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Phylogenomics and historical biogeography of the monocot order Liliales: out of Australia and through Antarctica

Thomas J. Givnish[a,*], Alejandro Zuluaga[a,b], Isabel Marques[c,d], Vivienne K. Y. Lam[c], Marybel Soto Gomez[c], William J. D. Iles[e], Mercedes Ames[a], Daniel Spalink[a], Jackson R. Moeller[a], Barbara G. Briggs[f], Stephanie P. Lyon[a], Dennis W. Stevenson[g], Wendy Zomlefer[h] and Sean W. Graham[c]

[a]*Department of Botany, University of Wisconsin-Madison, Madison, WI 53706, USA;* [b]*Departamento de Biología, Universidad del Valle, Cali, Colombia;* [c]*Department of Botany, University of British Columbia, Vancouver, Canada, V6T 1Z4;* [d]*Department of Agriculture (Botany), High Polytechnic School of Huesca, University of Zaragoza, Carretera de Cuarte Km 1, Huesca E22071, Spain;* [e]*University and Jepson Herbaria, University of California-Berkeley, Berkeley, CA 94720, USA;* [f]*Botanic Gardens Trust, Sydney, NSW 2000, Australia;* [g]*New York Botanical Garden, New York, NY 10458, USA;* [h]*Department of Plant Biology, University of Georgia, Athens, GA 30602, USA*

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Abstract

We present the first phylogenomic analysis of relationships among all ten families of Liliales, based on 75 plastid genes from 35 species in 29 genera, and 97 additional plastomes stratified across angiosperm lineages. We used a supermatrix approach to extend our analysis to 58 of 64 genera of Liliales, and calibrated the resulting phylogeny against 17 fossil dates to produce a new timeline for monocot evolution. Liliales diverged from other monocots 124 Mya and began splitting into separate families 113 Mya. Our data support an Australian origin for Liliales, with close relationships between three pairs of lineages (Corsiaceae/Campynemataceae, Philesiaceae/Ripogonaceae, tribes Alstroemerieae/Luzuriageae) in South America and Australia or New Zealand reflecting teleconnections of these areas via Antarctica. Long-distance dispersal (LDD) across the Pacific and Tasman Sea led to re-invasion of New Zealand by two lineages (*Luzuriaga, Ripogonum*); LDD allowed *Campynemanthe* to colonize New Caledonia after its submergence until 37 Mya. LDD permitted Colchicaceae to invade East Asia and Africa from Australia, and re-invade Africa from Australia. Periodic desert greening permitted *Gloriosa* and *Iphigenia* to colonize Southeast Asia overland from Africa, and *Androcymbium–Colchicum* to invade the Mediterranean from South Africa. Melanthiaceae and Liliaceae crossed the Bering land-bridge several times from the Miocene to the Pleistocene.

Introduction

The order Liliales as now circumscribed is a group of ten families, 64 genera, and ~1500 species (APG, 2009; Stevens, 2015). Most members of the order have tepal nectaries and extrorse anthers, but exceptions exist (e.g. nectaries absent or septal in some Melanthiaceae; anthers introrse in Campynemataceae, Colchicaceae, and some Alstroemeriaceae, Melanthiaceae, Philesiaceae, Ripogonaceae and Smilacaceae) (Stevens, 2015). The difficulty in identifying unreversed morphological synapomorphies that characterize Liliales is reflected in the quite different sets of families included in the order by Cronquist (1981), Dahlgren et al. (1985) and Thorne (1992). Their circumscriptions share only the family Liliaceae, which was much more widely defined by Cronquist. The current circumscription of Liliales is based on DNA sequence data, and even that has changed across different Angiosperm Phylogeny Group classification schemes (APG, 1998, 2003, 2009), with Corsiaceae only recently included in the order, Petermanniaceae

*Corresponding author:
E-mail address: givnish@wisc.edu

accepted as a family and Luzuriagaceae sunk in Alstroemeriaceae. The ten families now included in Liliales form a clade in the analyses of Fay et al. (2006), Petersen et al. (2013) and Mennes et al. (2015), but Kim et al. (2013) placed mycoheterotrophic Corsiaceae outside Liliales based on four plastid loci sequenced across 49 genera. Kim et al. (2013) included only one locus for Corsiaceae, however, and their data appear to be a contaminant sequence (Mennes et al., 2015).

Although there is substantial molecular support for the monophyly of Liliales, five areas of uncertainty regarding relationships within the order remain:

1. Relationships within Liliaceae. This family is by far the largest (610 spp.) in the order (Stevens, 2015), and subsumes extensive floral and vegetative variation and extraordinary range in genome size (Patterson and Givnish, 2002; Leitch et al., 2007). Patterson and Givnish (2002) found strong support for *Clintonia* and *Medeola* being sister to each other, and jointly sister to the remainder of Liliaceae *s.s.* based on plastid *rbcL* and *ndhF* sequences, and similar relationships have been documented by all other studies with a broad sampling of taxa (Givnish et al., 2005; Fay et al., 2006; Kim et al., 2013; Petersen et al., 2013). However, relationships among the five genera of Liliaceae outside this core group—Calochortaceae *sensu* Tamura (1998)—have varied among studies; the placements of *Calochortus* and *Tricyrtis* have proven unstable. Patterson and Givnish (2002) placed these two genera sister to each other, and jointly sister to a clade formed by *Streptopus, Prosartes* and *Scoliopus,* with all five then sister to core Liliaceae. Fay et al. (2006) analysed sequences for five plastid loci and *atp1* from the mitochondria to infer that *Tricyrtis* was sister to the core Liliaceae and *Calochortus* sister to the *Streptopus* clade, albeit with low support in both cases. Petersen et al. (2013) used sequences of plastid *ndhF* and *rbcL* and mitochondrial *atp1, cob* and *nad5* to place *Calochortus–Tricyrtis*, the *Streptopus* clade, and the core Liliaceae in an unresolved trichotomy. Kim et al. (2013) used sequences from four plastid loci to place *Calochortus* sister to core Liliaceae, *Tricyrtis* sister to the *Streptopus* clade and the last group of four genera sister to *Calochortus* plus core Liliaceae; support for the position of *Calochortus* was, however, quite weak. Mennes et al. (2015) used a Bayesian analysis of nuclear 18S rDNA and four mitochondrial loci to place *Calochortus* sister to *Clintonia* + *Lilium*, and *Tricyrtis* sister to all three, all with high support but excluding all other genera of the family. Differences in taxon sampling and phylogenetic techniques may both have contributed to the different inferences reached by the studies mentioned.

2. Relationships among the vine families. Several studies have placed Smilacaceae sister to Liliaceae, with Philesiaceae and Ripogonaceae sister to each other, and jointly sister to Liliaceae plus Smilacaceae (Patterson and Givnish, 2002; Givnish et al., 2005; Chase et al., 2006; Fay et al., 2006; Petersen et al., 2013; Mennes et al., 2015), often with strong support for all three nodes. However, Vinnersten and Bremer (2001) and Kim et al. (2013) concluded that the vine families formed a clade rather than a grade, with Smilacaceae sister to Philesiaceae-Ripogonaceae.

3. Placement of Melanthiaceae vs. Colchicaceae plus Alstroemeriaceae. With sparse taxon sampling, Patterson and Givnish (2002) placed Melanthiaceae sister to Liliaceae plus the vine families, but with low bootstrap support, with Colchicaceae sister to Alstroemeriaceae with 100% support; the latter two families were sister to all families of the order sampled except Campynemataceae. Fay et al. (2006) instead placed Colchicaceae–Alstroemeriaceae sister to Petermanniaceae, and both sister to Liliaceae plus the vine families, but with weak support in both cases. They found 98% bootstrap support for *Luzuriaga*, one of two genera of Luzuriagaceae, as the sister group of Alstroemeriaceae, which led APG (2009) to sink Luzuriagaceae in the latter. Mennes et al. (2015) resolved a similar topology with a five-locus Bayesian analysis, but the placement of this trio of families disappeared under maximum likelihood (ML). Petersen et al. (2013) found that Melanthiaceae, Alstroemeriaceae–Colchicaceae–Petermanniaceae and Liliaceae plus the vine families form an unresolved trichotomy, while Kim et al. (2013) inferred that Melanthiaceae–Petermanniaceae was sister to that core group, with Colchicaceae–Alstroemeriaceae sister to that broader combination.

4. Placement of Petermanniaceae. Chase et al. (2006), Fay et al. (2006), Graham et al. (2006), Petersen et al. (2013) and Mennes et al. (2015) placed the single species of *Petermannia* sister to Colchicaceae–Alstroemeriaceae, whereas Kim et al. (2013) placed *Petermannia* sister to Melanthiaceae. Mennes et al. (2015) also placed *Petermannia* as sister to Colchicaceae–Alstroemeriaceae in their five-locus Bayesian analysis, but this placement vanished in their ML analysis. Earlier studies generally did not include *Petermannia* or included a misidentified sample (see Chase et al., 2006; Graham et al., 2006).

5. Placement of Corsiaceae. Fay et al. (2006) placed the single species of Corsiaceae that they studied (*Arachnitis uniflora*) in a basal trichotomy with Campynemataceae and all other Liliales. Petersen et al. (2013) inferred instead that *Arachnitis* was sister to *Campynema* plus all other Liliales, and Kim et al.

(2013) placed *Arachnitis* entirely outside Liliales, Asparagales, Dioscoreales and the commelinid orders. Neyland and Hennigan (2003) used 26S rRNA gene sequences to place *Arachnitis* in Dioscoreales and *Corsia* sister to *Campynema* in Liliales, making Corsiaceae polyphyletic and increasing the mystery of its phylogenetic position. Mennes et al. (2015) used an analysis of nuclear and mitochondrial DNA sequences to place *Corsia* and *Arachnitis* sister to each other, both sister to *Campynema* and *Campynemanthe*, and all four sister to the remaining Liliales, with these relationships all having strong support; they also found this relationship with a plastid data set, although their family-level sampling was limited.

Vinnersten and Bremer (2001) used DIVA (Ronquist, 1997) to reconstruct the historical biogeography of Liliales, and concluded that the group arose in North and South America, Australia and New Caledonia roughly 82 Mya. Bremer and Janssen (2006) used a parsimony approach to infer that most monocot groups, including Liliales, arose in southern Gondwana. These analyses, however, were based on phylogenies that were weakly supported, a narrow set of monocot fossils, and somewhat unsophisticated analytical techniques. Mennes et al. (2015) used two to six fossils and more sophisticated dating using BEAST (Drummond et al., 2012) to estimate the crown age of Liliales as 90 ± 16 Mya, but did not conduct any formal analysis of historical biogeography. Chacón et al. (2012) used a relaxed clock and up to three fossil calibrations to reconstruct repeated movement of Alstroemeriaceae across the southern Pacific, but did not extend their analysis to many related groups.

To address the remaining uncertainties in the phylogeny, age and historical biogeography of Liliales, we present a phylogenomic analysis of relationships within the order here, based on 75 genes drawn from 35 plastomes representing 29 genera and all ten families of Liliales, and employing data from 97 more plastomes stratified across all monocot orders and other major lineages of angiosperms. We use 17 fossils to calibrate our molecular phylogeny against time, and extend this new timeline for monocot evolution to 58 of 64 genera of Liliales using a supermatrix analysis. Finally, we use the supermatrix phylogeny to infer the historical biogeography of Liliales, and use it to infer patterns of intercontinental dispersal in relation to events in Earth history.

