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RESEARCH ARTICLE

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Deep vicariance and frequent transoceanic dispersal shape the evolutionary history of a globally distributed fern family

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Abstract

Premise: The historical biogeography of ferns is typically expected to be dominated by long-distance dispersal due to their minuscule spores. However, few studies have inferred the historical biogeography of a large and widely distributed group of ferns to test this hypothesis. Our aims were to determine the extent to which long-distance dispersal vs. vicariance have shaped the history of the fern family Blechnaceae, to explore ecological correlates of dispersal and diversification, and to determine whether these patterns differ between the northern and southern hemispheres.

Methods: We used sequence data for three chloroplast loci to infer a time-calibrated phylogeny for 154 of 265 species of Blechnaceae, including representatives of all genera in the family. This tree was used to conduct ancestral range reconstruction and stochastic character mapping, estimate diversification rates, and identify ecological correlates of diversification.

Results: Blechnaceae originated in Eurasia and began diversifying in the late Cretaceous. A lineage comprising most extant diversity diversified principally in the austral Pacific region around the Paleocene–Eocene Thermal Maximum. Land connections that existed near the poles during periods of warm climates likely facilitated migration of several lineages, with subsequent climate-mediated vicariance shaping current distributions. Long-distance dispersal is frequent and asymmetrical, with New Zealand/Pacific Islands, Australia, and tropical America being major source areas.

Conclusions: Ancient vicariance and extensive long-distance dispersal have shaped the history of Blechnaceae in both the northern and southern hemispheres. The exceptional diversity in austral regions appears to reflect rapid speciation in these areas; mechanisms underlying this evolutionary success remain uncertain.

KEYWORDS

diversification, ferns, historical biogeography, long-distance dispersal, phylogeny, pteridophytes, vicariance

The various major land plant lineages are each defined by a combination of morphological characters that in most cases are distinctive, easily diagnosable, and often iconic traits of each particular group. Examples include the flowers and fruits of angiosperms and cones of gymnosperms. Ferns are similarly often characterized by one of their major reproductive features: they are seed-free and produce spores. Historically, this aspect of their biology (i.e., having spores as their major dispersal unit) has led ferns to be characterized as consummate dispersers (Tryon, 1986; Barrington, 1993; Wolf et al., 2001; Moran, 2008; Kessler, 2010), since their minuscule, dust-like spores are capable of traveling up to thousands of kilometers (Muñoz et al., 2004). Indeed, fern spores have even been recovered from the wings of transoceanic airplanes and were shown to germinate (Gradstein and van Zanten, 1999). While a role for vicariance in the historical biogeography of ferns has been acknowledged (Barrington, 1993; Kato, 1993; Haufler, 2007; Kessler, 2010), ferns' exceptional dispersal abilities have led to the general assumption that long-distance dispersal (LDD) should be the dominant feature discernable in their biogeographic histories, with little evidence expected for vicariance (Tryon, 1985; Wolf et al., 2001) or dispersal limitation (Karst et al., 2005; Qian, 2009).

Although LDD has widely been considered the main process shaping fern distributions at a global scale, credible evidence for vicariance has nonetheless been recovered for several fern genera, including *Dryopteris* (Sessa et al., 2012a, 2012b), *Pteridium* (Der et al., 2009), *Adiantum* (Paris and Windham, 1988), *Onoclea* (Gastony and Ungerer, 1997), *Nephrolepis* (Hennequin et al., 2010), *Deparia* (Kuo et al., 2016), *Trichomanes* (Dubuisson et al., 2022), *Polystichum* (Le Péchon et al., 2016), *Diplazium* (Wei et al., 2015), *Ptisana* (Lehtonen et al., 2020), *Eupodium* (Lehtonen et al., 2020), *Dicksonia* (Noben et al., 2017), and *Cyathea* and *Sphaeropteris* (Korall and Pryer, 2014). Other than the Gondwanan origin posited for the last five lineages (Korall and Pryer, 2014), these studies have found vicariance to have played a larger role in the northern than in the southern hemisphere, while LDD has dominated in the south and is consistent with the findings of Muñoz et al. (2004) that "wind highways" have played a prominent role in shaping floristic similarities of the southern continents. Indeed, recent studies have presented ample evidence for long-distance dispersal in southern-hemisphere fern lineages such as grammitid ferns (Sundue et al., 2014; Bauret et al., 2017a), *Rumohra* (Bauret et al., 2017b), and *Microgramma* (Almeida et al., 2021). These contrasting hemisphere-level patterns appear to reflect differences in geographic connectivity during the Cenozoic, with landmasses in the northern hemisphere having been more frequently connected by land bridges during this period (Tiffney and Manchester, 2001). In comparison, austral landmasses have been relatively isolated from each other for much of the Cenozoic, although a dynamic history of trans-Antarctic connectivity played an important role in the biogeography of some lineages (Sanmartín and Ronquist, 2004; Wang and Ran, 2014; Duellman et al., 2016).

Recent advances in methods for studying biogeographic and diversification processes now allow more sophisticated analyses of biogeographic history and the abiotic and biotic correlates of diversification and dispersal. The time is therefore ripe to re-examine the historical patterns of fern movements and revisit "the most basic arguments in fern biogeography", regarding the relative roles of long-distance dispersal and vicariance (Barrington, 1993, p. 276). Here, we used a robust phylogenetic framework to reconstruct and analyze the biogeographic history of a large, globally distributed family of ferns that is species-rich in the southern hemisphere: Blechnaceae. Blechnaceae is an excellent group for a study of this kind, as it has a cosmopolitan distribution and is well represented in all major geographic regions (except the poles). Blechnaceae is a primarily tropical family, though a substantial number of species are in temperate regions. The family is particularly prominent in south temperate regions, thereby allowing for the relative roles of dispersal and vicariance as drivers of diversity in austral groups to be assessed.

A member of the eupolypods II group of ferns (order Polypodiales, suborder Aspleniineae [PPG I, 2016]), Blechnaceae includes approximately 265 species and has two major centers of diversity, in the neotropics and Australasia/Oceania (PPG I, 2016; Gasper et al., 2017). Individual taxa occupy a wide range of habitats and growth forms, and members of the family are characterized (and easy to identify) by several morphological synapomorphies: the

FIGURE 1 Characteristics of Blechnaceae taxa. (A) Reddish young leaves. (B) Parallel, linear sori on either side of pinna midveins. (C) Multiple vascular bundles in the petiole. (A, B) *Blechnum occidentale*. (C) *Blechnum* sp. Images by E. B. Sessa.

tendency for young leaves to be reddish (Figure 1A), linear sori (spore-bearing structures) that are generally parallel and open toward the mid-veins (Figure 1B), and the presence of multiple vascular bundles in the petiole (as opposed to two bundles, which occurs in the remaining members of eupolypods II; Figure 1C) (Gasper et al., 2016, 2017). Recent taxonomic and phylogenetic work on the family has clarified the relationships among major lineages and expanded the number of genera to 25 (Gasper et al., 2016, 2017; Molino et al., 2019a). Some of these genera are relatively large, including *Parablechnum* (65 spp.), *Austroblechnum* (40 spp.), and *Blechnum* (30 spp.), while most are fairly small, with 15 genera having 10 or fewer species (including seven that are monospecific) (Gasper et al., 2016, 2017). Here, we reconstructed a dated phylogeny for Blechnaceae and used model fitting to test alternate models for the historical biogeography of the family. We also evaluated the diversification history of Blechnaceae and quantified dispersal and diversification in time and space.

MATERIALS AND METHODS

Phylogenetic inference

We used existing DNA sequence data from recent phylogenetic studies (Perrie et al., 2014; Gasper et al., 2017; Vicent et al., 2017; Molino et al., 2019a) to infer the evolutionary relationships of 156 Blechnaceae taxa, which represent 59% of extant diversity (of 265 estimated species in the family [Gasper et al., 2016; PPG I, 2016]). When necessary, taxonomy was resolved to match the most recent taxonomic treatment for Blechnaceae (Gasper et al., 2016). Thirty-five additional species belonging to Onocleaceae, Woodsiaceae, and Athyriaceae were chosen as outgroups based on recent phylogenies of eupolypods II ferns (Sundue and Rothfels, 2014; Gasper et al., 2017), for a total of 191 species in the data set. Sequence data for chloroplast markers *rbcL*, *rps4-trnS*, and *trnL-F* were downloaded from GenBank, and data for each region were aligned separately using the MAFFT v. 1.3.5 plugin (Katoh and Standley, 2013) in Geneious R9 (Kearse et al., 2012) before being concatenated. PartitionFinder v. 2.1.1 (Lanfear et al., 2017) was used to identify the optimal partition and model scheme for the concatenated matrix, with each marker evaluated independently.

