxulub crater in the Yucatán Peninsula in Mexico (Mann 2018); (3) Collision of Indian and Eurasian plates 55-42 Ma (Ashton and Gunatilleke 1987, Briggs 2003); (4) Orogeny of the Himalayas 55-20 Ma (Antonelli et al. 2015); (5) Separation of South America from Antarctica 40-30 Ma (Barker and Burrell 1977), and Antarctica and Australia ~30 Ma (Sanmartín and Ronquist 2004); (6) GAARLandia (Antonelli et al. 2015), and the beginning of Antarctic inland glaciation 35-32 Ma (Zachos and Klump 2005); (7) Two periods of proposed connectivity across the Panama Isthmus 20 and 6 Ma, after Bacon et al. (2015). PALEOC – Palaeocene; OLIGOC. – Oligocene; P – Pliocene; p – Pleistocene; Q – Quaternary. Subfamily and tribe annotation as in Fig. 3.

Our stochastic mapping analysis likewise highlights East Asia, as defined in Table 2 (Area N in Fig. 5) as a major source of dispersals to both Sundaland and Wallacea & New Guinea (with 12.95 BSM modelled dispersal events) as well as to the Indian plate noted above, Europe (subtribe Ramondinae), and Africa (subtribe Streptocarpinae and *Epithema tenue*) (Fig. 4, Table 5). In contrast, it was the recipient of relatively few dispersal events (Fig. 4, Table 5). This is consistent with the meta-analysis of De Bruyn et al. (2014)

which resolved continental Southeast Asia to be a major evolutionary hotspot in Asia. We recommend further analysis of this highly diverse and important subregion separately in the future (following Matzke, 2016) separating, for example, continental southeast Asia from the rest of East Asia to further elucidate the speciation and dispersal dynamics in such a scenario would be valuable.

Hilliard and Burtt (1971, p. 380) had suggested a Gondwana origin for what is now subtribe

Streptocarpinae (see Nishii et al. 2015). However, this can be rejected because the estimated stem (31.59 Ma) and crown (17.72 Ma) ages of the Streptocarpinae lineage are at least five times younger than the break-up of Gondwana in the mid Jurassic (~180-160 Ma) (Fig. 4, Fig. S8). Instead, the BGB analysis suggests a dispersal of the lineage into Africa to have occurred in the Oligocene-Early Miocene. One plausible route would have been overland migration after the closure of the Tethys seaway during the Early Miocene, although the route still requires crossing of some narrow seaways (Bialik et al. 2019). This would fit a southward migration route within Africa and two separate colonisations of Madagascar that was proposed by Hilliard and Burtt (1971) and later supported by molecular data (Möller and Cronk 2001). A second more recent dispersal from East Asia into Africa in the Late Miocene involved *Epithema tenue* (7.66 Ma), and could have followed a similar route, although direct LDD is also possible.

Dispersal of the Ramondinae lineage from East Asia (N) into Europe (E) occurred during the Oligocene, consistent with Petrova et al. (2015) (Fig. 4). At that point the European and Asian plates were firmly sutured, and hence overland migration to the contemporary Balkan Peninsular (and later further on to Spain for *R. myconii*) is the most likely hypothesis.

Other dispersals from East Asia (N) involved more than a dozen mainly southwards overland migrations to cross the Isthmus of Kra and into the Sunda Shelf & Philippines (S) over a wide period of time spanning the mid Oligocene and Miocene (e.g., Loxocarpinae p.p., 22.75 Ma; *Codonoboea*, 18.88 Ma; *Liebigia*, 15.56 Ma; *Paraboea p.p.*; 8.71 Ma) (see also Puglisi et al. 2016) (Figs 3-6). During periods of glaciations when sea levels were lower, the Sunda Shelf was part of the Eurasian landmass (Hall 2002, 2012a, b) and overland dispersal was possible. Several dispersals from East Asia (N) directly to the Sunda Shelf & Philippines (S) involved larger genera such as *Aeschynanthus* and the widespread *Rhynchoglossum*, but these species-rich genera were undersampled here.