Methods

Plastid phylogenomic analyses

Taxon sampling. We included 35 species of Liliales in our plastome study, representing 29 genera stratified across all ten families of the order (Table 1). New draft plastomes were generated for 19 of these taxa. We included plastome data for another 79 species stratified across all 12 monocot orders and 21 representatives of all major groups of eudicots and other major angiosperm lineages. We used *Amborella*, the sister group of all other angiosperms in most analyses (Jansen et al., 2007; Moore et al., 2007; Drew et al., 2014) as the outgroup.

Plastome sequencing. We used next-generation sequencing to produce plastid genome sequences. Total genomic DNA was extracted from fresh or silica-dried leaf tissue using DNeasy plant mini kits (Qiagen, Valencia, CA, USA) or a modified CTAB protocol (Rai et al., 2003). Depending on the quality and quantity of available genomic DNA, we made libraries with a BIOO Nextflex DNA sequencing kit, a BIOO Nextflex Rapid DNA sequencing kit (BIOO Scientific Corp., Austin, TX, USA) or a NuGEN Ovation Ultralow Library System (NuGEN Technologies, San Carlos, CA, USA). Sequencing of 100-bp paired-end reads was performed on an Illumina HiSeq 2000 platform (Illumina, San Diego, CA, USA).

Assembly of plastomes from resulting reads was performed using a pipeline based on the reference-based assembler YASRA (Ratan, 2009; www.bx.psu.edu/miller_lab), and Velvet (Zerbino and Birney, 2008) or the CLC Genomics Workbench 7.0.3 (www.clcbio.com) for *de novo* assemblies. Contigs from both analyses were aligned together using MAFFT v7.0 (Katoh and Kuma, 2002) as implemented in Geneious v7.1.2 (www.geneious.com) to produce longer contigs. These longer contigs were mapped to the *Lilium longiflorum* plastome in GenBank to create a plastome draft for each species. Disagreements between the two assemblies were very limited and resolved by mapping back the original reads to the resulting exon sequences using BOWTIE 2 (Langmead and Salzberg, 2012). Final annotation was confirmed and gene sequences were extracted using the DOGMA webserver (Wyman et al., 2004) with additional manual inspection using Sequencher v. 4.8 (GeneCodes, Ann Arbor, MI, USA). Individual gene alignments were conducted using MUSCLE (Edgar, 2004) and ClustalW (Larkin et al., 2007) as implemented in Geneious v. 7.1.2 (www.geneious.com), and then concatenated for phylogenetic analysis. Gaps were treated as missing data. Individual exons were uploaded to GenBank (Table 1).

Phylogenomic analyses. We derived phylogenies from 75 genes from the plastome data set (Table S1) under maximum parsimony (MP) and ML. MP analyses were conducted in PAUP* version 4b10

Table 1
Taxa for which plastome data were included in this study; voucher data are indicated for this study, voucher data for other sequences are provided in the original reports cited. Aligned data for all species, including those newly sequenced for this, will be deposited in Dryad

Major clade	Order	Family	Species	Citation or GenBank accession numbers	Voucher data (this study)
Basal angiosperms	Amborellales	Amborellaceae	*Amborella trichopoda* Baill.	Goremykin et al., 2003a	
	Austrobaileyales	Schisandraceae	*Illicium oligandrum* Merr. & Chun	Hansen et al., 2007	
	Nymphaeales	Nymphaeaceae	*Nuphar advena* Aiton	Raubeson et al., 2007	
Magnoliids	Canellales	Winteraceae	*Drimys granadensis* L. f.	Cai et al., 2006;	
	Laurales	Calycanthaceae	*Calycanthus floridus* L.	Goremykin et al., 2003b	
	Magnoliales	Magnoliaceae	*Liriodendron tulipifera* L.	Cai et al., 2006	
	Piperales	Piperaceae	*Piper cenocladum* Diels	Cai et al., 2006	
Eudicots	Apiales	Apiaceae	*Anethum graveolens* L.	Jansen et al., 2007	
	Apiales	Araliaceae	*Panax ginseng* C. A. Mey	Kim and Lee, 2004	
	Asterales	Asteraceae	*Helianthus annuus* L.	Jansen et al., 2007	
	Buxales	Buxaceae	*Buxus microphylla* Siebold & Zucc.	Hansen et al., 2007	
	Caryophyllales	Amaranthaceae	*Spinacia oleracea* L.	Schmitz-Linneweber et al., 2001	
	Cucurbitales	Cucurbitaceae	*Cucumis sativus* L.	Plader et al., 2007	
	Fabales	Fabaceae	*Medicago truncatula* Gaertn.	Matsushima et al., 2008	
	Gentianales	Rubiaceae	*Coffea arabica* L.	Samson et al., 2007	
	Malpighiales	Salicaceae	*Populus alba* L.	Okumura et al., 2006	
	Proteales	Platanaceae	*Platanus occidentalis* L.	Moore et al., 2006	
	Ranunculales	Berberidaceae	*Nandina domestica* Thunb.	Raubeson et al., 2007	
	Vitales	Vitaceae	*Vitis vinifera* L.	Jansen et al., 2006	
Monocots	Acorales	Acoraceae	*Acorus americanus* (Raf.) Raf.	Givnish et al., 2010	
			Acorus calamus L.	Goremykin et al., 2005	
	Alismatales	Araceae	*Colocasia esculenta* (L.) Schott	Ahmed et al., 2012	
			Lemna minor L.	Mardanov et al., 2008	
			Wolffia australiana (Benth.) Hartog & Plas	Wang and Messing, 2009	
		Hydrocharitaceae	*Elodea canadensis* Michx.	Huotari and Korpelainen, 2012	
			Najas flexilis (Willd.) Rostk. & W. L. E. Schmidt	Peredo et al., 2013	
	Arecales	Arecaceae	*Bismarckia nobilis* Hillebrandt & H. Wendl.	Barrett et al., 2013	
			Calamus caryotoides A. Cunn ex Mart	Barrett et al., 2013	
			Chamaedorea seifrizii Burret	Givnish et al., 2010	
			Elaeis oleifera (Kunth) Cortés	Leebens-Mack et al., 2005	
			Pseudophoenix vinifera (Mart.) Becc.	Barrett et al., 2013	
			Ravenea hildebrandtii C. D. Bouché	Givnish et al., 2010	
	Asparagales	Amaryllidaceae	*Agapanthus praecox* Willd.	Givnish et al., 2010	
		Asparagaceae	*Albuca kirkii* (Baker) Brenan	Givnish et al., 2010	
			Asparagus officinalis L.	Givnish et al., 2010	
			Chlorophytum rhizopendulum Bjorå & Hemp	Givnish et al., 2010	
			Hesperaloe parviflora (Torr.) J. M. Coult.	Givnish et al., 2010	
			Hosta ventricosa (Salisb.) Stearn	Givnish et al., 2010	
			Lomandra longifolia Labill.	Givnish et al., 2010	

Table 1
(Continued)

Major clade	Order	Family	Species	Citation or GenBank accession numbers	Voucher data (this study)
			Nolina atopocarpa Bartlett	Givnish et al., 2010	
			Yucca schidigera Ortgies	Givnish et al., 2010	
		Asteliaceae	*Neoastelia spectabilis* J. B. Williams	Givnish et al., 2010	
		Hypoxidaceae	*Curculigo capitulata* (Lour.) Kuntze	Givnish et al., 2010	
		Iridaceae	*Iris virginica* L.	Givnish et al., 2010	
		Orchidaceae	*Apostasia wallichii* R. Br.	Givnish et al., 2010	
			Dactylorhiza fuchsii (Druce) Soó	Givnish et al., 2015	
			Phalaenopsis aphrodite Rchb. f.	Chang et al., 2006	
			Phragmipedium longifolium (Warsz. & Rchb. F.) Rolfe	Givnish et al., 2015	
			Vanilla planifolia Jacks. Ex Andrews	Givnish et al., 2015	
		Xanthorrhoeaceae	*Phormium tenax* J. R. Forst. & G. Forst.	Givnish et al., 2010	
	Commelinales	Commelinaceae	*Belosynapsis ciliata* (Blume) R. S. Rao	Givnish et al., 2010	
			Tradescantia ohiensis Raf.	Givnish et al., 2010	
		Haemodoraceae	*Xiphidium caeruleum* Aubl.	Barrett et al., 2013	
	Dasypogonales	Dasypogonaceae	*Dasypogon bromeliifolius* R. Br.	Givnish et al., 2010	
			Kingia australis R. Br.	Givnish et al., 2010	
	Dioscoreales	Dioscoreaceae	*Dioscorea elephantipes* (L'Hér.) Engl.	Hansen et al., 2007	
		Nartheciaceae	*Lophiola aurea* Ker Gawl.	Lam et al., 2015	
	Liliales	Alstroemeriaceae	*Alstroemeria aurea* Graham	Kim and Kim, 2013	
			Alstroemeria longistaminea Mart.	KU302816-93	Zomlefer et al. 2312 (NY)
			Bomarea sp. 878	KU302970-3046	Telos Rare Bulbs
			Drymophila moorei Baker	KU303651-726	Briggs 10023 (NSW)
			Luzuriaga radicans Ruiz & Pav.	Kim et al. (NC_025333)	
		Campynemataceae	*Campynema linearis* Labill.	Mennes et al. (2015)	MF Duretto 1842 (HO)
			Campynemanthe viridiflora Baill.	KU303580-650	Pillon, Barrabé, Maudet, Richard & Dumontet 24 (NOU)
		Colchicaceae	*Burchardia umbellata* R.Br.	KU304026-102	Stevenson 3458 (NY)
			Uvularia grandiflora Sm.	KU303354-430	Ames & Givnish v0305422 (WIS)
			Uvularia sessilifolia L.	KU303431-504	Alverson DOB 9522013 (WIS)
			Wurmbea pygmaea (Endl.) Benth.	KU303505-79	A Case 77 (PERTH)
		Corsiaceae	*Arachnitis uniflora* Phil.	Mennes et al. (2015)	R Neyland 1928 (MCN)
			Corsia cf. boridiensis P.Royen	Mennes et al. (2015)	S Lyon SPL470-2 PNG (L)
		Liliaceae	*Calochortus albus* (Benth.) Douglas ex Benth.	KU303047-123	Patterson 13 (WIS)
			Clintonia borealis (Aiton) Raf.	KU303124-200	Givnish v0305424 (WIS)
			Fritillaria cirrhosa D. Don	Li et al., 2014	
			F. taipaiensis P. Y. Li	Li et al., 2014	
			F. hupehensis P. K. Hsiao & K. C. Hsia	Li et al., 2014	
			Lilium longifolium Thunb.	Kim et al., 2013	
			L. superbum L.	Givnish et al., 2010	
			Medeola virginiana L.	KU303799-873	Patterson 1065 (WIS)
			Prosartes lanuginosa (Michx.) D. Don	KU304179-255	Givnish v0305423 (WIS)
			Tricyrtis macropoda Miq.	KU303874-949	B Zhuang UBCBG-33743 (UBC)
			Tulipa pulchella (Regel) Baker	KU303278-353	Patterson 1066 (WIS)

Table 1
(Continued)