We conducted maximum likelihood analyses using IQTree 1.6.10 (Nguyen et al., 2015) with ultrafast bootstrapping (Hoang et al., 2018) and a partitioned data set (Chernomor et al., 2016) where each locus was modeled independently. BEAST v. 2.4.7 (Bouckaert et al., 2014) was used to reconstruct a dated phylogeny for Blechnaceae. We employed three fossil constraints, modeled as follows: the crown node of subfamily Woodwardioideae and the node uniting *Onoclea* with *Onocleopsis* plus *Matteuccia* were both constrained to 55.8 million years ago (Mya), based on fossils attributed to *Woodwardia* (Collinson, 2001) and *Onoclea sensibilis* (Rothwell and Stockey, 1991), respectively, and the crown node of Athyriaceae was constrained to 37.2 Mya based on an athyrioid fossil (Stockey et al., 1999). All three fossils were modeled using a gamma prior distribution, and we used R (R Core Team, 2016) to explore various combinations of the alpha and beta parameters that would make the median age for each node slightly older than its respective fossil, with a tail long enough that the ages estimated for these nodes in two previous studies (Schuettpelz and Pryer, 2009; Testo and Sundue, 2016) were included in the 95% confidence intervals. The values for the gamma distribution that achieved these criteria were the same for all three fossils: alpha = 2.0 and beta = 3.0, with the offset equal to the age of the fossil (55.8, 55.8, and 37.2, respectively). We conducted two independent BEAST runs for 50,000,000 generations each, using an uncorrelated, lognormal relaxed clock model with a birth–death process tree prior, and the optimal partitioning scheme and models identified by PartitionFinder. Trees and parameters were sampled every 20,000 generations, resulting in a total of 2500 trees. We examined the posterior distribution and estimated sample sizes (ESS) for all parameters using Tracer v. 1.6 (Drummond and Rambaut, 2007). We concluded that the posterior distribution had accumulated enough independent samples when ESS values for all parameters were above 200. We then used TreeAnnotator v. 2.4.7 (Bouckaert et al., 2014) to combine and summarize a post-burn-in (10%) set of trees (2250 trees), compute the 95% highest posterior density intervals (HPD) for ages for all nodes in the tree, and generate a maximum clade credibility (MCC) tree for use in downstream analyses.

Species distributions and historical biogeography

Current distributions for all taxa were determined from the literature (e.g., Giudice et al., 2008; Perrie et al., 2014; Dittrich et al., 2017; Gasper et al., 2017; Vicent et al., 2017; Molino et al., 2019a, 2019b), and from online databases of georeferenced herbarium specimen data (Global Biodiversity Information Facility [GBIF; https://www.gbif.org/] and Integrated Digitized Biospecimens [iDigBio; https://www.idigbio.org/]). Based on these current ranges, we defined nine geographic areas (Figure 2): North America, tropical America, temperate South America except southeastern Brazil, southeastern Brazil, Africa (including Madagascar), Eurasia, Australia, Southeast Asia (including India), and New Zealand and Pacific Islands. We chose these areas because they allow us to capture significant historical movements while maintaining a computationally tractable level of model complexity. We used the UpSetR R package (Conway et al., 2017) to calculate and visualize the number of taxa in each individual region and in each combination or intersection of regions.

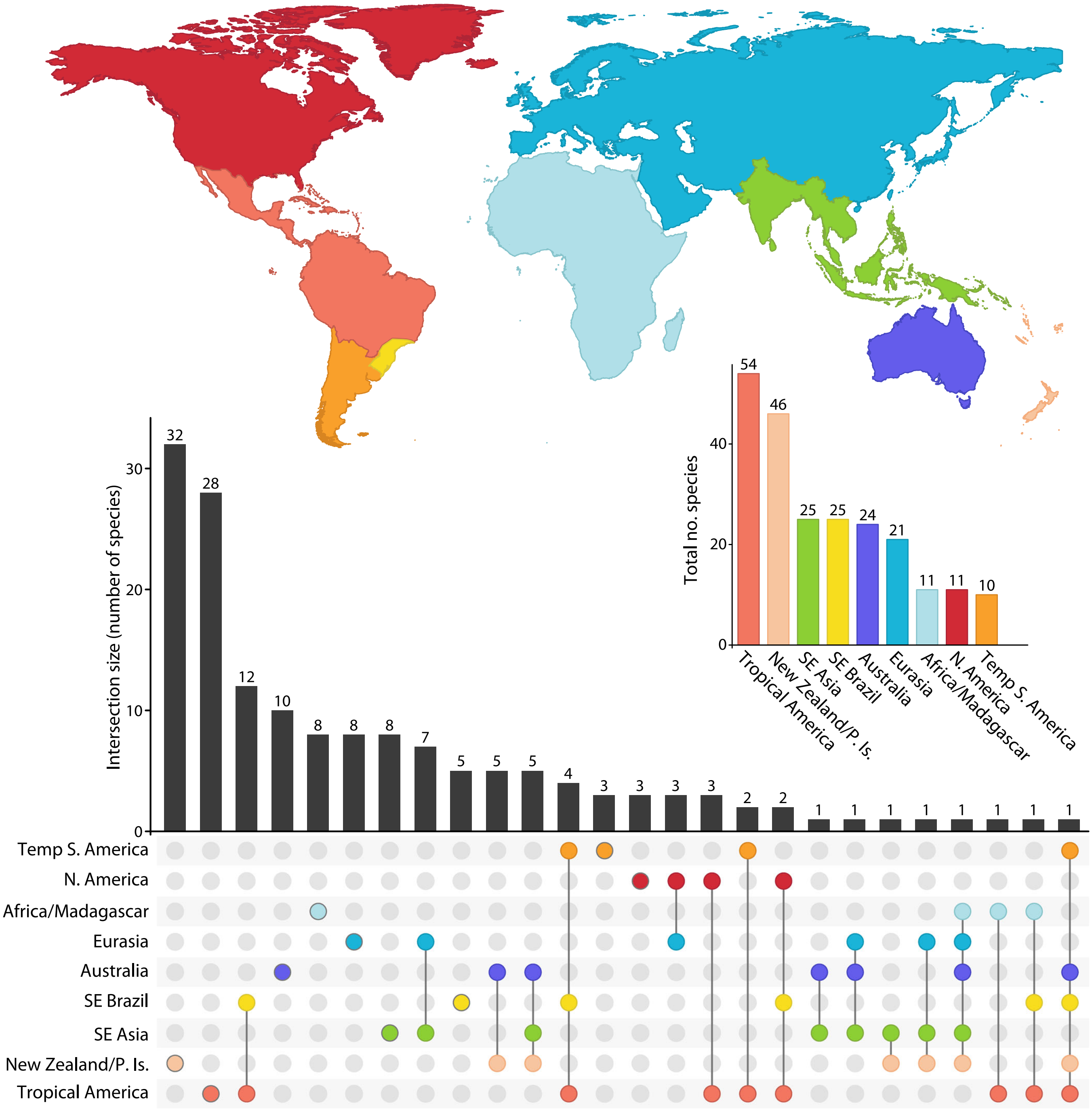

FIGURE 2 Summary of Blechnaceae species numbers and their distributions. The inset, colored graph shows total numbers of species in each region; the lower graph shows all the combinations of regions inhabited by members of the family. Reading across a row in the lower graph and totaling the numbers of the intersections gives the values in the upper graph. For example, the lower graph indicates that there are 28 species whose range is the single region tropical America; 12 species whose range is tropical America and southeastern Brazil; four species whose range is tropical America, southeastern Brazil, and temperate South America, etc. Reading across the lowest row and adding up the numbers corresponding to the colored circles gives us a total of 54 species whose range includes tropical America, as indicated in the upper graph. P. Is. = Pacific Islands; Temp = temperate.

We used the MCC tree as the basis for ancestral range estimation with BioGeoBEARS (Matzke, 2013, 2014) and tested the three basic models available in the software package (DEC, DIVA-like, and BAYAREA-like), each with and without the "founder event" +*j* parameter. We also tested for model sensitivity to the dispersal multiplier matrices by assessing the impact on model fit of two settings for the +*w* parameter (zero and "free"), which acts as an exponent for these matrices (as described by Dupin et al. [2016]). Setting *w* to zero negates the presence of the dispersal matrices in the analyses, effectively setting the probability of dispersal between all areas to the default value of 1. Setting *w* to be "free" allows its value to be optimized during the analysis. All analyses were time-stratified with four time bins to account for historical movements that have altered the proximity of continents/regions over time: 105–60 Mya, 60–30 Mya, 30–10 Mya, and 10 Mya–present. Model fit of the 18 different nested and non-nested models was tested using the Akaike information criterion with a correction for uneven sample size (AICc). Ree and Sanmartín (2018) suggested that models including the +*j* parameter are not statistically comparable to those without it, and so we treated those particular statistical results with caution. We used the best-fit model from the above analyses (the one with the lowest AICc score) to perform stochastic character mapping, with 50 replicates, as described by Dupin et al. (2016). Summarized results of stochastic character mapping were used to estimate the number of dispersal events between regions.

