



Orchid historical biogeography, diversification, Antarctica and the paradox of orchid dispersal

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ABSTRACT

Aim Orchidaceae is the most species-rich angiosperm family and has one of the broadest distributions. Until now, the lack of a well-resolved phylogeny has prevented analyses of orchid historical biogeography. In this study, we use such a phylogeny to estimate the geographical spread of orchids, evaluate the importance of different regions in their diversification and assess the role of long-distance dispersal (LDD) in generating orchid diversity.

Location Global.

Methods Analyses use a phylogeny including species representing all five orchid subfamilies and almost all tribes and subtribes, calibrated against 17 angiosperm fossils. We estimated historical biogeography and assessed the importance of different regions for rates of speciation, extinction and net species diversification. We evaluated the impact of particular LDD events on orchid diversity by asking how many species evolved in the new range subsequent to those events.

Results Orchids appear to have arisen in Australia 112 Ma (95% higher probability distribution: 102.0–120.0 Ma), then spread to the Neotropics via Antarctica by 90 Ma (HPD: 79.7–99.5 Ma), when all three continents were in close contact and apostasioids split from the ancestor of all other orchids. Ancestors of vanilloids, cypripedioids and orchidoids+epidendroids appear to have originated in the Neotropics 84–64 Ma. Repeated long- and short-distance dispersal occurred through orchid history: stochastic mapping identified a mean total of 74 LDD events or 0.8 Ma⁻¹. Across orchid history, Southeast Asia was the most important source and maximally accelerated net diversification; across epidendroids, the Neotropics maximally accelerated diversification.

Main conclusions Our analysis provides the first biogeographical history of the orchids, implicating Australia, the Neotropics and Antarctica in their origin. LDD and life in the Neotropics – especially the Andes – had profound effects on their spread and diversification; > 97% of all orchid species are restricted to individual continents.

Keywords

Asparagales, BioGeoBEARS, BiSSE, long-distance dispersal, Neotropics, Southeast Asia

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INTRODUCTION

Orchids are the largest family of angiosperms, with roughly 880 genera and 27,800 species. They comprise ~8% of all

vascular plants, grow in almost all terrestrial habitats except the driest deserts and are native to all continents except Antarctica (Pridgeon *et al.*, 1999–2014; The Plant List, 2015). Givnish *et al.* (2015) recently showed that the drivers of

extraordinary orchid diversity include the evolution of pollinia, epiphytic habit, CAM photosynthesis, pollination via Lepidoptera, euglossine bees, and deceit, and life in extensive tropical cordilleras such as the Andes and New Guinea Highlands. The defining characteristics of orchids – minute seeds, germination aided by fungal symbionts, and floral column of fused male and female parts – appear not to have accelerated orchid speciation themselves but to have interacted in several cases with the traits just mentioned to generate exceptional levels of orchid diversity.

Across angiosperms, species richness is greater in families with broader geographical ranges and latitudinal extents (Ricklefs & Renner, 1994). Indeed, the area of ecozones or continents occupied explains 50% of the variance in log-transformed species richness in a phylogenetically structured analysis of 409 angiosperm families (Vamosi & Vamosi, 2011). There remains the central question of whether large areas or ecological volumes occupied cause large numbers of species or vice versa (Ricklefs & Renner, 1994, 2000; Dodd *et al.*, 1999; Givnish *et al.*, 2014). But given that orchids occur on all continents save Antarctica, and have one of the widest latitudinal ranges of any plant family – from 72°N for *Corallorhiza trifida* in the Canadian Arctic Archipelago to 55°S for *Chloraea*, *Codonorchis* and *Gavilea* in Tierra del Fuego (Pridgeon *et al.*, 1999–2014) – it seems plausible that high orchid diversity may partly reflect their broad distribution.

This raises what we term the ‘paradox of orchid dispersal’. On one hand, the broad distribution of orchids (and their great diversity) might partly reflect their excellent dispersal, conferred by the dust-like seeds of almost all species. On the other hand, frequent long-distance seed dispersal should work against differentiation within species and thus, ultimately, speciation (Givnish, 2010). Dressler (1981) suggested that only 34 orchid genera had been able to cross tropical oceans and establish disjunct distributions on continents long isolated from each other (i.e. South America, Africa and Southeast Asia). Such disjunctions are seen within genera or pairs of closely related genera in all orchid subfamilies except Apostasioideae, suggesting that they may often have arisen early enough for continental drift to affect present-day distributions (Dressler, 1981; Chase, 2001; but see Guo *et al.*, 2012). Such inferences are not based, however, on actual calculations tied to the ages of specific fossils. Only three orchid species reached the Hawaiian Islands by natural means (Wagner *et al.*, 1990), suggesting limits imposed by seed dispersal or by missing pollinators or fungal symbionts. Dozens of closely related species of *Teagueia* appear to have speciated within a few kilometres of each other in Andean Ecuador (Jost, 2004), which also seems consistent with short-distance dispersal of orchid seeds or their mutualists (Givnish *et al.*, 2015).

Where did the orchids originate? To what extent do relationships above the generic level reflect intercontinental dispersal or vicariance events? Does the remarkable diversity of orchids reflect their ability to disperse among continents, or

is that ability limited? Where did the key plant traits that appear to have accelerated net rates of orchid diversification arise?

Answers to these questions have been blocked by the lack of a well-resolved, strongly supported backbone phylogeny for the orchids. Givnish *et al.* (2015) recently derived such a phylogeny using a phylogenomics approach, calibrated against time using 17 angiosperm fossils. Here, we use this tree to estimate the historical biogeography of Orchidaceae, identify its area of origin, assess the roles of vicariance and intercontinental dispersal, and locate the origin of epiphytism, a key trait that appears to have accelerated orchid diversification (see also Chomicki *et al.*, 2015). We test whether occurrence on different continents had a significant effect on rates of speciation, extinction and net species diversification. Finally, we assess the extent by which long-distance dispersal (LDD) may have increased orchid diversity by asking how many species evolved in new ranges after LDD events. These across-family biogeographical analyses complement those that have been conducted on several smaller groups of orchids (Gravendeel *et al.*, 2004; Bouetard *et al.*, 2010; Smidt *et al.*, 2011; Guo *et al.*, 2012, 2015; Dueck *et al.*, 2014; Freudenstein & Chase, 2015).