Major clade	Order	Family	Species	Citation or GenBank accession numbers	Voucher data (this study)
		Melanthiaceae	*Amianthium muscaetoxicum*	KU302894-969	Zomlefer 716 (FLAS)
			Chionographis japonica (Willd.) Maxim.	Bodin et al., 2013	
			Paris verticillata M. Bieb.	Do et al., 2014	
			Trillium luteum (Muhl.) Harb.	KU303950-4025	Givnish (WIS)
			Veratrum patulum O. Loes.	Do et al., 2013	
		Petermanniaceae	*Petermannia cirrosa* F. Muell.	KU304256-331	Briggs 10019 (NSW)
		Philesiaceae	*Lapageria rosea* Ruiz & Pav.	KU303727-798	Hollermayer 188 (UC)
			Philesia buxifolia Lam. ex Poir.	KU303201-77	Chase 545 (K)
		Ripogonaceae	*Ripogonum album* R. Br.	KU304103-78	Briggs 10014 (NSW)
		Smilacaceae	*Smilax china* L.	Liu et al., 2012	
	Pandanales	Cyclanthaceae	*Cyclanthus bipartitus* Poit. ex. A. Rich	Lam et al., 2015	
		Pandanaceae	*Freycinetia banksii* A. Cunn	Lam et al., 2015	
			Pandanus utilis Bory	Givnish et al., 2010	
		Velloziaceae	*Xerophyta retinervis* Baker	Lam et al., 2015	
	Petrosaviales	Petrosaviaceae	*Japonolirion osense* T. Nakai	Davis et al., 2013	
			Petrosavia stellaris Becc.	Logacheva et al., 2014	
	Poales	Bromeliaceae	*Brocchinia micrantha* (Baker) Mez	Givnish et al., 2010	
			Fosterella caulescens Rauh	Givnish et al., 2010	
			Navia saxicola L. B. Sm.	Givnish et al., 2010	
			Neoregelia carolinae (Beer) L. B. Sm. 'Argentea'	Givnish et al., 2010	
			Pitcairnia feliciana (A. Chev.) Harms & Mildbr.	Givnish et al., 2010	
			Puya laxa L. B. Sm.	Givnish et al., 2010	
		Centrolepidaceae	*Centrolepis monogyna* Benth.	Givnish et al., 2010	
		Cyperaceae	*Cyperus alternifolius* L.	Givnish et al., 2010	
			Mapania palustris (Hassk. Ex Steud.) Fern.-Vill.	Leebens-Mack JLM3024 (GA)	
		Ecdeiocoleaceae	*Ecdeiocolea monostachya* F. Muell.	Givnish et al., 2010	
			Georgeantha hexandra B. G. Briggs & L. A. S. Johnson	Givnish et al., 2010	
		Eriocaulaceae	*Syngonanthus chrysanthus* Ruhland	Givnish et al., 2010	
		Flagellariaceae	*Flagellaria indica* L.	Givnish et al., 2010	
		Joinvilleaceae	*Joinvillea ascendens* Gaudich. ex Brongn. & Gris	Givnish et al., 2010	
			Joinvillea plicata (Hook. f.) Newell & B. C. Stone	Leseberg and Duvall, 2009	
		Juncaceae	*Juncus effusus* L.	Givnish et al., 2010	
		Mayacaceae	*Mayaca fluviatilis* Aubl.	Givnish et al., 2010	
		Poaceae	*Agrostis stolonifera* L.	Saski et al., 2007	
			Anomochloa marantoidea Brongn.	Morris and Duvall, 2010	
			Bambusa oldhamii Munro	Wu et al., 2009	
			Eleusine coracana (L.) Gaertn.	Givnish et al., 2010	
			Hordeum vulgare L.	Saski et al., 2007	
			Oryza sativa L.	Hiratsuka et al., 1989	

Table 1
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Major clade	Order	Family	Species	Citation or GenBank accession numbers	Voucher data (this study)
			Puelia olyriformis (Franch.) Clayton	Givnish et al., 2010	
			Saccharum officinarum L.	Asano et al., 2004	
			Sorghum bicolor (L.) Moench	Saski et al., 2007	
			Streptochaeta angustifolia Soderstr.	Givnish et al., 2010	
			Triticum aestivum L.	Ogihara et al., 2002	
			Zea mays L.	Maier et al., 1995	
		Rapateaceae	*Potarophytum riparium* Sandwith	Givnish et al., 2010	
		Restionaceae	*Thamnochortus insignis* Mast.	Givnish et al., 2010	
		Sparganiaceae	*Sparganium eurycarpum* Engelm.	Givnish et al., 2010	
		Thurniaceae	*Thurnia sphaerocephala* Hook. f.	Givnish et al., 2010	
		Typhaceae	*Typha latifolia*	Guisinger et al., 2010	
		Xyridaceae	*Abolboda macrostachya* Spruce ex Malme	Givnish et al., 2010	
	Zingiberales	Cannaceae	*Canna indica* L.	Barrett et al., 2014	
		Heliconiaceae	*Heliconia collinsiana* Griggs	Barrett et al., 2013	
		Musaceae	*Musa acuminata* Colla	Leebens-Mack et al., 2005	
		Zingiberaceae	*Renealmia alpinia* (Rottb.) Maas	Givnish et al., 2010	

(Swofford, 2003), with 1000 bootstrap replicates to assess the relative degree of support for individual nodes. ML analyses were conducted in RAxML v. 8.0.9 (Stamatakis, 2014), using the GTRCAT approximation in the CIPRES Science Gateway (Miller et al., 2010). We used this simplified approach to make computations tractable, and acknowledge the recent caution by Simmons and Norton (2014) on the possibility of inflated support values arising from this method. We assessed tree topology using ten "thorough" optimizations *sensu* Stamatakis (2014), which all yielded the same most likely tree. We assessed bootstrap support using 1000 replicate resamplings of the data matrix. For ML analyses, we used PartitionFinder (Lanfear et al., 2012) with Akaike's information criterion (AIC) to select the best-fit partitioning schemes and models among those available in RAxML. Partitioning splits sites into sets that appear to have evolved under different models; fitting different ML models to these sets, rather than using a single model for all, is thought to improve phylogenetic inference (Lanfear et al., 2012). We initially coded each gene as an independent data block. Our set of 75 genes is based on the 81 genes used by Jansen et al. (2007) and Givnish et al. (2010), but excluding the four rDNA loci, as well as *accD* (not present in several samples, or present as a pseudogene impossible to align across angiosperms) and *ycf1* (often hard to retrieve). Preliminary analyses including and excluding partial data for *ycf1* produced the same topology.

Plastid supermatrix analysis

To increase sampling of key Liliales lineages, we assembled a second dataset consisting of two plastid regions (*matK* and *rbcL*) downloaded from GenBank for 146 more species of Liliales (Table S2). These sequences were combined with the plastome data to construct a supermatrix of 281 species, including representatives of 58 of the 64 genera of Liliales; 22 of the 58 genera were represented by single species. Data for the other 73 plastid genes for these additional species were treated as missing (Soltis et al., 2013; Givnish et al., 2014). We excluded *Arachnitis* due to its extremely long branch, which would probably have distorted estimates of branch ages in nearby parts of the supermatrix tree. Long branch lengths in Corsiaceae (and especially in *Arachnitis)* reflect the effect of mycoheteroptrophy on the rate of molecular evolution on retained plastid genes in this achlorophyllous family (Mennes et al., 2015). Individual gene alignments, data concatenation and ML phylogenetic analyses were conducted as with the plastome data. A total of 24.7% of the data were missing in the plastome data set; 63.5% were missing in the supermatrix.

Divergence times

We estimated divergence times among inferred ancestors in a Bayesian framework using BEAST v1.8.0 (Drummond and Rambaut, 2007; Drummond et al., 2012) using the supermatrix taxa. Given computational limitations and concerns about the effects of missing data on divergence time estimates, we conducted analyses based only on the two plastid coding regions (*matK, rbcL*) shared by all taxa (only *matK* present in *Corsia*). We used the ML tree from the supermatrix analysis as a topological constraint to retain the relationships recovered in the total evidence analysis, thereby restricting the Markov chain Monte Carlo exploration to parameters associated with branch length by unselecting the tree arrangement operators in BEAUti (Drummond and Rambaut, 2007; Drummond et al., 2012). We used an uncorrelated, relaxed lognormal clock, a Yule branching process, and unlinked site and clock models for the two plastid genes. Models of nucleotide substitution were selected for each gene region using the Bayesian information criterion in jModelTest 2.1.4 (Guindon and Gascuel, 2003; Darriba et al., 2012). These were identified as GTR + I + G for *rbcL* and *matK*.

A total of 17 fossils were utilized as calibration priors, with offsets corresponding to their minimum estimated ages (Table 2). All fossil priors were assigned a lognormal distribution (SD = 2), accounting for uncertainty in both absolute fossil age estimation and phylogenetic placement. Priors were also placed on the rosid and magnoliid crowns and the crown node of the Caryophyllales + asterids. Due to a lack of fossils easily attributed to these clades, normal priors were placed on these nodes with mean offsets and 95% confidence intervals mirroring the posterior ages from the exponential clock analysis of Bell et al. (2010). Finally, uniform priors were placed on the root node and the stem of *Illicium* based on the best practices described by Sytsma et al. (2014), who demonstrated the importance of root calibrations for divergence time estimations. Sytsma et al. (2014) found that providing a broad prior on the rosid stem was essential to obtaining realistic dates of origin for the rosid orders. Following their recommended best practices, the XML file used in these analyses and the aligned data have been archived in Dryad (http://dx.doi.org/10.5061/dryad.mc736). Two independent chains of 100 000 000 generations were run simultaneously on CIPRES, with samples logged every 10 000 generations. Effective sample sizes of all parameters were calculated and convergence among chains was visualized in Tracer v1.5 (Rambaut and Drummond, 2009). Tree files from the independent chains were combined after removing 25% as burn-in, and annotated using TreeAnnotator v1.8.0 (Drummond and Rambaut, 2007; Drummond

Table 2
Priors and offsets used to calibrate the supermatrix tree

Node	Prior*	Offset or mean	SD or range	Source
1. Poaceae PACMAD stem (crown of *Bambusa* through *Triticum*)	L	66	2	Iles et al. (2015); Prasad et al. (2011)
2. Poaceae subfamily Pooideae crown (*Agrostis, Hordeum, Triticum*)	L	40	2	Iles et al. (2015); Prasad et al. (2011)
3. Poaceae *Leersia* stem (crown of *Leersia* and *Oryza*)	L	30.44	2	Iles et al. (2015)
4. Typhaceae crown (*Sparganium, Typha*)	L	70	2	Iles et al. (2015); Givnish et al. (2005, 2010); Sulman et al. (2013)
5. Arecaceae subfamily Coryphoideae stem (crown of *Elaeis, Chamedorea, Ravenea, Pseudophoenix, Bismarckia*)	L	83.6	2	Iles et al. (2015)
6. Zingiberales crown	L	83	2	Iles et al. (2015)
7. Asparagaceae *Yucca* stem (crown of *Yucca, Hesperaloe*)	L	14.5	2	Iles et al. (2015)
8. Hemerocallidaceae stem (crown of *Xanthorrhoea* and *Phormium*)	L	38	2	Iles et al. (2015)
9. Ripogonaceae: *Ripogonum, Philesia, Lapageria*	L	51	2	Iles et al. (2015)
10. Cyclanthus stem (*Cyclanthus* through *Freycenettia*	L	47	2	Iles et al. (2015)
11. Araceae subfamily Lemnoideae stem (stem of *Lemna, Wolffia*)	L	66	2	Iles et al. (2015)
12. Monocot stem	L	113	1.5	Iles et al. (2015)
13. Caryophllales+Asterids crown	N	111	100–122	Bell et al. (2010)
14. Rosid crown (*Vitis, Populus, Cucumis, Medicago*)	N	114.5	97–132	Bell et al. (2010)
15. Magnoliid crown	N	123	108–138	Bell et al. (2010)
16. *Illicium* stem	U	144	138–150	Bell et al. (2010)
17. Root (stem of all—*Amborella*)	U	147.5	141–154	Bell et al. (2010)

*L, lognormal; N, normal; U, uniform.

et al., 2012) to construct the maximum clade credibility chronogram.