Diversification analyses

Diversification rate estimation

Lineage diversification rates were estimated from the MCC tree obtained from our BEAST analyses in RevBayes (Höhna et al., 2016), implementing a branch-specific birth–death model. We accounted for incomplete taxon sampling by assigning genus-level sampling proportions, using species-richness estimates from the Pteridophyte Phylogeny Group (PPG I, 2016). We specified a prior on the number of rate categories at $k = 6$ and assigned lognormal distributions for speciation and extinction rates with means equal to 0.913 [(number of taxa in phylogeny/root age)/2] and standard deviations set to 0.5. We allowed for rate shifts to occur across the tree and set a uniform distribution on the number of shifts scaled between 0 and 10. This model was sampled with an MCMC on the University of Florida's HiPerGator 2.0 high-performance computing cluster for 24,000 generations, with 4000 generations specified as burn-in. Convergence and mixing were assessed using Tracer 1.7 (Rambaut et al., 2018) to evaluate run convergence and to ensure that all parameters had an effective sample size >200.

Spatial diversification analyses

To evaluate patterns of diversification within a spatial context, speciation tip rates were extracted from the output of our RevBayes analysis and associated with occurrence data for the 156 Blechnaceae taxa included in our analysis. Occurrence data associated with a total of 39,578 georeferenced herbarium specimens were obtained from GBIF (GBIF, 2019; https://doi.org/10.15468/dl.fogds3). Taxonomy of all collections was adjusted to match the classification of the Pteridophyte Phylogeny Group (PPG I, 2016), and occurrences with ambiguous synonymization in this classification scheme were removed from the analyses using the approach of Suissa et al. (2021). These data were cleaned using the R package CoordinateCleaner (Zizka et al., 2019) to remove all occurrences that included coordinate–country mismatches, were localized in country capitals and centroids, were referenced at the coordinates of biodiversity institutions, and those with rounded coordinates. We then passed these data through an additional cleaning step in which interactive maps for all genera were generated using the R package leaflet (Cheng et al., 2022), then occurrences outside the ranges reported by Gasper et al. (2016) were manually removed. Finally, to reduce biases introduced by large numbers of occurrences associated with a few common and well-collected species, we filtered our occurrences to retain a single representative of each taxon per 25 × 25 km grid cells using the Join attributes by location tool in QGIS 3.2.0 (QGIS Development Team, 2018). The final occurrence data set included 4960 georeferenced records (Appendix S1).

We assessed patterns of species richness and rates of speciation along a latitudinal gradient by generating kernel density plots derived from specimen-associated values using the density base function in R. Density estimates in these plots were bounded at 65°N and 65°S to reflect the actual distribution of the family. To evaluate differences of speciation rates across regions, we extracted occurrence data for each of the regions delimited in our biogeographic analyses using Join attributes by location in QGIS 3.2.0 and custom-drawn shapefiles. Tip speciation rates obtained from our RevBayes analyses were then associated with occurrences of the same species, and the distribution of speciation rates within each region was then visualized using kernel density plots as described above. We also visualized the global distribution of speciation rates by plotting specimen occurrences on a map (using an equal area Mollweide projection) and interpolating specimen-associated rates between occurrences using the idw function in the R package gstat (Pebesma, 2004). To ensure that the geographic extent of speciation rates reflected the current distribution of the family, the resulting raster of interpolated rates was then clipped with a polygon defined by a 250-km buffer around each occurrence point from our occurrence data set. Additional information on this workflow and code are available at GitHub (https://github.com/wtesto/Speciation-Rate-Interpolation).

RESULTS

Phylogenetic analyses and divergence time estimation

The final data matrix included 191 species (156 Blechnaceae plus 35 outgroup taxa; Appendix 1) and was 2882 bp long (Appendix S2; Dryad Digital Repository: https://doi.org/10.5061/dryad.t4b8gtj3g [Testo et al., 2022]), with 1160 (40%) parsimony-informative sites, 1428 (50%) constant sites, and

294 (10%) autapomorphic sites. Maximum likelihood and Bayesian inference phylogenetic analyses produced highly congruent, well-resolved topologies with strong support throughout each tree. The ML tree score was ln L = –34,145.098, and 176/190 internal nodes had bootstrap support values ≥70%, indicating strong support (93 of these received 100% BS support) (Appendix S3). In the MCC tree from BEAST, 133/190 internal nodes had PP ≥0.90, with 110 of these having PP = 1.0 (Appendix S4). Divergence times estimated by BEAST (Figures 3A, B) indicate that the ancestor of Blechnaceae diverged from its closest relative (the ancestor of Onocleaceae) approximately 89 Mya (95% HPD interval = 107.5–72.3 Mya). Within Blechnaceae, the major genera had largely diverged from one another by roughly 27 Mya, while species-level divergences have continued until within the most recent 1 My. Broadly speaking, within the well-sampled clades (i.e., where additional taxon sampling is unlikely to break up long branches), the family includes both ancient single-species lineages (e.g., *Blechnidium melanopus*, which diverged from its sister clade 26.99 Mya), and recently diversified clades (e.g., *Parablechnum*, where many divergence events have occurred in the last 1–5 My (Figures 3 and 4).

Ancestral range estimations

The best fitting biogeographic model was BAYAREA-like+j (AICc = 1097.32; ln L = −544.55) with w set to free (optimal value of $w = 1.58$) (Appendix S5). Eurasia was inferred to be the most probable ancestral area for the Blechnaceae crown node as well as most other deep backbone nodes in the phylogeny (Figures 3 and 4). For each of the three subfamilies of Blechnaceae (Woodwardioideae, Stenochlaenoideae, and Blechnoideae), we found evidence of Eurasian origins followed by migration to other regions. Within Woodwardioideae, we found support for four migrations from Eurasia to North America, once each in monotypic *Lorinseria* and *Anchistea* and twice in *Woodwardia* (Figure 3). The timings of these events in the first two genera were uncertain due to their occurrence on long branches; those within *Woodwardia* appeared to have occurred in the early to mid Miocene. In Stenochlaenoideae, we recovered Eurasia as the most probable ancestral area, with subsequent migrations to tropical America in *Salpichlaena*, Southeast Asia and Africa in *Stenochlaena*, and throughout tropical regions of the world in *Telmatoblechnum* (Figure 3).

As in the other subfamilies, we found support for a Eurasian origin for subfamily Blechnoideae; however, this clade was substantially larger than Woodwardioideae and Stenochlaenoideae, and its biogeographic history was much more complex. A relatively small clade comprising *Brainea*, *Sadleria*, *Cleistoblechnum*, *Blechnopsis*, *Spicantopsis*, *Struthiopteris*, and *Blechnidium* was sister to the rest of the subfamily; this clade had a clearly Eurasian origin, with subsequent migration into the paleotropics in *Blechnopsis* and *Brainea*, expansion throughout the north temperate zone in *Struthiopteris*, and a single long-distance dispersal event to the Hawaiian Islands in *Sadleria* (Figure 3). The origin of *Sadleria* predates the emergence of today's Hawaiian Islands, suggesting that the initial colonization event must have occurred on a now-submerged part of the archipelago, with subsequent island hopping, as inferred for other Hawaiian endemic fern clades, such as the diellia clade of *Asplenium* (Schneider et al., 2005) and *Adenophorus* (Ranker et al., 2003). The clade comprising the remainder of the subfamily is inferred to have originated in Eurasia and then migrated to New Zealand/Pacific Islands in the early Eocene. Our reconstructions indicated at least 20 subsequent migration events of the New Zealand/Pacific Islands region in this clade, especially to Australia and tropical America. Most of these migration events occurred within the last 10 My, though we recovered evidence for Eocene migrations from New Zealand/Pacific Islands to Africa and the Americas in the stem lineages of the genera *Blechnum* and *Lomaridium*. Our stochastic character mapping analyses indicate highly asymmetric patterns of migration amongst regions, with New Zealand/Pacific Islands and tropical America being the principal source regions, followed by Australia (Figure 5). Australia and Southeast Asia were the principal recipients of migration from New Zealand/Pacific Islands, and most migration out of tropical America was to southeastern Brazil and temperate South America; migration from Australia was mostly to New Zealand/Pacific Islands and Southeast Asia.