MATERIALS AND METHODS

Phylogenetics and tree calibration

Our study uses the supermatrix tree of Givnish *et al.* (2015), based on sequences of 75 plastid genes for 39 orchid species and 96 angiosperm outgroups, and three plastid genes for another 162 orchid species. This analysis includes placeholders for all five subfamilies, 18 of 19 tribes, and 40 of 43 subtribes recognized by Chase *et al.* (2003), collectively representing 99.6% of all orchid species. We continue using the tribal and subtribal nomenclature of Chase *et al.* (2003) rather than its recent re-arrangement by Chase *et al.* (2015), to make our results regarding biogeography directly comparable to those in our earlier article devoted to plant traits (Givnish *et al.*, 2015).

Givnish *et al.* (2015) calibrated the single maximum-likelihood tree resulting from the supermatrix analysis against the ages of 17 angiosperm fossils using BEAST 1.80 (Drummond *et al.*, 2012) and branch lengths based on *atpB*, *psaB* and *rbcl* sequences. Dates and 95% highest posterior densities (hereafter, HPD) were calculated for each node. Here, we replace our sampling of Cyripedioideae with the more extensive set of taxa studied by Guo *et al.* (2012). We were unable to incorporate these directly in our dating analyses, as the only locus shared between the two datasets was *rbcl*. Instead, we replicated the BEAST analysis of Guo *et al.* and grafted the resulting time-calibrated phylogeny of cyripedioids onto ours. To refine modelling of geographical diversification in tribe Vanillaee, we grafted 12 *Vanilla* tips onto our tree, matching the topology and divergence times of representatives of the lettered clades in groups β and γ of

Bouetard *et al.* (2010), and used their results to graft *Pogonia japonica* as sister to *Pogonia minor* and *Cleistopsis* as sister to *Pogonia*. We included placeholders for a total of 173 orchid genera (21.7% of those tabulated by Chase *et al.* (2003).

Historical biogeography

We estimated ancestral areas on the modified BEAST chronogram using the maximum-likelihood approach implemented in BIOGEOBEARS (Matzke, 2014). BIOGEOBEARS incorporates a founder-event parameter for 'jump speciation', which allows cladogenetic dispersal outside parental areas. To test the effect of the J-parameter on ancestral-area estimation, we conducted two independent runs using DEC (dispersal–extinction–cladogenesis analysis) and DEC+J; two using DIVA and DIVA+J; and two using BayArea and BayArea+J. *A priori*, we considered DEC superior to the other models because it permitted speciation via the biologically relevant mechanisms of widespread vicariance and subset sympatry. We conducted likelihood ratio tests based on AICc scores on nested models to assess goodness of overall fits.

All tips were coded as present/absent in seven geographical regions (North America, Neotropics, Eurasia, Africa, Southeast Asia, Australia, Pacific) based on generic distributions acquired from Pridgeon *et al.* (1999–2014), eMonocot Team (2015) and WCSP (2015). Regional boundaries are discussed in Appendix S1. Representatives of individual genera were coded based on the entire distribution of that genus, except for species of Cypripedioideae and Vanilloideae grafted onto the phylogeny to represent lineages from different regions. In this placeholder analysis, terminal branch lengths to the taxa included are assumed to be accurate proxies for branch lengths to all species within genera, subtribes or tribes; deviations from this assumption are negligible at the scale of the entire orchid phylogeny. Ancestral-area estimations included representatives of Iridaceae and all astelid families (Asteliaceae, Blandfordiaceae, Boryaceae, Hypoxidaceae, Lanariaceae); the clade composed of the latter five families root at the node immediately above Orchidaceae in order Asparagales.

Relative dispersal probabilities among regions were constrained based on their emergent areas (particularly for Pacific islands) and widths of water barriers between areas during five time slices (0–2, 2–30, 30–60, 60–90 and 90–150 Ma; see Table S1 of Appendix S1). Dispersal probabilities between Australia and South America take into account their connection via then-warmer Antarctica during the two oldest periods (Givnish *et al.*, 2015). We considered movement between regions to be (1) long-distance dispersal (LDD) if it occurred over a substantial distance of water at the time of dispersal; (2) short-distance dispersal (SDD) across the short distances of water that separate Southeast Asia and Australia at Wallace's Line, or intermittently separate Eurasia and North America at Beringia; and (3) simple

geographical spread if regions were contiguous at the time of dispersal (e.g. Southeast Asia and Eurasia, or North America and the Neotropics after these areas came into near contact by the Middle Miocene [Montes *et al.*, 2012]). Distributions were considered a result of vicariance if ancestors had spread across formerly contiguous regions and then became extinct in an intervening region (e.g. Antarctica).

Stochastic mapping

We performed biogeographical stochastic mapping to estimate the number of dispersal events between each region, based on the dispersal and extinction parameters of our model, presence/absence of the terminal taxa in each region, and our ancestral-area estimation using BIOGEOBEARS. Following Matzke (2014), we calculated the average numbers of anagenetic range expansions (e.g. A→A+B), extinctions (e.g. A+B→A), range switches (A→B), cladogenetic range expansions involving sympatry or vicariance, and jump-dispersal events (e.g. A→A, B) from 50 stochastic maps to estimate the total number and directionality such events during orchid evolution. Although the number of placeholder taxa (~250) is small relative to the total number of species, the excellent representation at the subtribal level combined with many subtribes being restricted to a single region reduces the noise expected in this analysis. Conversely, distributional variation among species within genera or subtribes unaccompanied by dense sampling within those groups is likely to increase the variation detected via stochastic mapping.