Historical biogeography

Ancestral area reconstruction (AAR) was conducted with an ML approach using the recently developed program BioGeoBEARS (Matzke, 2013a,b). BioGeoBEARS incorporates a founder-event parameter (the "J-parameter"), which allows for simultaneous dispersal and cladogenetic events where daughter lineages inhabit unique areas disjunct from their parental lineages. This option is not present in other popular AAR models, such as DEC (dispersal–extinction–cladogenesis analysis: Ree and Smith, 2008), S-DIVA (statistical dispersal–vicariance analysis: Yu et al., 2010) or BayArea (Bayesian ancestral area reconstruction: Landis et al., 2013), but simulation studies have demonstrated its ability to significantly improve reconstruction likelihoods in many cases (Matzke, 2014). To test the influence of the J-parameter on reconstructions in Liliales, we conducted two independent runs in BioGeoBEARS, including DEC and DEC+J analyses. Likelihood ratio tests of corrected AIC (AICc) scores were conducted on the nested models in BioGeoBEARS to measure overall model fits.

All analyses were conducted on a pruned version of the BEAST chronogram, limiting sampling within Liliales to a single species per genus. We grafted *Arachnitis* onto that tree, at a distance above the Corsiaceae stem proportional to the distance from it to the end of the *Corsia* branch in the supermatrix ML phylogram. All terminal taxa were coded as present/absent in nine geographical areas, including (1) **Eastern North America**, (2) **Western North America** (including northern Mexico), (3) **Neotropics** (South America to southern Mexico), (4) **Eurasia** (including Europe and northern Asia), (5) **Africa**, (6) **Himalayas** (which did not exist prior to the collision of India with the rest of Asia, (7) **Southeast Asia**, (8) **East Asia** (China, Korea, Japan) and (9) **Australia** (including New Guinea and nearby islands thrown up by the collision of the Australian and Pacific Plates, as well as smaller rafts fragmented from the Australian Plate or Gondwana, i.e. New Caledonia and New Zealand). This atomization was based partly on known areas of endemism for individual genera or families of Liliales, the existence of water barriers between several of the continental regions and the need for a small number of regions to permit efficient operation of BioGeoBEARS. Relative dispersal probabilities among areas were constrained based on area availability (particularly for oceanic Pacific islands) and distances and water barriers between areas during six time slices: 0–2, 2–8, 8–30, 30–60, 60–90 and 90–150 Mya (Table S3). For genera having broad distributions, we attempted to identify ancestral areas using previously published analyses. Using this approach, we coded *Lilium* as Eastern Asia (Thomas J. Givnish, unpubl. data), *Schoenocaulon* as Neotropics (Zomlefer et al., 2006) and *Toxicoscordion* as Western North America (Zomlefer et al., 2001). We were unable to resolve a small number of ancestral areas for Smilacaceae based on Qi et al. (2013).

Results

Phylogenomic analyses

The plastome dataset included 78 826 aligned bases for 135 taxa and 75 genes. ML yielded a single tree and recovered monophyly for the monocots as a whole, each monocot order and all families of Liliales represented by more than one species with 100% bootstrap support (Fig. 1). Eudicots were sister to *Ceratophyllum* among the non-monocots sampled, with 99% bootstrap support under ML; together they formed the sister clade to the monocots, with 80% bootstrap support. Among the commelinid orders, Poales was resolved as sister to Commelinales + Zingiberales, and Arecales as sister to Dasypogonales, with the last relationship only moderately well supported. Acorales was sister all other monocots, Alismatales sister to the remaining orders, then Petrosaviales, Dioscoreales + Pandanales and Liliales, with Asparagales sister to the commelinids; each of these relationships had 100% bootstrap support, and 100 of 112 nodes within the monocots had bootstrap support ≥ 97% (Fig. 1). Within Liliales, Liliaceae *s.s.*—the clade subtended by *Clintonia–Medeola*—had 100% bootstrap support; *Tricyrtis* was sister to this clade with 82% bootstrap support, *Calochortus* was sister to *Prosartes* with 87% bootstrap support and Liliaceae as a whole had 100% support. Smilacaceae was sister to Liliaceae with < 50% support; Philesiaceae was sister to Ripogonaceae, with 100% bootstrap support for it and the clade formed by them, Smilacaceae and Liliaceae. Melanthiaceae was sister to Liliaceae plus the vine families with 100% bootstrap support. Alstroemeriaceae was sister to Colchicaceae, with Alstroemeriaceae *s.s.* (tribe Alstroemerieae) sister to the former Luzuriagaceae (tribe Luzuriageae); *Petermannia* was sister to all of these, and Alstroemeriaceae + Colchicaceae + Petermanniaceae were sister to the previously named families, all with 100% bootstrap support. Finally, Corsiaceae was sister to Campynemataceae, and the resulting clade sister to all other Liliales, all with 100% bootstrap support (Fig. 1). The ML partition analysis produced ten data partitions from the 75 genes input, and yielded the same branching topology as the unpartitioned analysis, with only small differences in branch lengths and support values (Fig. S1).

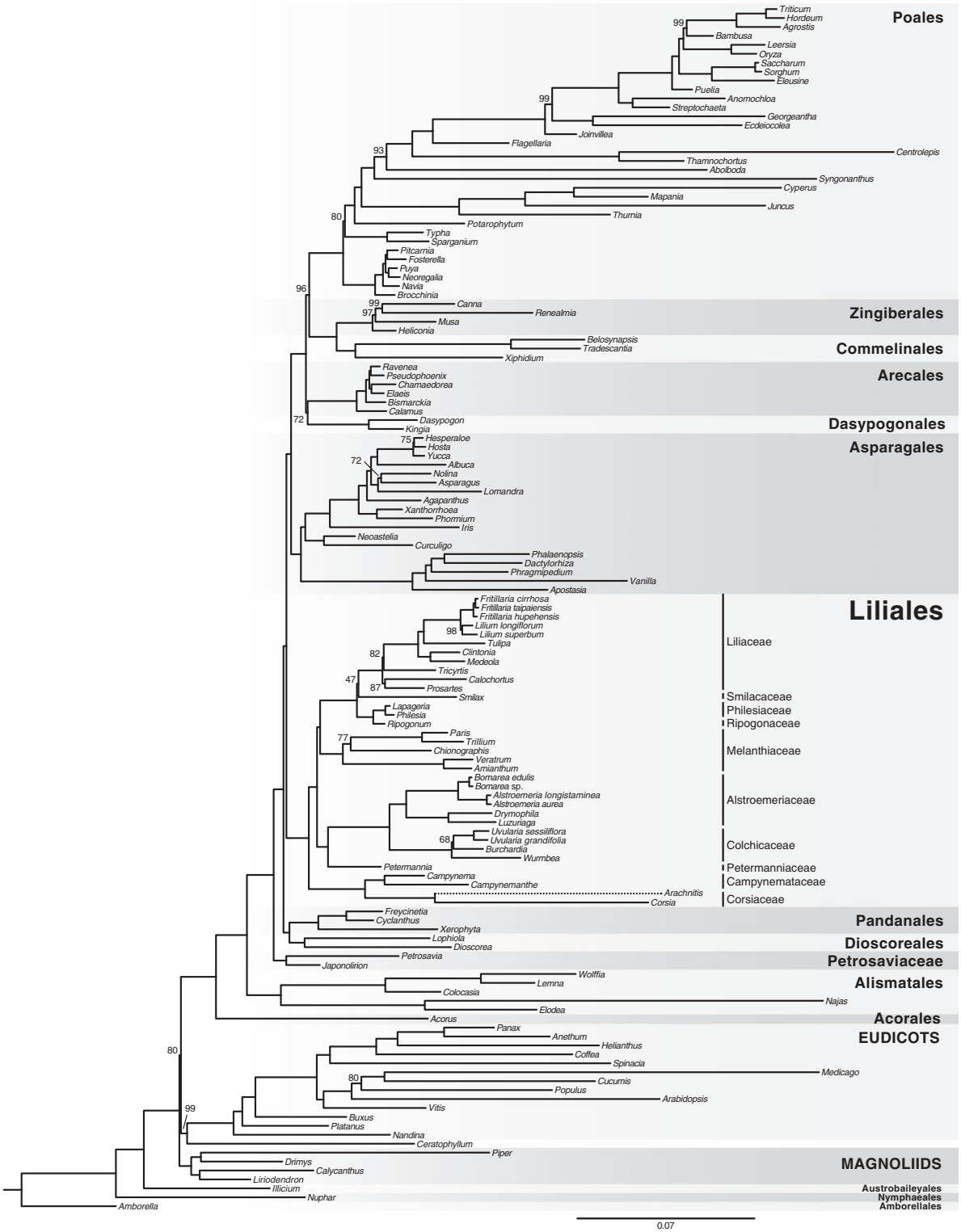

Fig. 1. ML phylogram showing relationships across Liliales, other monocots and angiosperm outgroups based on an unpartitioned analysis of sequences for 75 genes from the plastid genome. Branch lengths are proportional to the number of substitutions inferred along each lineage; the exceptionally long branch for the mycoheterotroph *Arachnitis* (dotted line) is shrunk 5 : 1 to allow it to be displayed. Bootstrap values are 100% unless otherwise indicated above branches.

Inferred branch lengths for the mycoheterotrophs *Corsia* and especially *Arachnitis* were over six times longer, on average, than those of other Liliales relative to the Liliales crown in the unpartitioned analysis (Fig. 1; 0.3363 ± 0.3011 vs. 0.0510 ± 0.0115, from species tips to stem of Liliales). The branch for *Arachnitis* was more than ten times longer than the average for all other Liliales (0.5492 vs. 0.0510), more than 29 standard deviations from the Liliales mean and more than twice as long as that for any other angiosperm included in the analysis. The three shortest internal branches within Liliales were those for the stem groups of *Tricyrtis* + Liliaceae *s.s.* (0.0005), of *Smilax* + Liliaceae (0.0006) and of *Burchardia* + *Uvularia* (0.0007). These branches correspondingly had three of the four lowest levels of support within the order. Across monocots, branch lengths were exceptionally short among palms and bromeliads, and unusually long in *Najas* in Alismatales and among cyperids, xyrids, restiids and graminids in Poales (Fig. 1). The mycoheterotroph *Petrosavia* sat on a branch 3.4 times longer than its green sister *Japonolirion* relative to the Petrosaviales crown, and 1.8 times longer relative to the monocot crown, but both branches were shorter than the average across monocots.

Under MP, 32 052 characters were informative, 11 840 were variable but uninformative and 34 934 were constant. MP yielded a single tree 231 366 steps long (CI = 0.319, CI' = 0.494 without autapomorphies) identical in topology to the ML tree, except that within Liliales, Philesiaceae + Ripogonaceae were sister to Liliaceae with 77% MP support, and Smilacaceae was sister to all three with 100% support (Fig. 2). In addition, the xyrids sampled (Eriocaulaceae, Xyridaceae) formed a clade with 98% bootstrap support, and were sister to Centrolepidaceae + Restionaceae, albeit with weak bootstrap support (52%). In the ML tree, the restiids were instead resolved as sister to the graminids and the xyrids formed a grade, with *Abolboda*, then *Syngonanthus* sister to the graminids + restiids with 93 and 100% ML bootstrap support, respectively (Fig. 1). Overall, 95 of 112 nodes within monocots in the MP tree had MP bootstrap support $\geq$ 97% (Fig. 2).

Supermatrix analyses

The supermatrix included 78 854 aligned bases for 275 taxa, including 177 within Liliales (CI = 0.318, CI' = 0.273). ML produced a single tree with the same topology at the familial level within Liliales as the plastome MP tree, departing from the ML tree only in placing Ripogonaceae + Philesiaceae sister to Liliaceae, then Smilaceae sister to both groups, rather than Smilacaceae sister to Liliaceae, with Ripogonaceae + Philesiaceae as sister to those two families. Thirty-four of the 36 genera in Liliales represented by multiple species were resolved as monophyletic; *Smilax* (Smilacaceae) and *Androcymbium* (Colchicaceae) were paraphyletic, with *Heterosmilax* and *Colchicum* embedded in each as subclades, respectively (Fig. S2).