Diversification and richness analyses

Branch-specific speciation rates varied 6-fold across the family, from 0.05 to 0.31 events My^{-1}. Genus-level mean speciation rates were lowest in *Lorinseria* and *Anchistea* (both 0.05 events My^{-1}) and highest in *Parablechnum* and *Doodia* (both 0.29 events My^{-1}) (Appendix S6). We detected a pattern of increased speciation rates in the southern hemisphere, with a peak at 35–40°S, principally due to the presence of rapidly speciating lineages (e.g., *Doodia*) in Australia and New Zealand (Figure 6). Another peak in speciation rates occurred at high latitudes (45–55°N) due to the circumboreal *Struthiopteris*, which is species-poor but very recently diverged. Speciation rates varied across the biogeographic regions delimited in our study, though overlap in rate distributions was generally high (Appendix S7). Mean rates were lowest in North America and Eurasia and highest in Australia and New Zealand (Figure 6).

Amongst the biogeographic regions delimited in our study, species richness was highest in tropical America (54 spp.), followed by 46 species in New Zealand/Pacific Islands (Figure 2). The next-richest regions were Southeast Asia, southeastern Brazil, and Australia; temperate regions and Africa/Madagascar harbored the lowest species

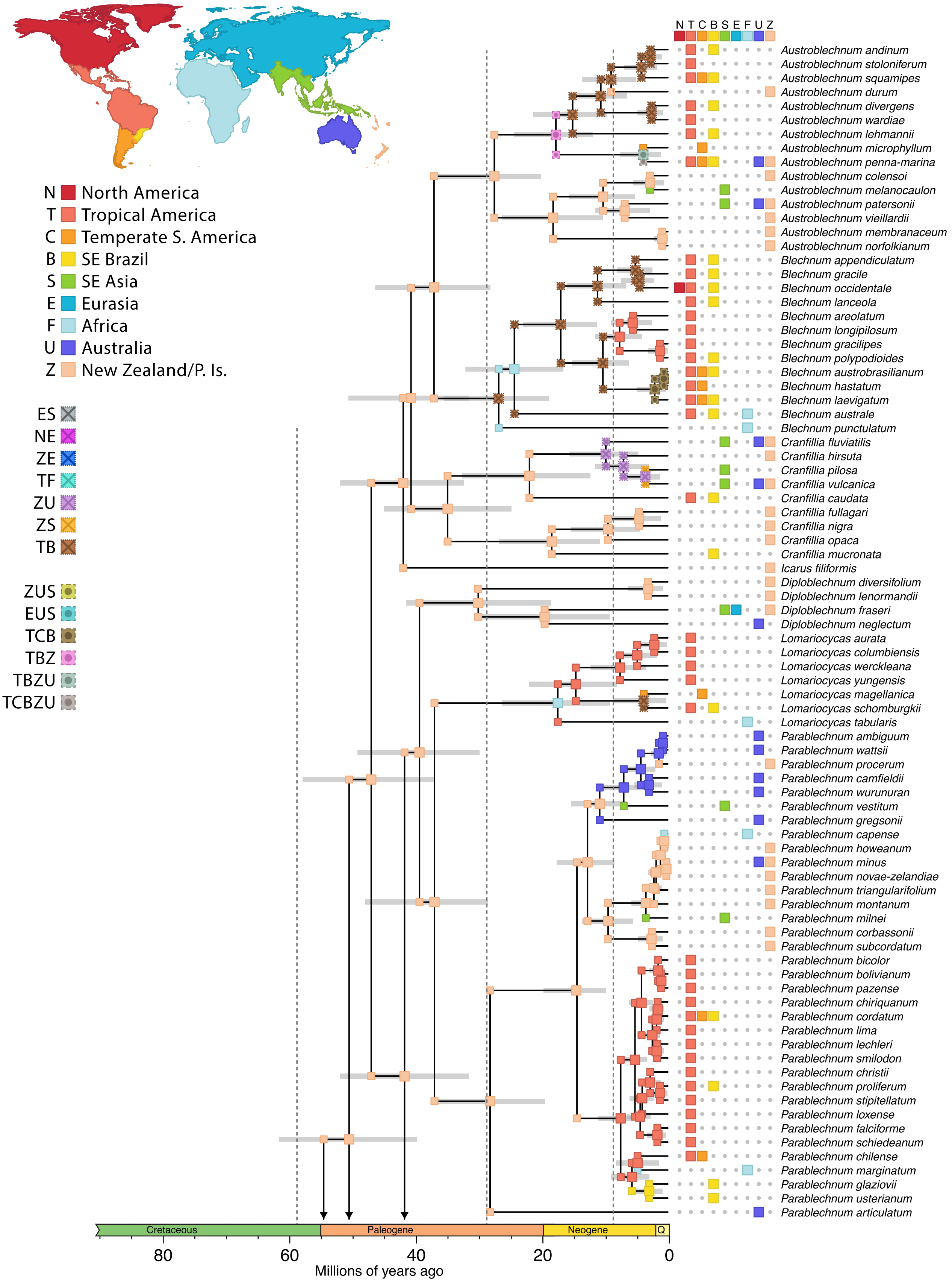

FIGURE 3 Results of historical biogeographic analyses of Blechnaceae, as inferred in BioGeoBEARS with a BAYAREA-like+j model. Outgroups of Onocleaceae, Athyriaceae, and Woodsiaceae are not shown; see Appendix S8.

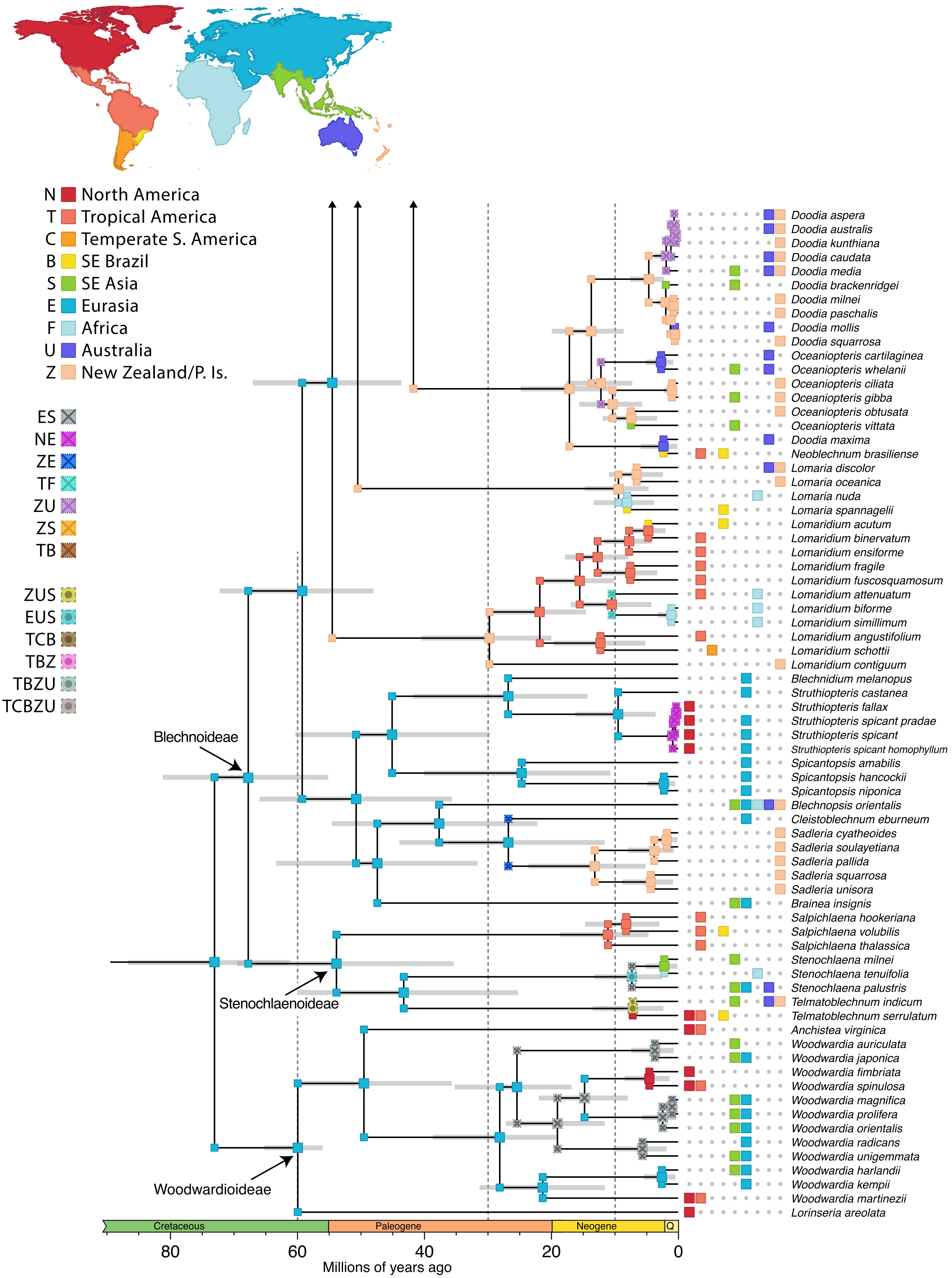

FIGURE 4 Results of historical biogeographic analyses of Blechnaceae, as inferred in BioGeoBEARS with a BAYAREA-like+j model. Outgroups of Onocleaceae, Athyriaceae, and Woodsiaceae are not shown; see Appendix S8.