Geographical correlates of rates of speciation, extinction and net diversification

We explored correlations between distribution in different regions and apparent rates of speciation, extinction and net species diversification using the BiSSE model (Maddison *et al.*, 2007) implemented in the R package Diversitree (FitzJohn *et al.*, 2009). BiSSE cannot calculate likelihoods on unresolved tips representing more than 190 taxa, so the numbers of species at all tips were down-weighted by a factor of 25, with small clades rounded up to 1 (Givnish *et al.*, 2014, 2015).

To test whether presence in a region affected diversification, we estimated the proportion of species present in each region for each of the taxonomic units comprising the tips of a pruned chronogram restricted to the set of subfamilies, tribes and subtribes employed by Givnish *et al.* (2015). We conducted analyses for orchids as a whole and for Epidendroideae. Data on the numbers of species in each taxonomic unit were drawn from Chase *et al.* (2003); data on the fraction of species distributed within and outside each region were derived from Pridgeon *et al.* (1999–2014), eMonocot Team (2015) and WCSP (2015). Where necessary, tallies of species occurrences for individual genera in each of the regions were down-weighted by the ratio of currently tabulated species to the total fide Chase *et al.* (2003). This

approach sidesteps issues raised by species, subtribes or tribes occurring in multiple regions by focusing, one region at a time, on the apparent effects of species presence versus absence in that region. This simplification seems reasonable, given that many of our taxonomic units and the great majority of individual species are restricted to single regions.

For each region, an unconstrained model for diversification was compared to models where speciation (λ), extinction (μ) and character-state transition rates (q) were individually constrained ($\lambda_0 = \lambda_1$, $\mu_0 = \mu_1$, $q_{01} = q_{10}$). Likelihoods of constrained models were compared to the unconstrained model, and significance of likelihood scores assessed using ANOVA. Net rates of diversification were calculated as $\lambda - \mu$. For each region, we measured the advantage in net diversification per million years within lineages conferred by a character state as $\zeta = \exp((\lambda_1 - \mu_1) - (\lambda_0 - \mu_0)) - 1$ (Givnish *et al.*, 2015). We used q_{10} as a measure of the extent to which a region served as a source of dispersal per-taxon present; q_{01} measured the extent to which it served as a target for dispersal from other regions per-taxon present in those regions.

Some authors have criticized BiSSE analyses as being sensitive to small sample sizes and extreme tip bias (Davis *et al.*, 2013) or correlations with characters not studied (Rabosky & Goldberg, 2015). Even after down-weighting by a factor of 25, we have 249 tips in the main analysis – close to the 300 recommended by Davis *et al.* Our epidendroid analysis, however, has only 99 tips, so inferences from it must be viewed with caution. Three of our seven regions (North America, Eurasia, Pacific) have <10% of the taxa (the threshold identified by Davis *et al.*), but none have especially high rates of speciation or diversification, so the reduced precision of rate inference for these would likely not be of great consequence (see Results). We have previously summarized the morphological and ecological correlates of high rates of orchid speciation and diversification (Givnish *et al.*, 2015) and discussed their wide distribution in the tropics, so confounding factors are unlikely to be an issue here.

Effects of intercontinental movements on orchid diversity

We calculated the number of species resulting from each of several selected LDD events across tropical oceans, based on the position of such events in the pruned chronogram and the number of species found per region in each tip. We studied (1) all LDD events, (2) the LDD event preceding the rise of the upper epidendroids and (3) the LDD events preceding the origins of the pleurothallid alliance, of Cymbideae minus Cymbidineae and of Angraecinae and Aerangidinae. We also identified the region associated with the origin of epiphytism at the base of the upper epidendroids – inferred by Givnish *et al.* (2015) – and whether the spread of epiphytism required additional LDD events.

RESULTS

Models including jump speciation provided a significantly better fit than those without (Table S2), so we used them to estimate historical biogeography. There were very few differences in ancestral age estimation using DEC+J, DIVA+J and BayArea+J, and so here we report the findings based on the biologically more reasonable DEC+J model. All dates described below are stem ages unless otherwise indicated. This model places the most likely origin of orchids in Australia 112 million years ago (Ma) (HPD: 102.0–120.0 Ma) (Fig. 1), when Africa and India/Madagascar had already separated from Antarctica and Australia, but Australia and South America remained connected via Antarctica. By the time that apostasioids diverged from other orchids 90 Ma (HPD: 79.7–99.5 Ma), the most likely distribution of the orchid crown was Australia+Neotropics, with the common ancestors of the vanilloids, cyripedioids and orchidoideae+epidendroids then originating most likely in the Neotropics roughly 84, 76 and 64 Ma, respectively (HPDs: 74.4–92.9, 64.6–87.4 and 54.8–73.7 Ma) (Fig. 1). Stem orchids arose in Australia under both DIVA+J and BayArea+J as well, with the initial orchids in Australia and the Neotropics under DIVA+J and in the Neotropics alone in BayArea+J. Under Dec+J, apostasioids reached Southeast Asia sometime during the last 43 Ma (HPD: 24.2–65.0 Ma) (Fig. 1), presumably via collision of the Australian and Eurasian Plates and short-distance dispersal.

Within vanilloids, tribe Pogonieae apparently underwent long-distance dispersal from the Neotropics to North America ca. 44 Ma (HPD: 33.5–54.9 Ma), spawning *Cleistosiopsis*, *Isotria* and *Pogonia*, with the latter moving to Eurasia within the last 11 Myr (HPD: 9.1–26.2 Ma) (Fig. 1). Tribe Vanilleae originated in the Neotropics and underwent long-distance dispersal across the Pacific 64–59 Ma (HPDs: 55.1–73.4 Ma, 47.9–69.0 Ma) to New Caledonia, leading to *Clematepistephium* and *Eriaxis*. *Vanilla* originated in the Neotropics ca. 61 Ma (HPD: 51.6–70.0 Ma), underwent LDD to Africa 26–18 Ma, and then moved from Africa via LDD into the Indian Ocean 13 Ma, and from Africa to the Caribbean 12–4 Ma (last several dates based on grafted branches) (Fig. 1). The remaining clade (*Pseudovanilla* through *Cyrtosia*) appears to have originated in Australia or Southeast Asia 61 Ma (HPD: 51.6–70.0 Ma) after LDD from the Neotropics, and then spread into Southeast Asia and further overland into East Asia in some *Cyrtosia*. *Pseudovanilla* appears to have undergone LDD to Pohnpei and Fiji in the Pacific 31–6 Ma (HPDs: 22.3–58.5 Ma, 2.1–11.2 Ma).