Within Liliaceae, *Lilium* was sister to *Fritillaria*, with *Cardiocrinum*, then *Notholirion*, then ((*Erythronium*, *Tulipa*), *Gagea*) and finally *Clintonia* + *Medeola* sister to this core group (Fig. S2). *Tricyrtis* was sister to this larger group, and *Calochortus* plus ((*Scoliopus*, *Prosartes*), *Streptopus*) were sister to all other Liliaceae.

Within the vine families, the supermatrix tree maintained the monophyly of *Ripogonum* and embedded *Heterosmilax* in a paraphyletic *Smilax*. Within Melanthiaceae, all five tribes were resolved as monophyletic, with Melanthieae (*Schoenocaulon* through *Veratrum*) sister to remaining tribes, Helioniadeae (*Helonias* through *Heloniopsis*) sister to Chionographideae (*Chamaelirium* and *Chionographis*) and both sister to Xerophylleae plus Parideae (*Pseudotrillium* through *Paris*) (Fig. S2).

Within Colchicaceae, the supermatrix analysis supported three clades, with *Burchardia* sister to *Uvularia* + *Disporum* sister to the remaining taxa, and *Tripladenia* then *Kuntheria* + *Schelhammera* sister to the remaining elements of the third clade (*Iphegenia* through *Colchicum*). Within Alstroemeriaceae, *Luzuriaga* and *Drymophila* of Luzuriageae were sister to each other, and jointly sister to *Alstroemeria* + *Bomarea* of Alstroemerieae. Monotypic Petermanniaceae was sister to Colchicaceae + Alstroemeriaceae. Finally, *Campynemanthe* was sister to *Campynema*, which in turn were sister to Corsiaceae; Campynemataceae + Corsiaceae were sister to all other Liliales (Fig. S2).

Divergence times and historical biogeography

The order Liliales appears to have diverged from other monocots by 124 Mya [95% highest posterior density (HPD) 116–131 Mya], and to have begun splitting into its constituent families 113 Mya (100–130 Mya, 95% HPD) (Figs 3 and S3). Stem ages of individual families range from 51.1 to 103.9 Mya, while crown ages vary from 3.8 to 84.8 Mya (Table 3). The monocot stem is resolved as 141.7 Mya; the crown age, 136.0 Mya. Ripogonaceae, Philesiaceae and Smilacaceae are the most recently divergent families, while Melanthiaceae and Liliaceae are the oldest. Based on the relative lengths of the *Corsia* branch and the Corsiaceae stem in the plastome tree, we estimate that *Arachnitis* and *Corsia* diverged from each other 56.1 Mya. Based on our analyses, estimated mean stem ages of monocot orders vary with a relatively narrow window from 112 Mya in Commelinales and Zingiberales to 136 Mya in Acorales (Table 3).

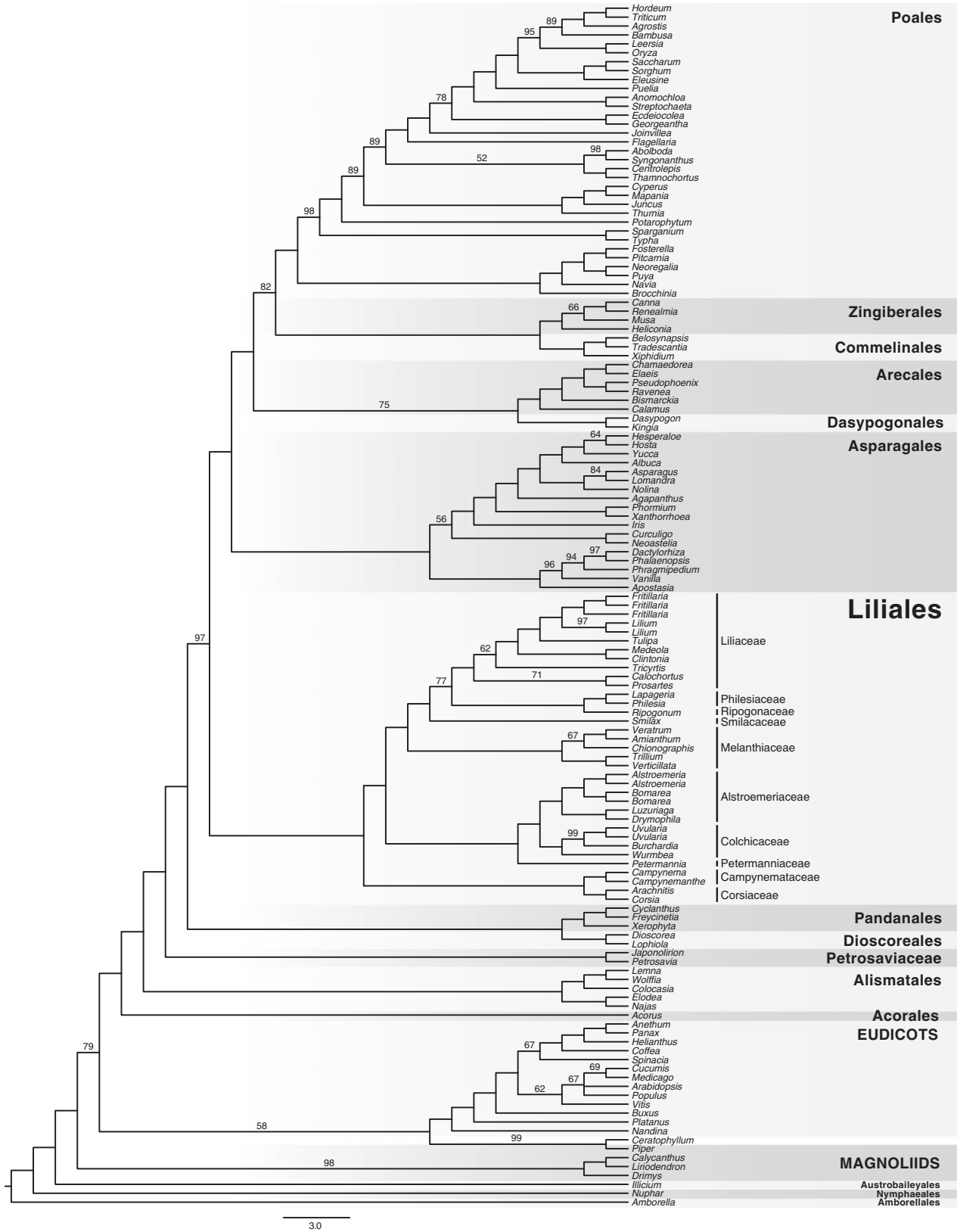

Fig. 2. MP cladogram showing relationships across monocots based on an unweighted analysis of 75 plastid genes. Bootstrap values are 100% unless otherwise indicated.

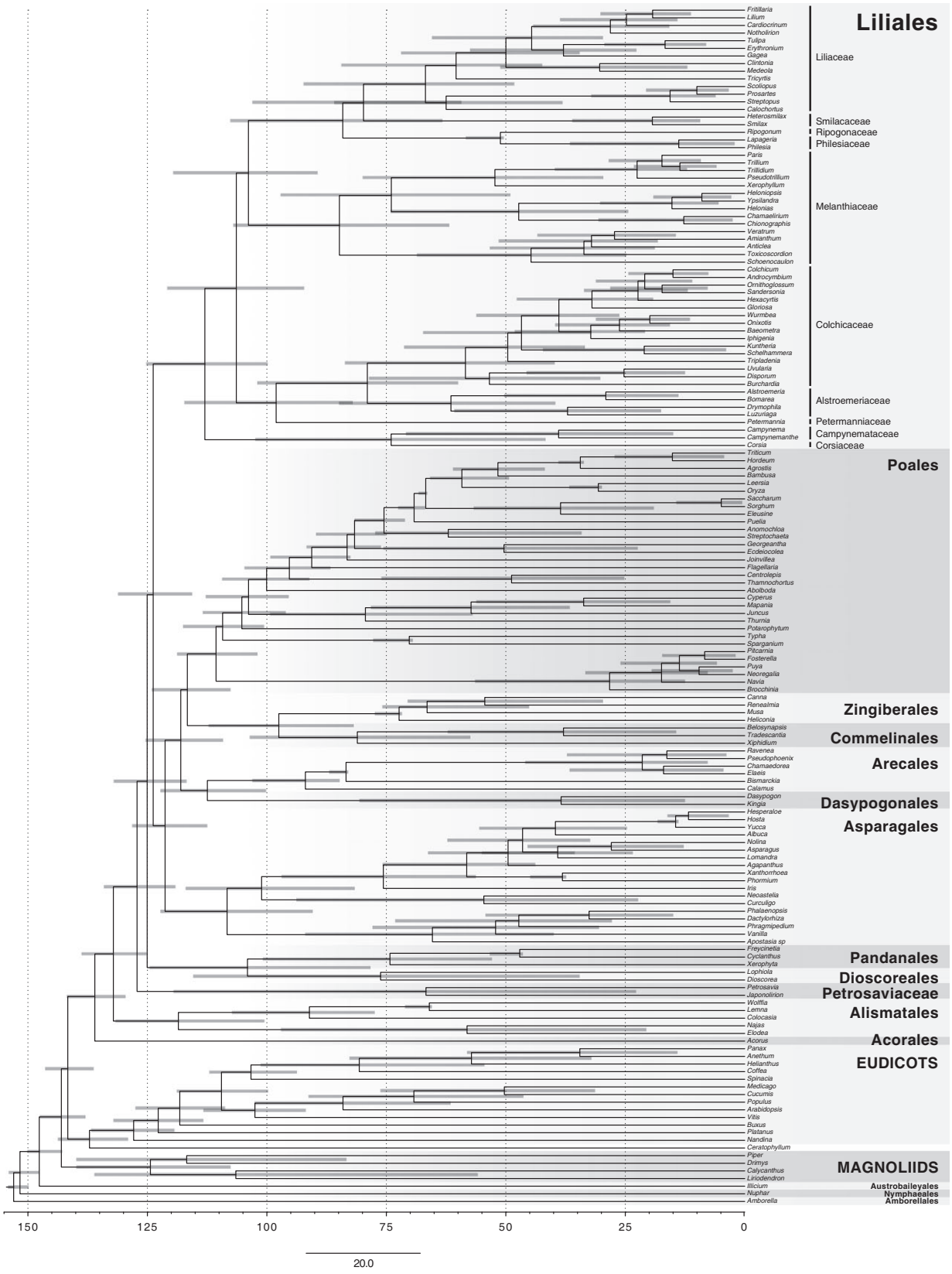

Fig. 3. Simplified timeline in millions of years for monocot evolution based on BEAST analysis, including single place-holders for each genus; grey bars represent 95% higher probability densities around each mean.