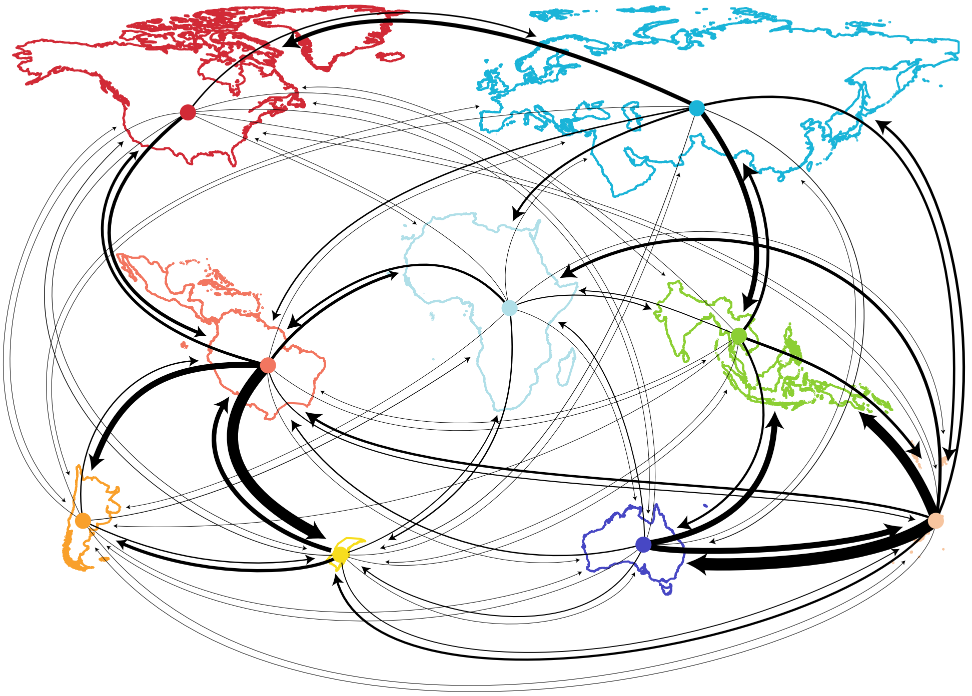

FIGURE 5 Results of biogeographic stochastic mapping. Line weights are proportional to the mean number of dispersal events from the source to the destination area, as indicated by the direction of the arrows. Thicker lines correspond to higher numbers of dispersal events in that direction, based on the results of 50 stochastic mapping replicates.

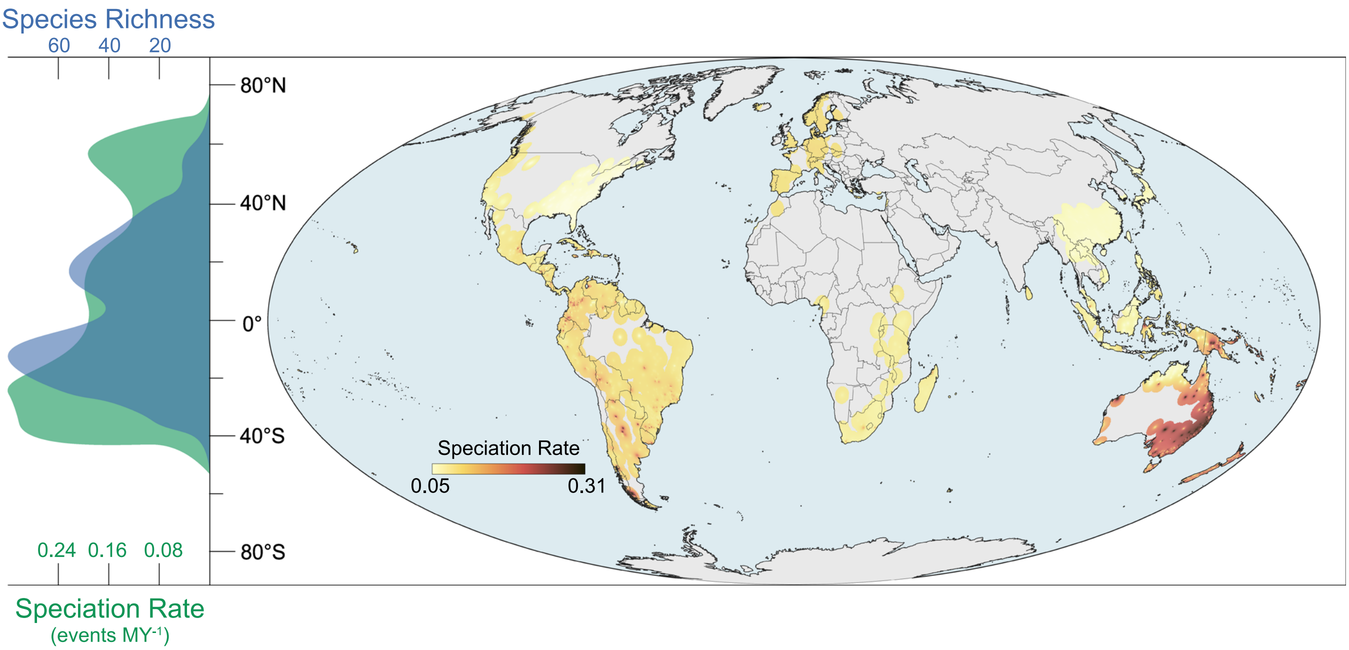

FIGURE 6 Map of speciation rates in Blechnaceae, based on rates inferred in RevBayes and species occurrence data obtained from Global Biodiversity Information Facility.

diversity. Our analysis of species–region interaction revealed high endemism in New Zealand/Pacific Islands (32 spp. found nowhere else) and tropical America (28 spp. found nowhere else). The only remaining species-region combinations represented by 10 or more species were tropical America + southeastern Brazil (12 spp.) and Australia (10 spp.); a total of 18 area combinations were occupied by five or fewer species (Figure 2). We found a bimodal distribution of species richness with respect to latitude, with peaks at ~5–15°N and 15–20°S (Figure 6).

DISCUSSION

A principal challenge in biogeography is understanding the relative roles of dispersal and vicariance in shaping taxon distributions. These processes differ in their relative contributions depending on the lineage's potential for LDD, with vicariance generally playing a minor role in the biogeographic histories of lineages with high dispersal capabilities. Few groups of organisms are better suited for LDD than ferns, which disperse via minute spores that can travel thousands of kilometers (Muñoz et al., 2004) and have been detected high in the atmosphere (Erdtman, 1937; Gradstein and van Zanten, 1999). Because of this and the ability of a considerable number of species to successfully establish from a single isolated spore (Haufler et al., 2016; Klekowski, 1969; Sessa et al., 2016), fern distributions are generally assumed to be largely shaped by dispersal rather than vicariance. Even so, vicariance cannot be ruled out as a driver of broad-scale fern biogeography a priori, as many fern families predate the breakup of the Laurasian and Gondwanan supercontinents (Testo and Sundue, 2016).

Our divergence-time estimates indicate that the diversification of Blechnaceae started in the late Cretaceous, with all three subfamilies (Woodwardioideae, Stenochlaenoideae, and Blechnoideae) likely diverging before the K–Pg boundary (Figure 3A, B). These ages are consistent with those reported by previous studies of leptosporangiate fern diversification and indicate that Blechnaceae is amongst the youngest fern families (Testo and Sundue, 2016). We found strong support for a Eurasian origin for the family, with subsequent migration within each subfamily early in the Cenozoic (Figure 3). Altogether, the biogeographic history of the family is complex, but mostly shaped by three processes: (1) climate-mediated vicariance, (2) frequent and strongly asymmetrical LDD, and (3) rapid speciation in tropical and austral regions.