Diversification through the Old World: Malesia and the Pacific

Dispersals between the Sunda Shelf and Wallacea & New Guinea require crossing Wallace's Line, a seaway that was never closed (Hall 2002, 2012a, b). In our study, these were on the whole more recent than dispersals from East Asia to the Sunda Shelf, and mostly eastwards into Wallacea & New Guinea (Figs 3-6), adhering to the more common pattern in this geographic area seen in numerous plant groups including *Begonia, Aglaia,* and *Pseuduvaria* (Richardson et al. 2012, Thomas et al. 2012, Grudinski et al. 2014, Su and Saunders 2009). Examples of this Sunda to Wallacea dispersal route included the large genera *Agalmyla* (16.2 Ma) and *Cyrtandra* (6.34 Ma) in tribe Trichosporeae, and the widespread *Epithema benthamii* and *E. saxatile* (2.5 Ma) in tribe Epithemateae (Figs 3-6). *Agalmyla* species have long hair-like seed appendages, as in *Aeschynanthus*, where this type of appendage was

shown to aid wind-dispersal or zoochory (perhaps on the feet of birds) across Wallace's Line (Hilliard and Burtt 2002, Kokubugata et al. 2011). Zoochory may also be involved in *Cyrtandra* species because of the presence of fleshy fruits (Atkins et al. 2020).

The BSM suggested one dispersal into and one out of Australia & Pacific Islands from Wallacea & New Guinea, split between the two genera *Boea* (11.42 Ma) and *Cyrtandra* (6.22 Ma). Both genera are undersampled here, and recent detailed biogeographic studies on *Cyrtandra* indicated that the direction of dispersal is predominantly from west to east in this region for the genus with three dispersals recorded from New Guinea to Australia and the Pacific (Johnson et al. 2017, Atkins et al. 2020). The directionality of dispersal events in eastern Malesia can, however, be highly complex (Low et al. 2022).

Conclusions

Our results provide new insights into the biogeographic history of the Gesneriaceae, particularly in the palaeotropics. With much denser sampling at genus level, particularly from the OW Didymocarpoideae subfamily, we have evidence to support the importance of rare LDD dispersal events in shaping the present-day distribution of the family, particularly the late Palaeocene arrival in the OW of a lineage from the Americas, most likely onto the Indian plate. This initial dispersal event to the OW ultimately led to the current diversity of the Didymocarpoideae, underlining the importance of rare, stochastic events in shaping diversity. Our work also indicates the importance of comprehensive sampling and the significance of endemics, such as *Championia* from Sri Lanka and *Jerdonia* from India in elucidating contemporary biogeographic patterns.

The analysis also highlights the importance of the Indian plate in the early history of Gesneriaceae in the Old World as both the source area of dispersals into the rest of Asia and as a later recipient. East Asia, including China and continental Southeast Asia, emerge as hotspots for Gesneriaceae where diversity evolved via both *in situ* speciation and subsequent emigration with lineages from this area dispersing to Europe, Africa and in high numbers to the Sunda Shelf and the Philippines and Wallacea and New Guinea.

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Author Contributions

MM, RM, and SR conceived this study. AK, GLM, HA, JLC, KN, MM, and SR provided samples and data. MM, KN, and SR analysed the data, with input from other authors. All authors contributed to the writing and revising of the manuscript.

Data Accessibility Statement

All newly generated sequences have been submitted to Genbank.

Supplemental Material

This material is available as part of the online article from https://escholarship.org/uc/fb

Table S1. Voucher information, GenBank numbers and country of origin (or distributions in brackets for cases of unknown origin) of the 408 samples used in the analyses of 356 Gesneriaceae and 52 other Lamiales and outgroup accessions.

Table S2. Details of the molecular markers used in the present study.