Subfamily Cyripedioideae and the genera *Cyripedium*, *Selenipedium*, *Phragmipedium* and *Mexipedium* appear to have arisen in the Neotropics roughly 76, 31, 28, 23 and 21 Ma, respectively (HPDs: 64.6–87.4, 30.2–43.0, 18.0–39.2, 14.1–33.3 and 12.4–31.5 Ma) (Fig. 1). *Cyripedium* spread into Eurasia (and rarely, Southeast Asia) and then back into North America several times. *Paphiopedilum* appears to have

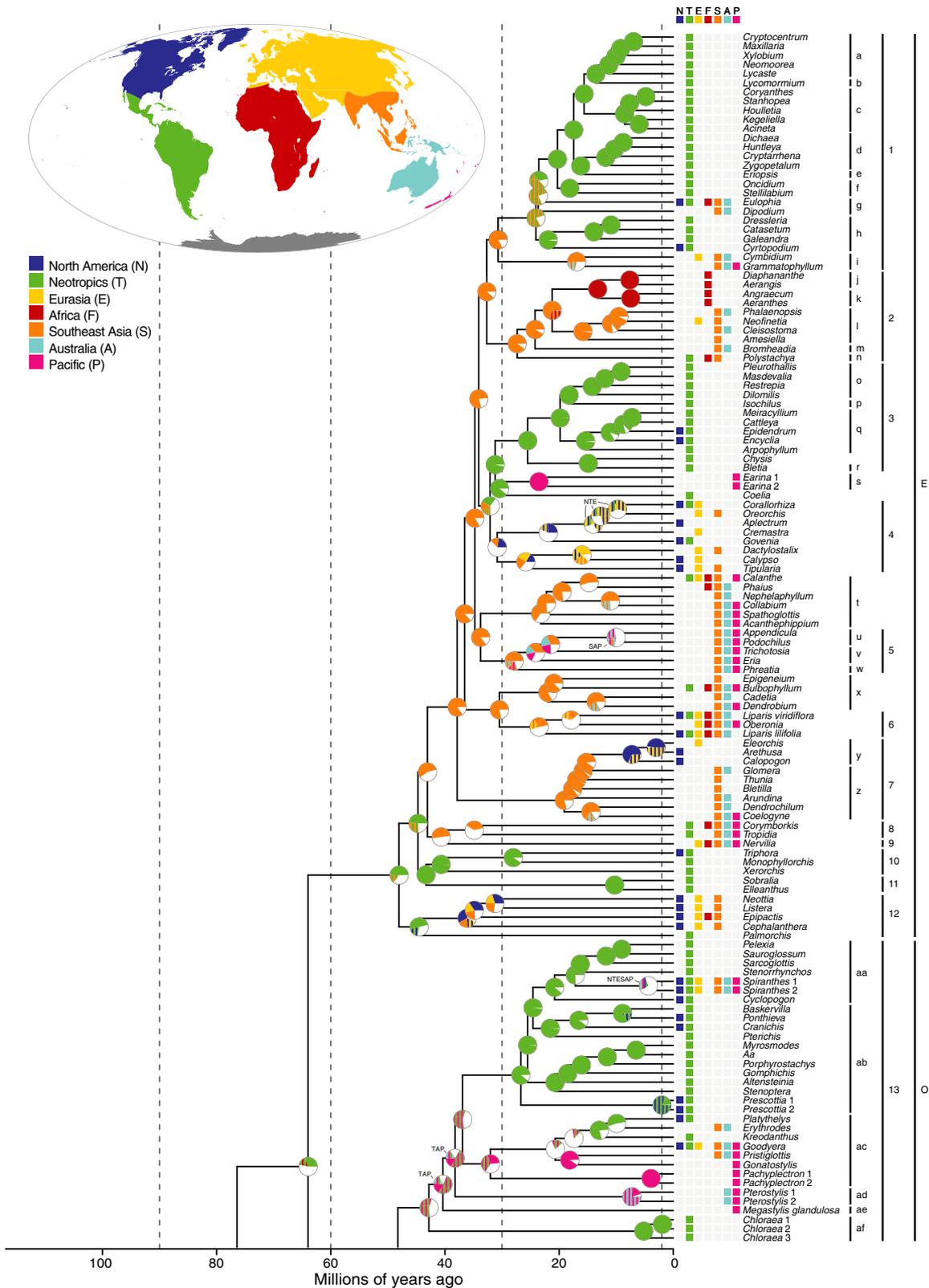


Figure 1 Diagram depicting estimation of orchid historical biogeography using BioGEOBEARS. Pie diagrams at each node denote the geographical regions (or combinations thereof) inferred to have been occupied by ancestral taxa. Wedge colour indicates ancestral region (see inset), wedge width, the probability of that region or combination of region. Combination of regions are indicated by hatching of colours or by lettering; white wedges indicate the sum of origins in regions (or regional combinations) with individual probabilities < 15%. Distributions of genera and individual species are indicated by coloured boxes. Vertical lines with numbers and letters indicate subtribes, tribes and subfamilies. Complete names for these lineages are provided in Figure S2, together with the pie diagrams on the shoulders of each node.