Role of vicariance in shaping distributions

Although the timescale of diversification in Blechnaceae precludes biogeographic scenarios involving the breakup of Gondwana (Sanmartín and Ronquist, 2004), continental-scale vicariance can explain the distributions of several genera. The three genera that comprise subfamily Woodwardioideae are principally distributed in North America and Asia, with the monotypic North American genus *Anchistea* being sister to *Woodwardia*, which includes both Eurasian and American species. *Lorinseria*, another North American genus with a single species, *L. areolata*, is sister to *Anchistea*+*Woodwardia*. Our divergence time estimates and ancestral area reconstructions suggest that these genera diverged in the early Cenozoic (ca. 60–50 Mya), with *Lorinseria* and *Anchistea* migrating to North America and *Woodwardia* remaining in Eurasia, with subsequent (late Oligocene onward) expansion to Southeast Asia and migration to North America. The divergence of these genera corresponds closely to the Paleocene–Eocene Thermal Maximum (PETM), when a well-documented boreotropical flora was widely distributed at high northern latitudes (Wolfe, 1975; Davis et al., 2002). Fossil evidence indicates that woodwardioid ferns were well represented in the floras of eastern Asia and northwestern North America at that time, including areas well north of where these genera occur today (Collinson, 2001). Together, these lines of evidence lead us to conclude that members of subfamily Woodwardioideae arose in Eurasia, expanded into North America across Beringia during periods of high global temperatures in the early Cenozoic, and subsequently became isolated as their ranges contracted southward due to global cooling during the Oligocene (Wolfe, 1975). This finding largely agrees with those of Li et al. (2016), except for the directionality of events: they inferred a North American, rather than Eurasian, origin for subfamily Woodwardioideae. Differences in sampling and methodology account for this discrepancy; Li et al. (2016) did not conduct formal ancestral area reconstructions in their study and did not consider the distributions of outgroups in their analyses.

A boreotropical connection may also explain the distribution of subfamily Stenochlaenoideae, but evidence supporting this scenario is less clear than in subfamily Woodwardioideae. Within this subfamily, the neotropical genus *Salpichlaena* diverged from the ancestor of the paleotropical genus *Stenochlaena* and pantropical *Telmatoblechnum* ca. 54 Mya, coincident with the PETM. As in subfamily Woodwardioideae, the timing of this divergence and the geography of the taxa involved are consistent with a scenario involving migration of *Salpichlaena* from Asia into the Americas through a boreotropical connection either through Beringia or the North Atlantic Land Bridge (Tiffney, 1985); however, paleobotanical evidence supporting such a history is limited. Fossils of ferns with large, apparently twice-pinnate leaves (like extant *Salpichlaena*) have been reported from the Paleocene of western North America (Lesquereux, 1878; Knowlton, 1930; Pabst, 1968); these have been placed in various genera by different authors, including *Salpichlaena*. The most complete fossils of these taxa were reported from Colorado by Knowlton (1930), who provided a detailed comparison of the fossils (treated as *Salpichlaena anceps*) to the extant neotropical species *Salpichlaena volubilis*, along with images and reconstructions of the fossil. We have studied these images and drawings presented by Knowlton and agree that the fossil bears a close resemblance to extant *Salpichlaena*; however, more complete material (especially fertile leaves) is needed to confirm its placement in this genus.

Members of subfamily Blechnoideae comprise most of the family's diversity and are a prominent component of many tropical and south temperate floras, especially in tropical America, Australia, and New Zealand (Perrie et al., 2014). Some authors (e.g., Cranfill, 2001) have postulated that this distribution reflects a Gondwanan origin for the clade, but our divergence-time estimates show that the clade is much too young to support such a hypothesis (Figure 3A, B; Appendices S8, S9). Instead, we suggest that the distributions of some genera in subfamily Blechnoideae likely result from a trans-Antarctic connection that linked most austral landmasses for an extended period following the breakup of Gondwana. Australia, New Zealand, Antarctica, and South America were physically connected until the separation of New Zealand (then joined with New Caledonia) by the opening of the Tasman Sea, starting in the late Cretaceous (ca. 80 Mya) and finishing near the end of the Paleocene (ca. 56 Mya) (Ladiges and Cantrill, 2007). A connection between Australia, Antarctica, and South America persisted considerably longer, until the formation of the South Tasman Sea separated Australia and Antarctica in the late Eocene (ca. 35 Mya) (Stickley et al., 2004). Shortly thereafter (ca. 30 Mya), the Drake Passage developed, ending the South America–Antarctica connection and allowing for the development of the Antarctic Circumpolar Current. Prior to the establishment of this current and subsequent glaciation, Antarctica had a warm temperate climate since the mid-Cretaceous and harbored a rich, *Nothofagus*-dominated flora (Hill and Scriven, 1995; Sanmartín and Ronquist, 2004). Although we are unaware of any records of Cenozoic Blechnaceae fossils from Antarctica, these habitats were likely similar to those favored by many extant Blechnoideae taxa (Saldaña et al., 2010), suggesting that the region was suitable for members of the family at least through the Eocene. The distributions and divergence times of *Austroblechnum*, *Lomaridium*, and *Lomariocycas* appear compatible with trans-Antarctic migration and vicariance (Figures 3 and 4), but some aspects of this interpretation are problematic. Our ancestral area reconstructions indicate that the timing of migration out of New Zealand/Pacific Islands in all three genera likely occurred in the late Eocene or early Oligocene, long after New Zealand and New Caledonia split off from Australia. While this incongruence could be used to preclude a history of trans-Antarctic migration in these groups, other possibilities could also result in the patterns observed here. First, the slow rifting of New Zealand and Australia following their initial separation would have permitted "stepping-stone" dispersal across the then-narrow Tasman Sea (Winkworth et al., 2015), effectively extending the period of time during which migration from New Zealand was achievable. Second, it is possible that our biogeographic models fail to capture the true history of these lineages because of extinction, a lack of information on historical distributions, and/or incomplete sampling of extant taxa (our phylogeny included ca. 70% of extant *Lomaridium* species and ca. 40% of known species in both *Austroblechnum* and *Lomariocycyas*). Conclusive evaluation of a potential trans-Antarctic migration history in these genera will require better taxon sampling and possibly more integrative models of range evolution (Silvestro et al., 2016). Although the biogeographic histories of some austral fern genera have been studied (Labiak et al., 2014; Bauret et al., 2017), the prominence of this distribution pattern suggests that the role of the Paleocene–Eocene Antarctic connection in shaping patterns of fern richness in the southern hemisphere warrants further study.

Long-distance dispersal and species diversification

Consistent with the well-established view that "long-distance dispersal is a dominant force in fern distribution" (Barrington, 1993, pp. 275–276), we found evidence for 113 (±63) dispersal events during the evolutionary history of Blechnaceae, totaling a rate of 1.55 events My^{-1} (Appendix S10). When dispersal events between adjacent areas were excluded (i.e., counting only long-distance dispersal events), a slightly lower rate of 1.23 events My^{-1} was recorded. These rates are higher than the rate of 0.8 events My^{-1} reported for orchids by Givnish et al. (2016) and similar to the 1.3 events My^{-1} reported by Sessa et al. (2012b) for the fern genus *Dryopteris*. The directionality of dispersal events is highly asymmetric, with New Zealand/Pacific Islands, Australia, and tropical America together being the source areas for 58% of all dispersal events (Figure 5). The elevated rates of dispersal observed among the southern continents likely are due to spore dispersal via the West Wind Drift, a prevailing wind pattern associated with the Antarctic Circumpolar Current that has existed since the opening of the Drake Passage in the Oligocene (Sanmartín et al., 2007). The West Wind Drift has previously been identified as an important dispersal route in other groups of spore-dispersed vascular plants (Labiak et al., 2014; Bauret et al., 2017, 2018; Testo et al., 2018; Morero et al., 2019) and likely has played an important role in shaping the conspicuous pattern of recent disjunctions between American and African fern and lycophyte groups (Moran and Smith, 2001). Within Blechnaceae, we find evidence for trans-Atlantic dispersals within the last 10 My from the Americas to Africa in *Lomaridium* and *Parablechnum* (Figures 3 and 4).

Along with shaping the distribution of lineages, LDD can lead to subsequent rapid speciation (Baldwin and Sanderson, 1998; Givnish et al., 2009; Sebastian et al., 2012). In Blechnaceae, the most prominent examples of rapid postdispersal diversification are in the genus *Parablechnum*, a clade of ca. 65 species that are well represented in south temperate and tropical montane floras. We found evidence for at least six LDD events of the genus from its ancestral range in New Zealand (Figures 3 and 4). Though most of these dispersal events are associated with minimal subsequent lineage diversification, a LDD event to tropical America preceded one of the most significant diversification events in the evolution of the family. Following this dispersal event in the mid Miocene, *Parablechnum* diversified rapidly in tropical and south temperate America, especially in the Andes, which is one of its centers of diversity. The timing of diversification in American *Parablechnum* corresponds closely with the rapid uplift of the Andes (Gregory-Wodzicki, 2000; Garzione et al., 2008), which numerous studies have shown to be a driver of exceptionally rapid speciation in various lineages (Madriñán et al., 2013; Lagomarsino et al., 2016; Testo et al., 2018). Along with having some of the highest rates of speciation observed in the family, South American *Parablechnum* are remarkable for the small geographic ranges of some species (Kessler et al., 2007) and evidence of unclear species boundaries (Smith and Kessler, 2018). Despite the prominence of this genus and other fern groups in tropical mountains, the interplay of mountain uplift and lineage diversification remains essentially unstudied in ferns; *Parablechnum* presents an excellent study group for such investigation.