Table 3
Inferred stem and crown ages (Ma) of major monocot clades, and the upper and lower bounds of the 95% higher posterior density (HPD) for those ages based on BEAST analysis

Clade	Stem age	95% HPD	Crown age	95% HPD
Monocots	141.7	136.2–146.3	136.0	129.6–141.7
Acorales	136.0	129.6–141.7		
Alismatales	132.1	125.1–138.7	118.5	100.5–131.6
Petrosaviales	127.2	119.1–134.0	66.7	22.9–119.5
Dioscoreales	104.1	78.3–124.5	76.1	34.7–115.4
Pandanales	104.1	78.3–124.5	74.2	53.0–100.8
Liliales	123.8	115.6–131.1	113.0	99.9–125.1
Campynemataceae	74.0	41.8–102.4	39.0	15.1–70.9
Corsiaceae	74.0	41.8–102.4	56.1*	
Alstroemeriaceae	79.0	60.1–102.0	61.5	39.7–84.9
Colchicaceae	79.0	60.1–102.0	58.5	39.9–83.6
Petermanniaceae	98.1	82.1–117.2		
Melanthiaceae	103.9	89.4–119.5	84.8	61.9–106.9
Philesiaceae	51.1	50.5–58.4	13.8	2.3–36.6
Ripogonaceae	51.1	50.5–58.4	3.8	0.6–12.0
Smilacaceae	79.8	59.3–103.0	19.3	9.5–36.1
Liliaceae	79.8	59.3–103.0	66.8	48.3–92.3
Asparagales	121.3	112.5–128.1	108.3	90.4–122.2
Arecales	112.5	100.2–122.2	83.4	84.8–103.0
Dasypogonales	112.5	100.2–122.2	41.2	12.7–80.6
Commelinales	97.5	81.8–112.1	80.5	57.5–103.5
Zingiberales	97.5	81.8–112.1	72.3	71.8–77.4
Poales	116.6	107.6–124.0	110.6	102.0–118.7

*Based on grafting *Arachnitis* onto the BEAST chronogram, at a distance above the Corsiaceae stem proportional to the distance from it to the end of the *Corsia* branch in the supermatrix ML phylogram.

Across monocots, the DEC + J model was not significantly better than DEC ($P > 0.22$), so we used the simpler model to reconstruct historical biogeography within Liliales. The order appears to have arisen in Australia, at a time when that continent and South America were attached to each other via Antarctica (Fig. 4). The distribution of *Arachnitis* in the Neotropics/South Atlantic Islands clearly appears to have arisen via vicariance. By the time that Campynemataceae and Corsiaceae diverged from each other 74 Mya, Australia and South America were still close to a temperate Antarctica, but Africa had diverged from the other southern landmasses by several hundred kilometres.

Alstroemeriaceae apparently spread mostly overland from Australia to the Neotropics between 79 and 61.5 Mya, while Australia and South America were both still close to Antarctica, with vicariance in these areas later resulting from continental drift. Within Colchicaceae, long-distance dispersal (LDD) from Australia to eastern Asia (including East Asia, Southeast Asia and the Himalayas) and eastern North America occurred in *Disporum* and *Uvularia*, respectively, sometime after 25.3 Mya (Fig. 4). LDD from Australia to Africa occurred after 46.7 Mya for the ancestor of the core, largely African Colchicaceae (*Iphigenia* through *Colchicum*), with independent movements from Africa to Southeast Asia in *Gloriosa* and *Iphigenia* roughly 32 Mya, from Africa to Europe in *Androcymbium–Colchicum* sometime after 20.9 Mya, and from Africa to Australia in *Wurmbea* sometime after 16.7 Mya (Fig. 4). The first two movements probably involved overland movement during periodic greening of the Saharan and Arabian deserts, while the latter involved LDD over the Indian Ocean (see Discussion).

Biogeographical movements at several points along the spine of the Liliales are not well resolved, especially for transitions to Melanthiaceae, the vine families and Liliaceae. Melanthiaceae appears most likely to have arisen in eastern North America ca. 104 Mya, with shifts to western North America and the Neotropics in the clade subtended by *Schoenocaulon* and *Veratrum*, with additional spread to the Himalayas in *Anticlea*, movement back to eastern North America in *Toxicocordion* and *Amianthium*, and throughout the northern hemisphere (excluding north Africa) in *Veratrum* (Fig. 4). Movement to East Asia occurred in *Chionographis* and *Helionopsis* + *Yspilandra*, with further movement to Southeast Asia and the Himalayas in the latter.

Movement from eastern to western North America occurred in Parideae (*Xerophyllum* through *Paris*) between 74 and 52.3 Mya (Fig. 4). Subsequent movement back to eastern North America occurred in *Xerophyllum*, and into eastern North America and East Asia occurred in the ancestor of the remaining Parideae, with origins of *Trillidium–Trillium–Paris* in East Asia, movement to the Himalayas in *Trillidium*, to North America in *Trillium*, and to Eurasia, Southeast

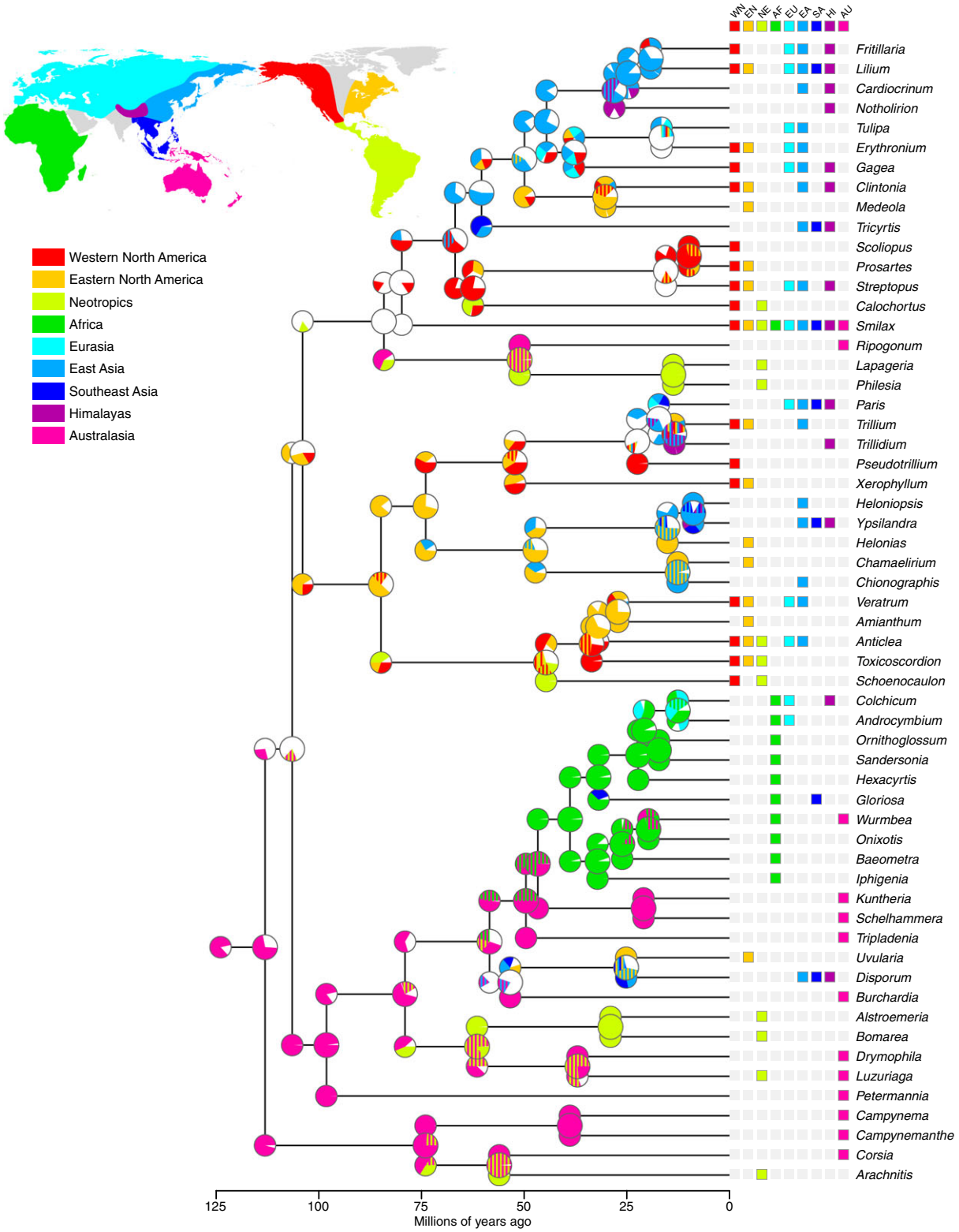

Fig. 4. Reconstruction of the historical biogeography based on BioGeoBEARS. Colours of pie wedges at each node represent geographical areas (or combinations thereof) inferred to have been occupied by ancestral taxa (see inset map); wedge width represents the chance individual areas were occupied. White is used to code for ancestral areas or combinations inferred to have had an individual probability < 15%. Dots over one terminal area indicate the inferred ancestral area for each genus (see text).

Asia and the Himalayas in *Paris*, with the split between *Trillium* and *Paris* occurring ca. 17.3 Mya, and the crown ages of these genera being ca. 13.6 and 13.7 Mya, respectively (Fig. 4).

Philesiaceae–Ripogonaceae arose in Australia and the Neotropics ca. 84 Mya, with movement to the Neotropics in Philesiaceae and to Australia in Ripogonaceae ca. 51.1 Mya, plausibly via teleconnections between these continents and Antarctica and subsequent vicariance induced by continental drift. Dispersal and vicariance within widespread Smilacaceae cannot be resolved by our genus-level analysis.

Liliaceae appears to have arisen in western North America or possibly East Asia (Fig. 5). The family spread overland into the Neotropics (Mexican plateau) in *Calochortus*, into eastern North America in some *Prosartes*, and into eastern North America, East Asia, the Himalayas and Eurasia in *Streptopus*. Spread from western North America into East Asia ca. 66.8 Mya, most likely overland via Beringia, is inferred for the ancestor of the remaining Liliaceae, with subsequent spread into Southeast Asia and the Himalayas in *Tricyrtis* (Fig. 4). The core Liliaceae (Medeoloideae + Lilioideae) appears to have originated 60.4 Mya in East Asia with overland spread via Beringia ca. 50 Mya into eastern North America for *Clintonia* + *Medeola*, and later movements into western North America and East Asia in some species of *Clintonia*. Lilioideae probably arose in East Asia 50 Mya, with later, independent movements (most likely overland) into Eurasia for the ancestor of *Gagea–Erythronium–Tulipa* ca. 44.6 Mya, and subsequent overland movement into East Asia, the Himalayas and western North America in *Gagea*, and into Eastern and Western North America in *Erythronium* (Fig. 4). The crown group of the four remaining genera of Liliaceae arose in East Asia 28.1 Mya, with overland movement of *Cardiocrinum* and *Notholirion* to the Himalayas and subsequent independent spreads of *Lilium* and *Fritillaria* into North America, Eurasia and the Himalayas, and of a few species of *Lilium* into Southeast Asia as well, beginning ca. 19.3 Mya. The crown ages of *Fritillaria* and *Lilium* are ca. 15.9 and 15.1 Mya, respectively (Fig. 4).