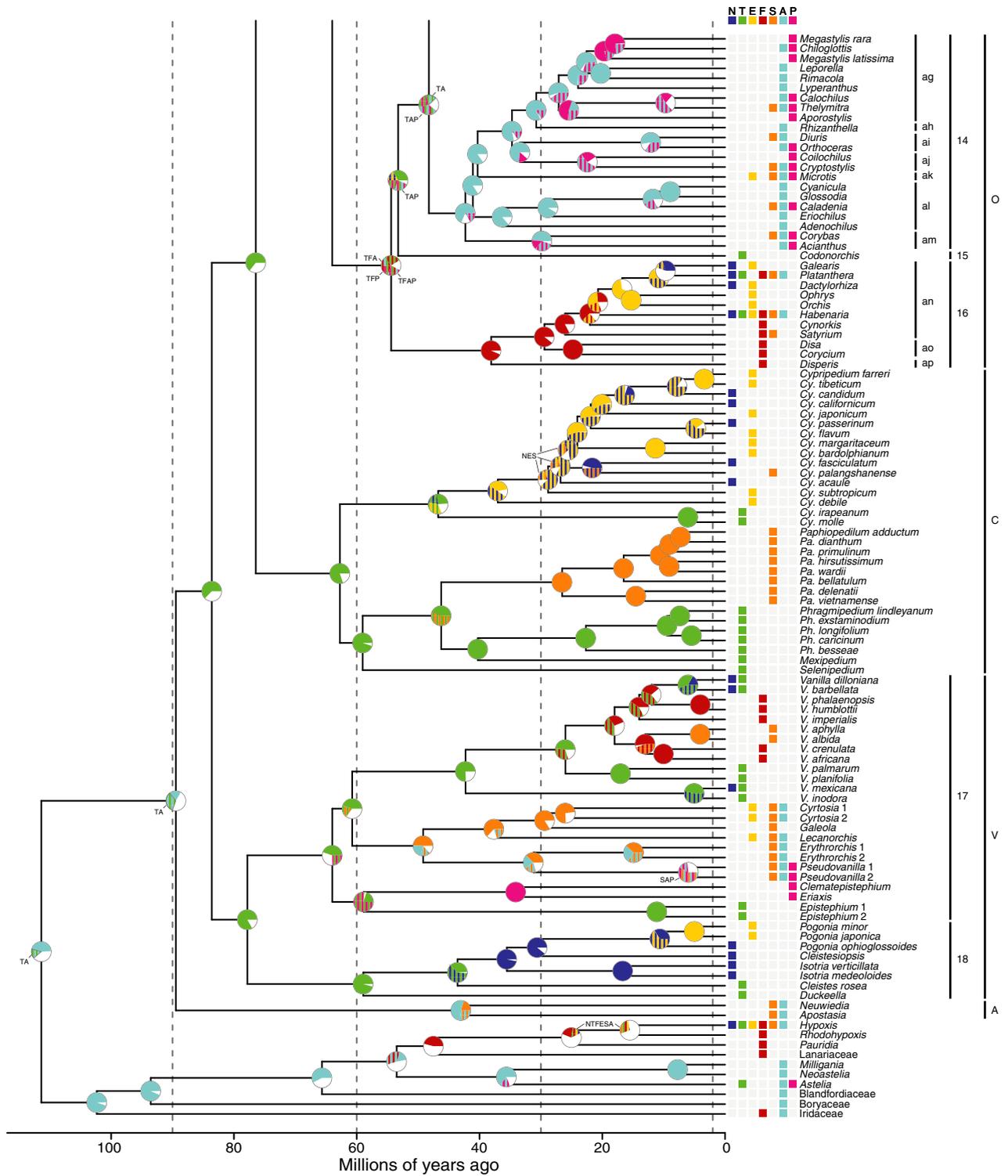


Figure 1 Continued.

colonized Southeast Asia from the Neotropics 46 Ma (from grafted branch), most likely involving long-distance dispersal via boretropical migration through Beringia.

Orchidoideae arose via range expansion from the Neotropics to include Africa, together with Australia and/or the Pacific, with Orchidoideae spreading from Africa into Eurasia and

ultimately North America and Japan. *Codonorchis* remained in South America, where it today occurs in the far south. Diurideae spread to Australia and then to Southeast Asia, New Zealand and New Caledonia. Cranichidae underwent a major diversification in the Neotropics, with dispersal to North America in *Cranichis* and *Spiranthes*, and dispersal to

Australia and the Pacific in *Pachyplectron*, *Pterostylis* and relatives (Fig. 1).

Epidendroids appear to have arisen in the Neotropics ca. 64 Ma (HPD: 54.8–73.7 Ma), with subsequent dispersal to Eurasia, Southeast Asia and North America in Neottieae. Dispersal to Southeast Asia occurred in the vast clade of epidendroids sister to Sobralieae + Triphoreae, including Tropideae and Nervileae (Fig. 1). Two long-distance dispersals back to the Neotropics from Southeast Asia appear to have occurred: in the large clade allied with the pleurothallids (Coelia-Agrostrophyllinae-Bletiinae-Laeliinae-Pleurothallidinae-Ponerinae) roughly 32 Ma (28.4–34.2 Ma), with LDD to the Pacific in Agrostrophyllinae (*Earina*) 30 Ma (HPD: 26.7–35.1 Ma); and in Cymbideae minus Cymbidinae, between 31 and 24 Ma (HPDs: 26.5–34.9 and 17.5–26.7 Ma), with dispersal in Cymbidinae to Australia, the Pacific basin, and Eurasia in the last 17 Ma (HPD: 10.3–24.0 Ma) (Fig. 1). Calypsoeae appears to have undergone LDD from Southeast Asia to North America 32 Ma (HPD: 28.4–35.9 Ma) and then spread back to Eurasia and Southeast Asia at least twice. Arethuseae appears to have undergone LDD from Southeast Asia from North America 15 Ma (HPD: 8.5–18.4 Ma) and then dispersed back to Southeast Asia to form *Eleorchis*. Aerangidinae and Angraecinae of Vandeeae appear to have arisen in Africa after LDD from Southeast Asia 21 Ma (HPD: 17.5–24.0 Ma). Secondary LDDs from Southeast Asia to Australia and the Pacific Basin appear to have occurred in Collabinae, Podochileae, Dendrobieae and *Phreatia* (Fig. 1). The main difference between the DEC+J and BAYAREA+J estimations is that movements to the Neotropics in Cymbideae and Epidendreae are from Southeast Asia in the former and from Australia and Southeast Asia in the latter (Fig. S1 of Appendix 1).