Global patterns of Blechnaceae diversity are complex, but latitudinal trends in both species richness and speciation rate highlight the clade's austral center of diversity. In contrast to most fern families, which generally exhibit highest diversity and speciation rates in montane forests near the Equator (Kessler et al., 2011; Weigand et al., 2020; Suissa et al., 2021), species richness in Blechnaceae peaks at ca 20°S and speciation rates are highest between ca. 20–40°S. Diversity of Blechnaceae taxa at these latitudes is centered in the Central Andes, southeastern Brazil, eastern Australia, and New Zealand (Figures 2 and 5), where most species are found in wet forests. Both species richness and speciation rates are especially high in Australia and New Zealand, where Blechnaceae taxa are overrepresented in the fern flora (7% and 11%, respectively; McCarthy, 1998; Breitwieser et al., 2010) relative to their global diversity (globally, Blechnaceae include just 2.5% (265/10,578) of fern species richness (PPG I, 2016). Although the goal of our study was not to examine drivers of species diversity, available data provide some possible explanations for the remarkable success of Blechnaceae lineages in these regions. First, these areas (especially New Zealand) have been colonized by various lineages within subfamily Blechnoideae for ca. 50 My, thereby providing a long period of time for members of the family to diversify within the region. In addition, there may be a physiological basis to the success of Blechnaceae in austral regions. In a study of Australian fern richness, Nagalingum et al. (2015) indicated that patterns of diversity in the mountains of eastern Australia were largely shaped by temperature seasonality, with Blechnaceae being one of only a few cold-tolerant fern families present. Generally, fern diversity declines with decreasing annual temperatures (Bhattarai et al., 2004; Khine et al., 2019) and fern assemblages in cold climates tend to be phylogenetically clustered (Kluge and Kessler, 2011; Suissa et al., 2021). Blechnaceae taxa are well represented in tropical alpine and temperate habitats—some *Parablechnum*, *Austroblechnum*, and *Lomariocycas* species grow at ca. 4500 m a.s.l. and *Struthiopteris spicant* can be found to 70°N latitude—suggesting that some lineages in the family are particularly well adapted to cold conditions.

CONCLUSIONS

Taken together, our results demonstrate that the diversification history of Blechnaceae began in the late Cretaceous in Eurasia and that the spread of the family globally likely involved both extensive long-distance dispersal and movements facilitated by land connections that have since vanished. The success of the family in south temperate regions may be due to the cold tolerance of many of its species; this physiological tolerance may also contribute to the group's prominence at high elevations in the tropics, which is unique among fern families that have high diversity in the tropics. While this study considerably advances our understanding of the complex biogeographic history of this family, more work is needed to understand how the interplay of plant physiology, climatic conditions, and historical processes have shaped the distribution of Blechnaceae taxa. Integrative approaches, particularly those that incorporate climatic, geological, and trait data within a modeling framework, are of particular promise.

AUTHOR CONTRIBUTIONS

E.B.S., W.L.T., A.L.G., and J.M.GyG. conceived the study. E.B.S., A.L.G., V.A.O.D., A.S., S.M. and J.M.GyG. collected sequence data that were analyzed in the study. E.B.S. and W.L.T. conducted analyses and wrote the first draft of the manuscript, with all authors contributing substantially to revisions.

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DATA AVAILABILITY STATEMENT

Alignments and trees have been uploaded to the Dryad Digital Repository (https://doi.org/10.5061/dryad.t4b8gtj3g [Testo et al., 2022]). GenBank accession numbers are provided in Appendix 1.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Cleaned occurrence data set obtained from GBIF.

Appendix S2. Nexus file of the final alignment used in the phylogenetic analyses.

Appendix S3. ML phylogeny from IQTree, with branches colored to represent bootstrap support values according to the included legend.

Appendix S4. MCC chronogram from BEAST, with branches colored to represent bootstrap support values according to the included legend.

Appendix S5. Results of BioGeoBEARS model comparison.

Appendix S6. Speciation rates estimated with RevBayes analysis.

Appendix S7. Density distribution plots of speciation rates, delimited by biogeographic region.

Appendix S8. MCC chronogram from BEAST, showing median node ages.

Appendix S9. MCC chronogram from BEAST, showing the age ranges for the 95% HPD intervals for node age.

Appendix S10. Matrix of inferred dispersal rates from biogeographical stochastic character mapping.

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APPENDIX 1: GENBANK ACCESSION DATA OF SAMPLES USED IN THIS STUDY. HYPHENS INDICATE MISSING SEQUENCES.

Taxon, rbcL, rps4-trnS, trnL-trnF.