Discussion

Phylogeny

Our plastome ML phylogeny resolves all five major areas of uncertainty in relationships within Liliales, but with varying degrees of support. First, within Liliaceae, *Tricyrtis* is sister to Lilioideae + Medeoloideae with 82% ML bootstrap support, *Calochortus* is sister to *Prosartes* with 87% bootstrap support, and the clade formed by these taxa and all other Liliaceae has 100% bootstrap support (Fig. 1). Our supermatrix analysis places *Prosartes* sister to *Scoliopus*, both sister to *Streptopus* and all three sister to *Calochortus*. Our

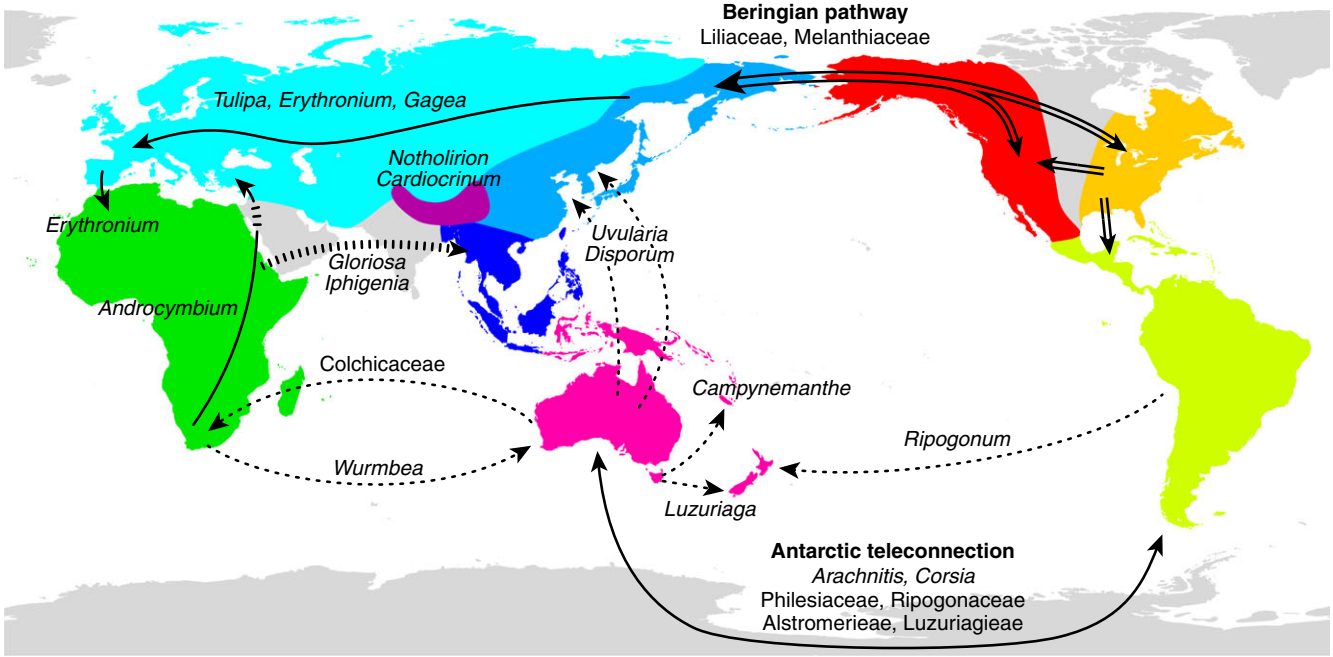

Fig. 5. Summary of overland movements within continents (solid arrows) or via the Bering land bridge (hollow arrows), the Antarctic teleconnection (heavy arrows) or the intermittent greening of the Sahara and Arabian deserts (hashed lines), and LDD over water (dashed lines).

placement of *Calochortus* and *Tricyrtis* confirms the phylogeny of Fay et al. (2006) but with much higher support, and contradicts those obtained by others (see Introduction). Calochortaceae *sensu* Tamura (1998) is not monophyletic. Our data support the branching topology within *Scoliopus–Prosartes–Streptopus* found by many (Patterson and Givnish, 2002; Givnish et al., 2005; Fay et al., 2006; Kim et al., 2013; Petersen et al., 2013).

Second, the plastome ML phylogeny places Smilacaceae sister to Liliaceae, not Philesiaceae–Ripogonaceae. Although this topology supports the conclusions of most authors other than Vinnersten and Bremer (2001) and Kim et al. (2013), the question of relationships among the vine families is not closed, given the low ML bootstrap support (47%) for the position of Smilacaceae and the exceedingly short branch on which that family sits in the ML plastome tree (Fig. 1). Furthermore, our MP plastome tree and ML supermatrix phylogeny place Philesiaceae–Ripogonaceae sister to Liliaceae, with Smilacaceae sister to all three. The sensitivity of the position of Smilacaceae to differences in taxon sampling and method of analysis leaves its evolutionary position unresolved even with analyses of 75 plastid genes. This situation is similar to that in Zingiberales, in which even the entire set of plastid coding regions was inadequate to resolve all of the deep branching events between families (Barrett et al., 2014), and inclusion of non-coding plastid regions was needed to resolve and adequately support all interfamilial relationships (C. F. Barrett, pers. comm.). The Bayesian analysis of five nuclear and mitochondrial gene sequences by Mennes et al. (2015) is consistent with our ML plastome tree, but relationships of all Lilialean families to each other collapse in their ML analysis, except for the ties of Philesiaceae to Ripogonaceae, Colchicaceae to Alstroemeriaceae and Campynemataceae to Corsiaceae (C. Mennes, pers. comm.).

Third, our plastome phylogeny identifies the sister groups of Liliaceae + the vine families as Melanthiaceae, then ((Colchicaceae, Alstroemeriaceae), Petermanniaceae), consistent with the findings of Patterson and Givnish (2002), although those authors did not include Petermanniaceae or Corsiaceae in their analysis. The disparity among previous reports of the position of Melanthiaceae vs. Colchicaceae–Alstroemeriaceae (e.g. see Givnish et al., 2005; Fay et al., 2006; Kim et al., 2013; Mennes et al., 2015) is probably the result of the very short branch on which Melanthiaceae sits (Fig. 1).

Fourth, our placement of *Petermannia* sister to Colchicaceae–Alstroemeriaceae affirms the conclusions of several authors (Chase et al., 2006; Fay et al., 2006; Graham et al., 2006; Petersen et al., 2013; Mennes et al., 2015) but not Kim et al. (2013). Finally, our plastome data support the conclusions of Mennes et al. (2015) that Corsiaceae is monophyletic, lies within Liliales and is sister to Campynemataceae, with both families jointly sister to all other families of the order. The aberrant placement of *Arachnitis* outside Liliales by Kim et al. (2013) appears to have been a result of DNA contamination (Mennes et al., 2015).

The three shortest branches within Liliales in the plastome tree—for the stem groups of *Tricyrtis* + Liliaceae *s.s.*, *Smilax* + Liliaceae *s.l.* and *Burchardia* + *Uvularia*—had three of the four lowest levels of support within the order. The connection between inferred branch length and support is expected, and helps account for two of the five "soft spots" in the Liliales phylogeny. The relatively short branches associated with *Petermannia* and the stem of Melanthiaceae account for two other soft spots. The extremely long branch of Corsiaceae accounts for the previous difficulty in placing this mycoheterotrophic taxon (Fig. 1).

Historical biogeography

Our supermatrix analysis places the stem and crown of Liliales at ca. 124 and 112 Mya, respectively (Figs 3 and S3; Table 3). These and the stem and crown ages of individual families are substantially further back in time than those inferred by Bremer (2000) and Vinnersten and Bremer (2001) using mean branch lengths calibrated against the ages of six Cretaceous fossils, by Givnish et al. (2005) using penalized likelihood analysis calibrated using the same six fossils, and by Mennes et al. (2015) using BEAST and the ages of two to six fossils of Liliales or monocots generally. We believe that our analysis—which used the more advanced dating algorithm in BEAST and the ages of 17 angiosperm fossils—provides the most credible age estimates for Liliales yet available. Our dating results are fairly similar to those obtained by Chacón et al. (2012) based on a relaxed clock and up to three fossil calibrations.

Our BioGeoBEARS analysis places the origin of Liliales in Australia, at a time when Australia, Antarctica and South America were in close proximity to each other. In other words, our analysis points to Gondwana minus Africa (and India) as the lilialean cradle. We estimate the divergence of Neotropical *Arachnitis* from Australasian *Corsia* as occurring 56.1 Mya, which precedes the estimated final split between Australia and Antarctica 35.5–52 Mya and that between South America and Antarctica 36 Mya (Scotese et al., 1988; Veevers et al., 1991; Woodburne and Case, 1996), although some small separations between the continents arose beginning as early as 80 Mya. We and Mennes et al. (2015) conclude that Corsiaceae acquired a disjunct distribution in the Neotropics and Australasia via continental drift and their teleconnection via Antarctica.

Campynemanthe most likely reached New Caledonia from Australasia via LDD, not vicariance, given that it diverged from Tasmanian *Campymena* ca. 39 Mya and that New Caledonia split from Australia no later than ca. 66 Mya (Grandcolas et al., 2008) and seems to have been completely submerged from the Palaeocene until 37 Mya (Pelletier, 2006). The 95% confidence interval about the divergence of *Campynema* and *Campynemanthe* is, however, unusually broad and extends back to 71 Mya (Figs 3 and S3), so that the possibility of vicariance via continental drift and persistence on some emergent islet on the nearby Norfolk or Loyalty Ridges (Herzer et al., 1997; Meffre et al., 2006; Pelletier, 2006; Ladiges and Cantrill, 2007) for millions of years while New Caledonia was submerged cannot be wholly excluded. However, our conclusion that *Campynemanthe* reached New Caledonia via LDD accords with recent studies pointing to the origins of several endemic lineages there no earlier than 37 Mya (Grandcolas et al., 2008; Pillon, 2012; Nattier et al., 2013; Kranitz et al., 2014).

The distribution of the ancestor of the remaining Liliales from 113 to 106 Mya is most likely Australia and South America, reflecting again their teleconnnection via Antarctica (Fig. 4). One descendant clade consists of Colchicaceae, Alstroemeriaceae and Petermanniaceae (CAP), while the other consists of Melanthiaceae, Ripogonaceae, Philesiaceae, Smilacaceae and Liliaceae (MRPSL). The CAP ancestor occurred in Australia, to which *Petermannia* remains restricted. The ancestor of Colchicaceae–Alstroemeriaceae appears to have been found in Australia or Australia and South America 61.5 Mya (Fig. 4). At the time, Australia and South America had a teleconnection via Antarctica, so this initial appearance on both continents may simply reflect vicariance by continental drift. The subsequent restriction of *Alstroemeria* and *Bomarea* to South America may represent either extinction in Australia or adaptation to seasonally dry conditions associated with the early uplift of the Andes (Chacón et al., 2012), with the latter reflected by their bulbous growth form. Chacón et al. (2012) reconstruct movement of *Alstroemeria* out of the Andes into the Brazilian Highlands about 9 Mya, at about the same time as the orchid tribe Laeliinae (Antonelli et al., 2010) and tank epiphytes of bromeliad subfamily Bromelioideae (Givnish et al., 2014).

Our generic-level reconstruction places the split between *Luzuriaga* (with three species in Chile and one in New Zealand) and *Drymophila* (with one species on mainland Australia and one on Tasmania) at 37.1 Mya, when Australia and South America still had an Antarctic teleconnection. Both genera have fleshy fruits capable of LDD. The split between *Luzuriaga parviflora* (the sole New Zealand species) and *L. radicans* (Chile) at 15.0 Mya implies recent LDD across the Pacific. The branching topology within *Luzuriaga* implies that the genus arose in South America (Chacón et al., 2012), and the late derivation of *L. parviflora* implies its relatively recent origin in New Zealand. Two scenarios are possible. First, given the existence of the genus in New Zealand ca. 23 Mya (Conran et al., 2014), *Luzuriaga* may initially have been present in New Zealand, then went extinct [perhaps due to inundation of up to 82% of its landmass before the time of maximum submergence 23 Mya (Neall and Trewick, 2008; Campbell and Landis, 2009; Sharma and Wheeler, 2013)], and then recolonized the archipelago via LDD (Chacón et al., 2012; Conran et al., 2014). The tribe Richeae of Ericaceae appears to have had a similar history (Jordan et al., 2010; Conran et al., 2014), although that group has capsular fruits.