Stochastic mapping

BIOGEOBEARS inferred an average total of 15.0 jump-dispersal events and 121 anagenetic dispersal events; there were also 225.9 cladogenetic events involving extinction but not dispersal (Tables S3–S5 of Appendix S1). Sixteen of 69 jump-dispersal scenarios had a mean occurrence ≥ 0.3 , totalling 10.3 of 15.0 events; 51 of 312 anagenetic scenarios had a mean occurrence ≥ 0.3 , totalling 121 of 138.7 events. Of the more common jump-dispersal events, 8.4 (82%) involved LDD, 1.5 (14%) involved SDD across Wallace's Line or Beringia and 0.44 (4%) involved simple spread over contiguous areas (Table S4). Of the more common anagenetic dispersal events, 65.9 (55%) involved LDD, 40.3 (34%) involved SDD and 12.6 (11%) involved simple geographical spread. Our analysis, thus, identified at least 74.3 LDD events in the history of orchid evolution (Table S5). Most anagenetic migrations were between adjoining regions.

Effects of geographical distribution on diversification

Different regions had different effects on speciation, extinction and net species diversification (Tables 1, S6). Across orchid history, presence in Southeast Asia led to the highest advantage in net diversification rate relative to other regions per million years ($\zeta = 15.4\%$), with the second highest advantage in Australia ($\zeta = 7.7\%$); the remaining regions had only small advantages or disadvantages in diversification. Speciation and extinction rates were significantly lower in Southeast Asia and Australia than elsewhere. In general, diversification rates were not correlated significantly with λ_1 or μ_1 , but – as expected – were highly correlated with

Table 1 Apparent rates of speciation (λ), extinction (μ) and character-state transition (q) associated with presence in particular regions for orchids as a whole and for epidendroids. States with significantly higher rates are indicated by * ($P < 0.05$), ** ($P < 0.01$) and *** ($P < 0.001$). $D_1 = (\lambda_1 - \mu_1)$ measures the diversification rate associated with a particular distribution; $\zeta = \exp((\lambda_1 - \mu_1) - (\lambda_0 - \mu_0)) - 1$ measures the advantage in net diversification ($r = \lambda - \mu$) per million years within lineages conferred by that distribution.

	λ_1	λ_0	μ_1	μ_0	D_1	ζ	q_{01}	q_{10}
Orchidaceae								
Southeast Asia	0.159	0.751***	4.4×10^{-5}	0.735***	0.159	15.4%	0.0014	0.117***
Australia	0.119	0.662***	2.5×10^{-6}	0.616***	0.119	7.7%	0.0015	0.0791***
Neotropics	0.471	0.311	0.388	0.260	0.083	3.2%	0.0075*	0.0006
Africa	0.280	0.503	0.236	0.454	0.044	–0.2%	0.0037	0.0309*
Eurasia	0.049	0.406***	1.5×10^{-5}	0.339***	0.049	–1.8%	0.0017	0.0467***
North America	0.143	0.440*	0.111	0.378	0.032	–3.0%	0.0057*	0.0007
Pacific	7.0×10^{-6}	0.477***	2.0×10^{-5}	0.422***	0.000	–5.6%	0.0047	0.0414**
Epidendroideae								
Neotropics	0.186	0.316***	4.9×10^{-6}	0.003***	0.186	11.5%	0.0033***	2.6×10^{-8}
Australia	0.126	0.372*	3.2×10^{-7}	0.255*	0.126	9.1%	0.0007	0.0000
Southeast Asia	0.129	0.425*	5.3×10^{-6}	0.310	0.129	1.5%	8.1×10^{-4}	0.0510***
Eurasia	0.042	0.281***	7.0×10^{-6}	0.153	0.042	1.5%	0.0410*	0.0015
Africa	0.193	0.464	0.086	0.381	0.107	0.2%	0.0028	0.0320*
Pacific	0.014	0.439***	2.5×10^{-8}	0.345***	0.014	–7.7%	0.0048	0.0444
North America	0.297	0.392***	0.756**	0.297	–0.459	–42.6%	0.0058	1.9×10^{-5}

($\lambda_1 - \lambda_0$) ($r = 0.988^{***}$) and ($\mu_1 - \mu_0$) ($r = -0.904^{***}$). Southeast Asia was also the strongest per-taxon source area, reflecting the proximity of Eurasia to New Guinea and off-shore islands. Australia was the second strongest source. Across epidendroids, presence in the Neotropics led to the highest diversification rate relative to other regions ($\zeta = 11.5\%$) (Table 1). Southeast Asia was again the strongest source; Eurasia was the strongest target. North America had by far the greatest disadvantage in diversification ($\zeta = -42.6\% \text{ Myr}^{-1}$), presumably because it is the least tropical of the regions and epidendroids are mostly tropical in distribution. Speciation and extinction rates were not correlated significantly with relative diversification rates, or relative advantage in extinction rates ($\mu_1 - \mu_0$), but speciation rates were highly correlated with ($\lambda_1 - \lambda_0$) ($r = 0.988^{***}$). Southeast Asia was both the strongest per-taxon source and target during epidendroid evolution (Table 1).

Effects of dispersal on diversification at large spatial scales

The products of all LDD events following the vicariant spread of the family to the Neotropics and Australia include all orchids save ca. 675 species, or 2.7% of all orchids tabulated by Chase *et al.* (2003). Just one LDD event, from the Neotropics to Southeast Asia roughly 48 Ma (HPD: 40.5–56.9 Ma) – in the common ancestor of Nervilieae, Tropidieae and the upper epidendroids (Fig. 1) – precedes diversification of 79.4% of all orchid species within the new range. A later LDD event, from Southeast Asia to the Neotropics roughly 31 Ma (25.0–38.9 Ma) – in the common ancestor of Blettiinae, Laeliinae, Pleurothallidinae and Ponerinae – accounts for 5857 species, or 23.5% of all orchid species. The LDD event in the same direction that led to Cymbideae minus Cymbidinae 24 Ma (HPD: 20.1–28.1 Ma) accounts for 14.9% of all orchids; the LDD event from Southeast Asia to Africa 21 Ma (HPD: 16.1–26.5 Ma) that led to Angraecinae and Aerangidae generated 3.1% of all orchids.