Table S3. Characteristics of the Bayesian inference analysis for 408 samples based on concatenated *mat*K, *ndh*F, *rps*16 and *trn*LF sequence data.

Table S4. Clade support of subfamilies, tribes and subtribes of Gesneriaceae found in MP, ML, BI analyses.

Table S5. Results of the biogeographic stochastic modelling (BSM) of Gesneriaceae for switching dispersal ('a'), anagenetic dispersal ('a' or 'd') and cladogenetic (founder 'j') events one the BAYAREAlike+s+j model in BioGeoBEARS.

Table S6. Summary of the biogeographic stochastic modelling (BSM) of Gesneriaceae on the BAYAREAlike+s+j model in BioGeoBEARS.

Figure S1. Phylogram of a single maximum parsimony (MP) tree based on 408 samples of Gesneriaceae and outgroup samples and concatenated *mat*K, *ndh*F, *rps*16 and *trn*LF sequence data of 22,434 steps length, CI=0.3441, and RI=0.8087.

Figure S2. 50% majority rule consensus tree based on 165,748 most parsimonious trees based on 408 samples of Gesneriaceae and outgroup samples and concatenated *mat*K, *ndh*F, *rps*16 and *trn*LF sequence data with frequency values along the branches.

Figure S3. Bootstrap 50% majority rule consensus tree of 10,000 random replicates based on 408 samples of Gesneriaceae and outgroup samples and concatenated *mat*K, *ndh*F, *rps*16 and *trn*LF sequence data with branch support values along the branches.

Figure S4. Maximum Likelihood (ML) tree based on 408 samples of Gesneriaceae and outgroup samples and concatenated *mat*K, *ndh*F, *rps*16 and *trn*LF sequence data, with ML bootstrap values along the branches.

Figure S5. Bayesian Inference (BI) tree with average branch lengths based on 408 samples of Gesneriaceae and outgroup samples and concatenated *mat*K, *ndh*F, *rps*16 and *trn*LF sequence data, with posterior probability values along the branches.

Figure S6. Histogram of SS values for the nine fossil calibration nodes, when each was used as the single calibration point.

Figure S7. Line graph illustrating the effect of consecutively removing fossil calibration points on the value of 's'.

Figure S8. BEAST chronogram of 408 Gesneriaceae and outgroup samples analysed, with ages shown along the branches.

Figure S9. Resulting BioGeoBEARS trees under the DEC and Dec+j models based on 359 samples of Gesneriaceae and outgroup samples.

Figure S10. Resulting BioGeoBEARS trees under the DIVAlike and DIVAlike+j models based on 359 samples of Gesneriaceae and outgroup samples.

Figure S11. Resulting BioGeoBEARS trees under the BAYAREAlike and BAYAREAlike+j models based on 359 samples of Gesneriaceae and outgroup samples.

Figure S12. Correlation between ML and BSM state probabilities in the biogeographic stochastic modelling (BSM) analysis one the BAYAREAlike+s+j model in BioGeoBEARS based on 359 samples of Gesneriaceae and outgroup samples.

Figure S13. Number of events counts in each category in the biogeographic stochastic modelling (BSM) analysis one the BAYAREAlike+s+j model in BioGeoBEARS based on 359 samples of Gesneriaceae and outgroup samples.

Figure S14. Summary of divergence times and HPD confidence intervals for selected clades/nodes in Gesneriaceae estimated in the present study (●) and previous studies, Roalson and Roberts (2016) (●), Petrova et al. (2015) (●), Perret et al. (2013) (●), and Fonseca et al. (2021, without Sanango) (●).

Figure S15. Possible scenarios of the initial LDD event at the Cretaceous-Paleogene boundary (=Cretaceous-Tertiary K-T boundary) coinciding with the dispersal of the ancestor of the OW Gesneriaceae into India; (Plate tectonic maps and Continental drift animations by C. R. Scotese, PALEOMAP Project (www.scotese.com), Scotese 2001).

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