Anchistea virginica, AY137660, AF533857, -; ***Anisocampium skinneri***, JF832058, -, KX656169; ***Athyrium decurrentialatum***, AB574936, JN168081, EU329106; ***Athyrium filix-femina***, JF832056, MG183458, MG183531; ***Athyrium otophorum***, EF463305, JN168076, MG183552; ***Athyrium yokoscense***, AB574933, JN168078, MG183575; ***Austroblechnum andinum***, KU898604, KU898550, KU925243; ***Austroblechnum colensoi***, KF975783, KF975739, DQ683379; ***Austroblechnum divergens***, KU898605, KU898548, KU898664; ***Austroblechnum durum***, KF975788, KF975744, DQ683383; ***Austroblechnum lehmannii***, KU898606, KU898551, KU898665; ***Austroblechnum melanocaulon***, KF975794, KF975750, KF975720; ***Austroblechnum membranaceum***, KF975795, KF975751, DQ683392; ***Austroblechnum microphyllum***, KU898607, KU892685, JQ907377; ***Austroblechnum norfolkianum***, KF975801, KF975757, DQ683401; ***Austroblechnum patersonii* subsp. *queenslandicum***, KJ170823, KJ170796, KJ170850; ***Austroblechnum pennamarina***, KU898609, KU898554, KU898668; ***Austroblechnum squamipes***, KU898610, KU898555, KU898669; ***Austroblechnum stoloniferum***, KU898611, KU898556, KU898670; ***Austroblechnum vieillardii***, KF975814, -, KF975730; ***Austroblechnum wardiae***, KU898612, KU898557, KU898671; ***Blechnidium melanopus***, KU898627, -, -; ***Blechnopsis orientalis***, KJ398411, KJ398407, KJ398409; ***Blechnum appendiculatum***, KU898613, KU898558, KU898672; ***Blechnum areolatum***, KU898614, KU898559, KU898673; Blechnum australe, KF992445, -, JQ907366; ***Blechnum austrobrasilianum***, KU898617, KU898562, KU898676; ***Blechnum gracile***, KU898620, KU898565, KU898678; ***Blechnum hastatum***, KU898619, KU898564, -; ***Blechnum laevigatum***, KU898621, KU898566, -; ***Blechnum lanceola***, KU898622, KU898567, KU898680; ***Blechnum longipilosum***, KU898626, KU898570, KU898683; ***Blechnum moorei***, KF975799, KF975755, KF975722; ***Blechnum occidentale***, KU898623, KU898568, KU898681; ***Blechnum polypodioides***, KU898624, KU925241, KU925244; ***Blechnum punctulatum***, KF975811, KF975767, DQ683412; ***Brainea insignis***, KU898628, KU898571, KU898684; ***Cleistoblechnum eburneum***, JN168003, JN168071, -; ***Cranfillia fluviatilis***, KJ398412, KJ398408, KJ398410; ***Cranfillia hirsuta***, KF975792, KF975748, KF975718; ***Cranfillia nigra***, KF975800, KF975756, DQ683399; ***Cranfillia opaca***, KF975805, KF975761, KF975725; ***Cranfillia pilosa***, KF975809, KF975765, KF975728; ***Cranfillia sampaioana***, KU898629, KU898572, KU898685; ***Cranfillia sprucei***, KU898630, KU898573, KU898686; ***Cranfillia vulcanica***, KJ170825, KJ170798, KJ170852; Deparia lancea, D43913, AF425153, AB106927; ***Deparia petersenii***, AB078601, JN168086, MG183579; ***Deparia unifurcata***, EF463307, JN168087, KX656167; ***Diplazium bellum***, KC254356, KC254507, KC254428; ***Diplazium cristatum***, EF463310, KC254515, KC254434; ***Diplazium maximum***, KC254385, KC254539, KC254459; ***Diplazium ovatum***, KC254355, KC254506, KC254427; ***Diplazium spectabile***, KC254388, KC254542, KC254462; ***Diplazium virescens***, KC254417, -, KC254496; ***Diplazium wichurae***, JN168018, JN168093, MG183580; ***Diploblechnum diversifolium***, KF975787, KF975743, KF975716; ***Diploblechnum fraseri***, KF975790, KF975746, DQ683390; ***Diploblechnum lenormandii***, KF975793, KF975749, KF975719; ***Diploblechnum neglectum***, KJ170835, KJ170808, KJ170862; ***Doodia aspera***, AY137673, AF533871, DQ683419; ***Doodia australis***, KF975817, KF975772, DQ683422; ***Doodia brackenridgei***, KF975818, KF975773, KF975732; ***Doodia caudata***, JF950808, -, JF950941; ***Doodia kunthiana***, AB040578, -, DQ683424; ***Doodia maxima***, U05921, -, -; ***Doodia media***, U05922, -, -; ***Doodia milnei***, KF975820, KF975775, DQ683425; ***Doodia mollis***, AB040579, -, DQ683428; ***Doodia squarrosa***, KF975822, KF975777, DQ683429; ***Icarus filiforme***, KF975789, KF975745, DQ683385; ***Lomaria discolor***, KF975786, KF975742, DQ683382; ***Lomaria nuda***, KJ170821, KJ170794, KJ170848; ***Lomaria oceanica***, KF975804, KF975760, KF975724; ***Lomaria spannagelii***, KU898643, KU898584, KU898698; ***Lomaridium acutum***, KU898638, KU892692, KU892709; ***Lomaridium angustifolium***, KU892707, KU892687, JQ907373; ***Lomaridium attenuatum***, KF992444, -, -; ***Lomaridium biforme***, AB040561, -, -; ***Lomaridium binervatum***, KU892699, KU892689, JQ907368; ***Lomaridium contiguum***, KF975784, KF975740, KF975714; ***Lomaridium ensiforme***, KU898639, KU892695, JQ907371; ***Lomaridium fragile***, KU898640, KU892686, JQ907372; ***Lomaridium fuscosquamosum***, KU898641, KU892684, KM001898; ***Lomaridium schottii***, KU892698, KU892691, KU892714; ***Lomaridium simillimum***, AB040570, -, -; ***Lomariocycas aurata***, KU898633, KU898576, KU898690; ***Lomariocycas columbiensis***, KU898634, KU898577, -; ***Lomariocycas magellanica***, AB040560, -, -; ***Lomariocycas schomburgkii***, KU898636, KU898579, KU898692; ***Lomariocycas tabularis***, KF992447, -, -; ***Lomariocycas werckleana***, KU898637, KU898580, KU898693; ***Lomariocycas yungensis***, KU898635, KU898578, KU898691; ***Lorinseria areolata***, AF425102, AF425155, -; ***Matteuccia struthiopteris***, AB232415, AF425158, KC254425; ***Neoblechnum brasiliense***, AB040545, -, JQ907369; ***Oceaniopteris cartilaginea***, KJ170816, KJ170789, KJ170843; ***Oceaniopteris gibba***, KF975791, KF975747, KF975717; ***Oceaniopteris obtusata***, KF975803, KF975759, KF975723; ***Oceaniopteris vittata***, KF975815, KF975770, KF975731; ***Oceaniopteris whelanii***, KJ170827, KJ170800, KJ170854; ***Onoclea sensibilis***, JF832076, AF425159, -; ***Onocleopsis hintonii***, JF832077, AF425160, -; ***Parablechnum ambiguum***, KJ170813, KJ170786, KJ170840; ***Parablechnum articulatum***, KJ170814, KJ170787, KJ170841; ***Parablechnum bicolor***, KU898645, KU898586, KU898700; ***Parablechnum bolivianum***, KU898646, KU898587, KU898701; ***Parablechnum camfieldii***, KJ170815, KJ170788, KJ170842; ***Parablechnum capense***, AB040547, -, -; ***Parablechnum chilense***, AB040550, -, -; ***Parablechnum christii***, KU898647, KU898588, KM001892; ***Parablechnum corbassonii***, KF975785, KF975741, KF975715; ***Parablechnum cordatum***, KU898648, KU898589, KU898702; ***Parablechnum falciforme***, KU898649, KU898590, KU898703; ***Parablechnum glaziovii***, KU898650, KU898591, KU898704; ***Parablechnum gregsonii***, KJ170819, KJ170792, KJ170846; ***Parablechnum howeanum***, JF950804, -, JF950940; ***Parablechnum lechleri***, KU898651, KU898592, KU898705; ***Parablechnum lima***, KU898652, KU898593, KU898706; ***Parablechnum loxense***, KU892700, KU892682, JQ907375; ***Parablechnum marginatum***, KF992446, -, -; ***Parablechnum milnei***, KF975796, KF975752, KF975721; ***Parablechnum minus***, KF975797, KF975753, DQ683395; ***Parablechnum montanum***, KF975798, KF975754, KJ187000; ***Parablechnum novae-zelandiae***, EF469957, KF975758, DQ683403; ***Parablechnum pazense***, KU898653, KU898594, KU898707; ***Parablechnum procerum***, KF975810, KF975766, DQ683411; ***Parablechnum proliferum***, KU898654, KU898595, KU898708; ***Parablechnum schiedeanum***, KU898655, KU898596, KU898709; ***Parablechnum smilodon***, KU898644, KU898585, KU898699; ***Parablechnum stipitellatum***, KU898656, KU898597, KU898710; ***Parablechnum subcordatum***, KF975812, KF975768, KF975729; ***Parablechnum triangularifolium***, KF975813, KF975769, DQ683415; ***Parablechnum usterianum***, KU898658, KU898599, KU898712; ***Parablechnum vestitum***, KC533882, -, -; ***Parablechnum wattsii***, KJ170826, KJ170799, KJ170853; ***Parablechnum wurunuran***, KJ170828, KJ170801, KJ170855; ***Pentarhizidium intermedium***, KC254354, KC254505, KC254426; ***Pentarhizidium orientale***, JF832079, -, -; ***Sadleria cyatheoides***, KJ716413, -, DQ683431; ***Sadleria pallida***, AB040588, -, -; ***Sadleria souleytiana***, AB040591, -, -; ***Sadleria squarrosa***, AB040592, -, -; ***Sadleria unisora***, AB040593, -, -; ***Salpichlaena hookeriana***, KJ628825, -, -; ***Salpichlaena thalassica***, KU898659, KU898600, KU898713; ***Salpichlaena volubilis***, KU898660, -, KU898714; ***Spicantopsis amabilis***, MH644111, -, MH644138; ***Spicantopsis hancockii***, MH644114, -, MH644141; ***Spicantopsis niponica***, MH644112, -, MH644140; ***Stenochlaena milnei***, AF425104, AF425157, -; ***Stenochlaena palustris***, KJ170829, KJ170802, KJ170856; ***Stenochlaena tenuifolia***, EF463163, -, -; ***Struthiopteris castanea***, MH644118, -, MH644128; ***Struthiopteris fallax***, MH644122, -, MH644132; ***Struthiopteris spicant var. homophyllum***, MH644120, -, MH644136; ***Struthiopteris spicant var. pradae***, MH644123, -, MH644134; ***Struthiopteris spicant***, MH644121, -, MH644135; ***Telmatoblechnum indicum***, KJ170830, KJ170803, KJ170857; ***Telmatoblechnum serrulatum***, KU898662, KU898602, KU898716; ***Woodsia andersonii***, JF833268, -, -; ***Woodsia cycloloba***, KP226762, -, -; ***Woodsia elongata***, JF832060, JN168079, -; ***Woodsia glabella***, KP226764, -, -; ***Woodsia ilvensis***, KP226765, -, -; ***Woodsia indusiosa***, KP226754, JN168080, -; ***Woodsia kangdingensis***, KP226755, -, -; ***Woodsia manchuriensis***, JN168021, MG183505, MG183582; ***Woodsia mollis***, JF832087, -, -; ***Woodsia montevidensis***, KP226771, -, -; ***Woodsia obtusa***, U05949, -, -; ***Woodsia oregana*** **subsp**. ***cathcartiana***, KF186523, -, -; ***Woodsia plummerae***, JF832088, -, -; ***Woodsia polystichoides***, U05657, HQ380220, -; ***Woodsia rosthorniana***, KP226776, -, -; ***Woodwardia auriculata***, AY137661, AF533858, -; ***Woodwardia fimbriata***, AY137662, AF533859, -; ***Woodwardia harlandii***, AY137663, AF533860, -; ***Woodwardia japonica***, KM606976, KM606989, DQ683432; ***Woodwardia kempii***, AY137665, AF533862, -; ***Woodwardia magnifica***, KM606985, KM606991, -; ***Woodwardia martinezii***, KU898663, AF533863, KU898717; ***Woodwardia orientalis var. orientalis***, AB575059, -, -; ***Woodwardia prolifera***, KM606974, KM606987, DQ683433; ***Woodwardia radicans***, AY137667, KU892690, JQ907391; ***Woodwardia spinulosa***, AY137668, AF533866, KU898718; ***Woodwardia unigemmata***, KM606975, KM606988, NC_028543.