Overall, 160 orchid species among the clades tabulated occur in North America, 11,448 in the Neotropics, 595 in Eurasia, 2583 in Africa, 5444 in Southeast Asia, 4405 in Australia and 777 in the Pacific. Given the total number of orchid species in these clades, this implies that only 2.6% of individual orchid species occur in more than one region. Epiphytism appears to have arisen in the upper epidendroids in Southeast Asia, with the spread of epiphytic orchids throughout the tropics requiring several subsequent LDD events.

DISCUSSION

Orchids appear to have arisen in Australia 112 Ma (see Results for HPDs of this and all other phylogeny-based dates mentioned below) and then migrated to South America via Antarctica by 90 Ma (Fig. 1). Between 100 and 48 Ma, global temperatures reached exceptional highs driven by rising

atmospheric CO₂ levels; Antarctica had a summer maximum temperature of ca. 20°C and supported tropical to subtropical vegetation (Pross *et al.*, 2012). A growing list of monocot genera and families are known to have a disjunct distribution in Australia and South America, represented by extant or fossil taxa, supporting an Antarctic connection (Conran *et al.*, 2015). The origin of Liliales in Australia (Givnish *et al.*, 2016) and the origin of the commelinid orders in South America – then connected to Antarctica and thus Australia (Givnish *et al.*, 1999) – bracket the origin of the orchids and reinforce the conclusion that orchids arose in Australia. Fossil pollen from Antarctica from 52 Ma indicates the presence of palms and near-tropical rain forests even at that late date (Pross *et al.*, 2012). It is ironic that Antarctica – the one continent where orchids currently are not found – appears to have played a key role in early orchid evolution.

Dressler (1981) argued that, of the 33 orchid genera with disjunct distributions on continents separated by tropical oceans (South America, Africa and Southeast Asia), only five might be old enough to reflect vicariance based on continental drift. However, our data indicate that these ‘old’ disjunctions – in *Vanilla*, *Corymborkis*, *Palmorchis-Diceratosteles*, *Epistephium-Clematepistephium* and *Tropidia* – are in fact too recent to reflect continental drift and instead seem to be products of long-distance dispersal. Dressler (1981) recognized the distinctiveness of the orchid floras on each of the three tropical continental regions and suspected that they evolved after they had separated from each other. Our data support a more complex scenario, with multiple introductions to each region. Dressler realized that exchanges between North America and Eurasia could have occurred frequently during the Cenozoic as a result of intermittent land bridges across Beringia and the North Atlantic. Based on early, time-calibrated broad-scale phylogenies for angiosperms, Chase (2001) concluded that orchids likely arose around 110 Ma and might have evolved on Gondwana. However, he argued that trying to identify the continent on which they arose was futile, given how close the continents were to each other then.

Our biogeographical estimation suggests that 15 transoceanic LDD events resulted in the origin of orchid tribes or smaller groups restricted or nearly so to individual continents, and occurred long after the breakup of Gondwana. These events were (1–2) from Southeast Asia to Neotropics twice, forming Cymbideae minus Cymbidinae and the pleurothallid alliance; (3) from Southeast Asia to Africa, forming Angraecinae + Aerangidae; (4) from Southeast Asia to North America, forming large parts of Calypsoeae; (5–6) from Neotropics to Southeast Asia twice, forming Neottieae and the upper epidendroids + Tropidieae + Nervilieae; (7–9) from Neotropics to Africa forming Orchideae, to Australia forming Diurideae, and to the Pacific forming Pterostylidinae and part of Goodyerinae; (10–11) from the Pacific to Neotropics twice, forming part of Goodyerinae and Spiranthininae; (12) from Neotropics to Africa, forming part of *Vanilla*; (13) from Africa back to the Caribbean, forming more of *Vanilla*;

(14) from Neotropics to Southeast Asia, forming part of *Vanilleae*; and (15) from Neotropics to the Pacific, forming *Clematopistephium* + *Eriaxis* (Fig. 1). The movement of apotasioids from Australia to New Guinea and thence across Wallace's Line to Southeast Asia presumably occurred after the Australian, Eurasian and Pacific plates began to collide 25 Ma, causing the uplift of New Guinea and nearby islands (Pigram & Davies, 1987).

Over time, relatively low rates of dispersal – and/or dispersal over relatively short distances – should maximize speciation and net rates of diversification. At the scale of our sampling, orchids underwent about 74 transoceanic LDD events in 90 Ma, or 0.8 events Ma^{-1} – not a very high rate, less than ca. 1.3 events Ma^{-1} for *Dryopteris* over the past 25 Ma (Sessa *et al.*, 2012), and far less if expressed in events $\text{species}^{-1} \text{Ma}^{-1}$.