Second, given the broad 95% confidence intervals around the timing of the split between *Luzuriaga parviflora* and *L. radicans* (4–32 Mya), which includes our estimated time of divergence of *L. parviflora*, it may simply be that *Luzuriaga* did not go extinct on New Zealand after the Miocene. Given that many elements of the fossil flora described from the site investigated by Conran et al. (2014) are present in New Zealand today [excepting some tropical elements (Lee et al., 2012)], this second scenario seems more plausible. Otherwise, we might have to posit repeated recolonizations by several lineages. Certainly, several animal lineages that appear incapable of LDD (e.g. kiwis, moas, tuatara) did manage to survive the partial submergence of New Zealand.

Colchicaceae probably also originated in Australia, with early divergent *Burchardia, Tripladenia, Schelhammera* and *Kuntheria* restricted to that continent (Fig. 4). LDD from Australia to northern temperate deciduous forests of East Asia and eastern North America occurred 53–25.3 Mya in *Disporum* and *Uvularia*. No direct connection between Australia and Asia or North America has ever existed, but Asian *Disporum* has fleshy fruits capable of LDD, and dispersal between East Asia and North America via Beringia has occurred in many groups (e.g. see Xiang and Soltis, 2001; Milne and Abbott, 2002). A Beringian land connection between eastern Asia and western North America was present before the late Miocene, and then again repeatedly during glacial periods during the Quaternary (Tiffney, 1985; Manchester, 1999). An epicontinental seaway separated eastern and western North America from the late Aptian (ca. 105–102 Mya) to the early Maastrichian (ca. 70 Mya) (Tiffney and Manchester, 2001; Milne, 2006). C_4 grasslands appear to have re-separated eastern and western forests in North America starting in the late Miocene (ca. 7 Mya) (Edwards et al., 2010).

Apparently, LDD from Australia to Africa ca. 38.9 Mya also initiated the largely African core

Colchicaceae (*Iphigenia* through *Colchicum*). Subsequently, *Gloriosa* invaded Southeast Asia while *Iphigenia* independently invaded Southeast Asia and Australia, both sometime after 32 Mya (Fig. 4). Both these invasions could have been completely overland during periods of heavier rainfall in the Sahara and Arabian deserts, with subsequent extinctions of intervening populations during dryer periods like those at present. Relatively wet periods have recurred repeatedly during the Pleistocene in Arabia and the Sahara, apparently tied to shifts in the Earth's orbit and strong, non-linear feedbacks between vegetation and the atmosphere (Foley et al., 2003; Rosenberg et al., 2011; Groucutt and Petraglia, 2012). Bulbous *Wurmbea* apparently re-invaded seasonal parts of Australia from Africa via LDD sometime after 16.7 Mya; our analysis places Australian and African subclades of *Wurmbea* sister to each other. Case et al. (2008) inferred dispersal of *Wurmbea* from Africa to Australia based on a sister relationship between *Wurmbea* clades in Africa and Australia/New Zealand, embedded in an African grade including *Onixotis, Baometra* and *Iphigenia*. They pointed as well to movement of *Wurmbea* from Western Australia to South Australia and New Zealand; our dating indicates that at least the latter (involving *"Iphigenia" novae-zelandiae*) used over-water dispersal. The phylogenetic analysis of del Hoyo et al. (2009) implies an Australian clade contained within a paraphyletic African (mainly Cape) lineage of *Wurmbea*; these authors expanded *Wurmbea* to include South African *Onixotis* and *Neodregea*. Finally, our species-level analysis places European *Colchicum* originating 12.7–7.3 Mya within a paraphyletic African (mainly Cape) *Androcymbium*. More extensive sampling and a detailed analysis led del Hoyo et al. (2009) to propose that *Androcymbium–Colchicum* arose in south-west Africa—a winter-rainfall hotspot for bulbous geophytes—and then dispersed via an intermittently arid pathway in East Africa to North Africa and ultimately Eurasia.

Melanthiaceae appears to have originated in North America ca. 104 Mya, more likely in the east than in the west (Fig. 4). Our supermatrix phylogeny is consistent with the division of the family into five tribes by Zomlefer et al. (2001), with Parideae (*Pseudotrillium* through *Paris*) sister to Xerophyllidae (*Xerophyllum*), Heloniadeae (*Helonias* through *Ypsilandra*) sister to Chionographideae (*Chionographis* and *Chamaelirium*) and Amiantheae (*Schoenocaulon* through *Veratrum*) sister to both of these pairs. The ancestral condition for the family appears most likely to have been eastern North America, or both eastern and western North America (Fig. 4). Amiantheae are distributed primarily in western North America and the Neotropics, with *Amianthum* becoming restricted to eastern North America sometime in the last 27 Myr; *Veratrum* spreading throughout the northern hemisphere and reaching Southeast Asia within the last 19 Myr; and *Anticlea* reaching Eurasia and East Asia in the last 4.3 Myr. The remaining tribes appear to have originated in eastern North America, with the ancestors of *Heloniopsis–Ypsilandra* and *Chionographis* moving, most likely overland, to East Asia in the last 15.2–12.8 Myr, respectively, and *Ypsilandra* subsequently reaching the Himalayas. Parideae–Xerophyllideae arose in North America 52.3 Mya, more likely in the west than in the east, as did Parideae, with *Pseudotrillium* becoming restricted to Western North America, *Trillidium* to the Himalayas, *Trillium* to East Asia and eastern and western North America, and *Paris* to Eurasia, East Asia, Southeast Asia and the Himalayas starting 22.5 Mya, involving at least two dispersal events across Beringia.

Based on our genus-level analysis, the distribution of the ancestor of the remaining four families is difficult to infer, due to the wide distribution of *Smilax*, although the Neotropics appears to be most likely (Fig. 5). A detailed phylogeny of Smilacaceae appears unlikely to clarify this situation, given the distributions of the four major clades within the family identified by Qi et al. (2013). *Smilax aspera*, sister to all other taxa, occurs in Eurasia, North Africa, Southeast and East Asia, and the Himalayas; the remaining species split into three clades, one mainly restricted to the New World, and two Old World clades sister to each other and occurring primarily in East Asia and western and eastern North America, and East Asia and Southeast Asia, respectively. The ancestor of Philesiaceae and Ripogonaceae appears to have been distributed in South America and Australia 84 Mya, when both continents had an overland teleconnection via Antarctica (see above). Subsequent restriction of Philesiaceae to southern South America and Ripogonaceae to Australia and New Zealand ca. 51.1 Mya based on our molecular phylogeny also occurred while South America and Australia were near Antarctica, but well after Zealandia separated from the Australian plate. This suggests that the occurrence of fleshy fruited *Ripogonum* in New Zealand today may represent a recent (ca. 1 Mya) instance of LDD from Australia across the Tasman Sea, given the strong similarity of the leaves of *R. album* from eastern Australia and New Guinea with those of *R. scandens*, the sole species from New Zealand, and our timeline of divergence among species of *Ripogonum*. A similar recent LDD event took place in *Wurmbea* (Case et al., 2008; see above). *Ripogonum* also dispersed to New Zealand in the Miocene and may later have become extinct, given the abundance of *Ripogonum* fossils from the Miocene in New Zealand (Conran et al., 2013). Carpenter et al. (2014) have recently described the fossil *Ripogonum americanum* from 52.2 Mya in Argentina, clearly indicating that

Ripogonaceae made it to southern South America and subsequently became extinct.

Finally, our genus-level analysis indicates that Liliaceae probably arose in western North America (and possibly East Asia) 67 Mya (Fig. 4), reflecting the present-day occurrence of *Calochortus, Prosartes, Scoliopus* and *Streptopus* at least partly in that region. By 60.4 Mya, the ancestor of the remaining taxa appears to have arrived in East Asia, with *Tricyrtis* presumably dispersing overland to Southeast Asia shortly thereafter and ultimately to the Himalayas after they arose. While the leading edge of India may have had a "soft" collision with Eurasia 55–70 Mya (Sclater and Fisher, 1974; Yin and Harrison, 2000), a continent–continent "hard" collision leading to massive Himalayan uplift probably did not occur until the Eocene/Oligocene transition 34 Mya (Aitchison et al., 2007) or even later (Uddin et al., 2010). Ancestors of Medeoloideae–Lilioideae appear to have occupied eastern North America by 50.0 Mya, with likely overland movement to western North America and East Asia via Beringia in *Clintonia* sometime after 30 Mya (Fig. 5). Movement overland to East Asia or Eurasia via Beringia ca. 50 Mya accompanied the evolution of bulbous Lilioideae. Our analysis suggests an origin of *Gagea–Erythronium–Tulipa* in western North America, East Asia or Eurasia, with dispersal into eastern Eurasia and divergence among these genera beginning 39.9 Mya. *Notholirion, Cardiocrinium, Lilium* and *Fritillaria* also originated in East Asia, with divergence among them beginning 28.1 Mya. *Notholirion* and *Cardiocrinum* either invaded or became restricted to the now uplifting Himalayas between 28.1 and 24.8 Mya, and *Lilium* and *Fritillaria* dispersed widely in the northern hemisphere beginning 19.3 Mya and presumably entered the New World via Beringia (Fig. 4).

More detailed phylogenies of individual groups do not currently clarify this picture. For example, *Gagea* now occurs in Eurasia, East Asia, the Himalayas and western North America, but widespread hybridization and conflict between nuclear and plastid phylogenies (see Peterson et al., 2009; Zarrei et al., 2009) preclude any detailed analysis of its phylogeography as yet. We see several phylogeographical scenarios as being consistent with the *Erythronium* phylogeny presented by Clennett et al. (2012), including independent overland invasions from Asia to western and eastern North America, or a single invasion of North America with a back-invasion of Eurasia. The phylogeny of *Tulipa* presented by Christenhusz et al. (2013) roots it solidly in Eurasia, with a single, relatively late invasion of North Africa by *T. sylvestris*. The historical biogeography of Liliaceae might be best clarified by detailed studies of relationships within the relatively small genera *Streptopus, Prosartes* and *Clintonia*, and especially by intensive studies within the large genus *Lilium*. While the nuclear ITS phylogeny presented by Gao et al. (2013) is consistent with an origin of *Lilium* in East Asia and the Himalayas and a single invasion of North America, conflict between plastid and nuclear trees is rampant (Thomas J. Givnish, unpubl. data), implying widespread hybridization and a need to re-examine relationships before reconstructing historical biogeography within this group. The same may be also be true of its sister genus *Fritillaria* (see Day et al., 2014).

Overall, however, our results point to an "out of Gondwana" origin of the order Liliales, with close relationships between three pairs of lineages (Corsiaceae and Campynemataceae; Philesiaceae and Ripogonaceae; Alstroemerieae and Luzuriageae of Alstroemeriaceae) distributed in South America and Australia, New Caledonia or New Zealand reflecting vicariance and teleconnections of these areas via Antarctica in the ancient past (Fig. 5). LDD appears implicated in the re-invasion of New Zealand by two lineages (*Luzuriaga, Ripogonum*) whose initial occurrence there may have succumbed to early inundation of most of its land mass. LDD, not vicariance, appears to have allowed *Campynemanthe* to colonize New Caledonia after it having been submerged for many millions of years. LDD also seems to have permitted Colchicaceae to invade East Asia and Africa independently from Australia, and to re-invade Africa from Australia. Periodic greening of the Sahara and Arabian deserts appears to have permitted *Gloriosa* and *Iphigenia* to colonize Southeast Asia overland from Africa, and *Androcymbium–Colchicum* to invade the Mediterranean overland from its roots in south-western South Africa. The historical biogeography of Melanthiaceae and Liliaceae appears consistent with several movements across Beringia leading to vicariance, consistent with their restriction to the northern hemisphere and the presence of a land bridge joining Asia and western North America before the late Miocene that permitted movement of the boreotropical flora, and the later, repeated re-formation of the land bridge during glacial periods of the Quaternary (Fig. 5).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Supplemental materials figures and tables.