Integrated across orchid history, Southeast Asia had the highest net diversification rates and was the strongest source area (Table 1). The geological history of Southeast Asia is unusually complex, reflecting early collisions of Gondwanan fragments with the Eurasian plate and later collisions of the latter with the Australian, Pacific and Philippine plates (Hall, 2009). By 80 Ma, Gondwanan fragments had sutured to Eurasia, forming western Malesia, much of which remained above water after 65 Ma. In the middle Eocene, rifting of the Makassar Strait formed a deep channel that persisted through the Cenozoic and separated the Australian plate from emergent parts of the Sunda Shelf (Hall, 2009). Numerous north–south mountain ranges (e.g. Tenasserim, Kayah-Karen, Luang Prabang) mark mainland Southeast Asia and grade into the Hengduan and Himalayan massifs to the west; all were uplifted by continuing collision of the Indian plate with Eurasia over the past 50 Myr and provide extensive venues for speciation (Yu *et al.*, 2015). Importantly, these mountains and the volcanoes of insular Southeast Asia are most likely where epiphytism evolved in epidendroids and then spread around the world. Repeated fluctuations in sea level and climate fragmented rain-forest areas during the Pleistocene and probably fostered extensive speciation in insular and mainland Southeast Asia (Guo *et al.*, 2012, 2015; Thomas *et al.*, 2012). Southeast Asia is one of the world's leading hotspots for plant diversity, with 42,000 species of vascular plants (Brooks *et al.*, 2006). Integrated biogeographical studies of 29 plant and animal clades clearly separate Southeast Asia west of Wallace's Line from Australia, New Guinea and Pacific islands (Turner *et al.*, 2001). Southeast Asia's position would have facilitated orchid dispersal into the adjoining Australian region and warmer parts of contiguous Eurasia.

Across all orchid history, Australia is second in net diversification rate and the second strongest source area for migration (Table 1). Most orchids in this region are restricted to New Guinea, Sulawesi and nearby islands, all of which have complex histories. Western Sulawesi rafted from Borneo in the middle Eocene; eastern Sulawesi, the Moluccas, the lesser Sunda islands and New Guinea resulted from collision of the

Australian, Eurasian and Pacific plates 25 Ma (Pigram & Davies, 1987; Hall, 2009). Much of this area emerged only during the late Miocene, but southeastern Sulawesi and smaller, short-lived islands emerged by 20 Ma (Hall, 2009) and presumably facilitated short-distance dispersal of apotasioids from the Australian mainland (see Results). The New Guinea orogeny began 10 Ma, with over 30 smaller terranes assembled on the northern periphery of the oncoming Australian plate (Hall, 2009; Baldwin *et al.*, 2012). The great area, height and topographic complexity of the New Guinea Highlands favoured the evolution of large numbers of orchids over the last 10 Myr (De Vogel & Schuiteman, 2001; Schuiteman *et al.*, 2010; Givnish *et al.*, 2015). New Guinea's position, in turn, would have facilitated dispersal into Southeast Asia and tall, wet islands of the southwest Pacific.

It is surprising that the Neotropics showed such a low advantage (3.2% Myr^{-1}) relative to other regions in net diversification, given that the fastest speciating groups of orchids (*viz.*, Pleurothallidinae, Laeliinae and close relatives [Givnish *et al.*, 2015]) are found in tropical America. However, the Neotropics were also the cradle of several ancient, low-diversity lineages (*viz.*, Vanilloideae, Cyrtipedioideae) with very low rates of diversification (Givnish *et al.*, 2015). When we restrict attention to more recent history and focus on epidendroids (crown group ca. 48 Ma), the Neotropics are indeed characterized by the highest rates of diversification ($\zeta = 11.5\%$ in Table 1) and speciation relative to other regions ($\lambda_1 - \lambda_0 = 0.186$). These unusually high rates may be tied to the uplift of the northern Andes over the past 15 Myr and increased access to Central America from South America over the same period (Givnish *et al.*, 2014). Both areas are geographically extensive and climatically and topographically complex. The Andes especially have been shown to foster rapid speciation in bromeliads and orchids (Givnish *et al.*, 2014, 2015) and many other groups (Hughes *et al.*, 2013), and they are the leading hotspot for plant biodiversity worldwide (Brooks *et al.*, 2006). Two exceptionally diverse groups – the pleurothallid alliance and Cymbideae minus Cymbidinae – are largely restricted to the northern Andes and Central America. Detailed phylogenies and biogeographical estimations at finer geographical scales of these two clades could be used to test these hypotheses. Both should show a substantial increase in speciation and the narrowness of species ranges starting 15 Ma.

Finally, the relatively low rate of long-distance dispersal by orchids worldwide appears to have played a key role in their diversification. The products of all LDD events following the vicariant origin of orchids in Australia and the Neotropics include 97.3% of present-day orchid species. This suggests that access provided by LDD to other continental areas – and the possibilities for speciation, range expansions and avoidance of extinction afforded by their landforms, geographical extent, pollinators and mycorrhizal partners – increased orchid diversity by 36-fold, directly and indirectly. LDD from the Neotropics to Southeast Asia at the base of the upper epidendroids + Sobralieae + Triphoreae alone

appears to have multiplied orchid diversity fivefold; LDD from Southeast Asia to the Neotropics 32 Ma to form the pleurothallid alliance alone appears to have generated nearly one-quarter of present-day species. Yet limited dispersal of dust-like seeds in tropical mountains is at least one possible driver of high local diversity (Givnish *et al.*, 2015). Thus, while pollinia, epiphytism, life in extensive tropical cordilleras and specialization on particular groups of pollinators all accelerated orchid diversification (Givnish *et al.*, 2015), infrequent long-distance dispersal also played an important role by permitting occasional access to new regions and pools of mutualists. Geographically, the three significant accelerations of net species diversification (Givnish *et al.*, 2015) correspond to (1) LDD from the Neotropics to Africa, Australia and the Pacific basin; (2) LDD from the Neotropics to Southeast Asia, followed by invasion of higher elevations and the evolution of epiphytism; and (3) invasion of the northern Andes by the pleurothallid alliance. We stand by our original interpretation of these accelerations as reflecting the origins of (1) pollinia, (2) epiphytism and (3) invasion of an extensive tropical cordillera, but here we identify where these key morphological and ecological shifts occurred.

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SUPPORTING INFORMATION

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

Appendix S1 Additional methods, tables and figure.

BIOSKETCH

This article is the product of an international collaboration among specialists in orchid systematics, phylogenetics, ecology and biogeography.

Author contributions: T.J.G. and D.S. designed the study and conducted the analyses; T.J.G., S.P.L, S.J.H, A.D., G.G.C. and J.M. compiled distributional data; T.J.G. wrote the first draft; all authors except A.D., G.G.C. and J.M. produced the time-calibrated phylogeny.

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