The “evil tribe” spreads across the land: A dated molecular phylogeny provides insight into dispersal, expansion, and biogeographic relationships within one of the largest tribes of the sunflower family (Vernonieae: Compositae)

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PREMISE: With over 1500 species, the globally distributed Vernonieae is one of the most successful members of the largest family of flowering plants, the Compositae. However, due to its morphological complexity and limited geographic representation in previous studies, subtribal and biogeographic relationships are unclear. Here, new DNA sequence data spanning the geographic range of the tribe provides a taxonomically robust time-calibrated phylogeny, estimates migration pathways and timing of important biogeographic events, and allows inference of environmental factors that have contributed to the success of the Vernonieae worldwide.

METHODS: Phylogenetic relationships were estimated for 368 taxa representing all Vernonieae subtribes. Molecular clock and ancestral range estimation analyses provide a framework for inference of the biogeographic history of the tribe.

RESULTS: Relationships among the subtribes were established and correct placement determined for problematic taxa, along with the first model-based assessment of the biogeographic history of the tribe. The Vernonieae were estimated to have evolved ~50 mya. Africa was the first center of diversity, from which a single dispersal event established the monophyletic New World lineage. Long-distance dispersal from Africa and Brazil established the tribe on five continents and Oceania.

CONCLUSIONS: The New World lineage is monophyletic, but Old World taxa are not. New subtribal taxonomies are needed. Moquinieae are nested in Vernonieae. Long-distance dispersal from Africa beginning 45 mya was key to establishing the tribe's near-global distribution. Migration corridors created by volcanic mountain chains and iron-rich soils in Africa and the Americas promoted radiation and range expansion.

KEY WORDS: Africa; ancestral range estimation; Asteraceae; edaphic specialization; long-distance dispersal; phylogenetic conservatism; South America; volcanic soils.

With 25,000–30,000 species, including one out of every 10 flowering plants, the sunflower family, Compositae or Asteraceae, is found everywhere except Antarctica (although fossil Compositae are known from there; Funk et al., 2005). Despite their near-universal presence in plant communities, detailed information on the biogeographic histories of most tribes remain largely unknown, including the sixth largest tribe, the Vernonieae (~1500 species). A taxonomically robust phylogeny including a broad geographic representation, time calibration, and ancestral range estimation can shed light on dispersal and migration routes for the Vernonieae and other tribes that emerged during the Compositae's explosive Eocene radiation out from southern Africa (Funk et al., 2009; Mandel et al., 2019), along with other factors that have promoted the worldwide success of this hyperdiverse family.

Vernonieae (aka the “evil tribe”) has an extensive distribution in both the New and Old Worlds, including on islands in both hemispheres (Fig. 1). The tribe is unique within the family in having two separate, but geographically parallel, bi-hemispheric lineages of similar age, one running nearly continuously northward from Argentina across Central America, Mexico, and eastern North...
America to Canada, and the other running the length of East Africa
continuing through the Arabian Peninsula, India into southern
China, Malaysia, Australia, and the northern Pacific. Separated by
the Atlantic Ocean, these parallel lineages have evolved in isolation
from one another after the initial colonization event from Africa to
South America that established the New World Vernonieae. From

FIGURE 1. Vernonieae photo plate. Selected taxonomic diversity of Tribe Vernonieae. (A) Distephanus angustifolius (DC.) H. Rob. & B. Kahn (Africa),
early-diverging lineage with trinervate leaves; (B) Baccharoides adoensis (Sch. Bip. ex Walp.) H. Rob. var. kotschyana (Sch. Bip. ex Walp.) Isawumi, El-
Ghazaly & B. Nord. (Africa); (C) Hilliardella capensis (Hourr.) H. Rob., Skvarla & V. A. Funk (Africa); (D) Gymnanthemum myrianthum (Hook. f.) H. Rob.
(Africa); (E) Hesperomania oahuensis (Hillebr.) O. Deg. (Hawai‘i); (F) Critoniopsis bogotana (Cuatrec.) H. Rob. (Colombia); (G) Chrysoallena desertorum
(Mart. Ex DC.) Dematteis (Brazil); (H) Oocephala staeheilinoides (Africa) (Harv.) H. Rob. & Skvarla; (I) Pseudopegolettia tenella (DC.) H. Rob., Skvarla & V. A.
Funk (Africa); (J) Vernonia noveboracensis (L.) Michx. (Eastern North America), capitulum dissection with disk florets removed; (K) Achenes on capitu-
lum of Hilliardella elaeagnoides (DC.) Swelank. & J. C. Mannin; (L) V. noveboracensis disk floret corolla, anthers, and vernonioid styles covered in pollen.
Photo credits (used with permission): (A–D, H–I, K) Marinda Koekemoer, National Herbarium, Pretoria, South Africa; (E) Susan Ching, Plant Extinction
Prevention Program, Hawai‘i; (F, J, L) Jason T. Cantley; (G) Carol Siniscalchi, Benoit Louille, Fed. Univ. Pernambuco, Brazil. Scale bars: (A, E, G) 2 cm; (B) 1
cm; (C, D, H) 20 cm; (F) 30 cm; (I) 5 cm; (J, K) 1 cm; (L) 0.25 cm.
these two centers of diversification, the tribe has continued to expand across continents and islands, including Australia and Hawaii, reaching a near-global distribution (Keeley and Robinson, 2009).

Despite the potential of the Vernonieae to provide insight into the evolution and biogeography of the largest family of flowering plants on Earth, it has received limited attention from systematists until recently. Problematic aspects of its biology and biogeography have made it so refractory to systematic understanding that it has earned the nickname the “evil tribe” (Funk et al., 2005; Keel and Robinson, 2009). Principal among these difficulties is a lack of discrete boundaries to reliably distinguish among taxa at every level from the species to the subtribe. There is a continuum of overlapping characters/states in both vegetative and reproductive morphologies that obscure species boundaries. And this is not a small problem. There are >1000 similar-appearing species distributed across the globe. Unable to resolve taxonomic boundaries using then-available tools, the historical solution was to place the vast majority of taxa into a single worldwide “core” genus, *Vernonia* Schreb. While this solution solved one kind of problem, it did not work for the remaining 80% of genera in the tribe. These taxa have individually unique morphologies, are typically represented by only one or a very small number of species, and lack synapomorphies to suggest their relationships with other members of the tribe. Absent any obvious affinities with each other, let alone similarities with taxa that make up the “hell” of a thousand look-alikes in *Vernonia* s.l., the solution was to recognize each taxon as unique, creating a multitude of separate genera floating around the “core” genus in a kind of phylogenetic purgatory (summarized in Keeley and Robinson, 2009).

Issues with the hard-to-distinguish *Vernonia* s.l. were eventually resolved for many taxa through the detailed morphological studies of Harold Robinson (US) and colleagues over the past 40 years and by the addition of molecular studies (Keeley et al., 2007). The “core” genus, *Vernonia* s.l., was reduced to ~25 New World species, while those removed from it were placed into other, often newly established genera. These, in turn, were assigned to newly recognized subtribes (Robinson, 1999a, b). The first phylogeny for the tribe was provided using molecular data by Keeley et al. (2007). Continuing work combining molecular and morphological data resulted in the establishment of additional subtribes and recognition of new genera (Keeley and Robinson, 2009). However, several subtribal relationships remain problematic, especially for monotypic genera—for example, *Stokesia* L’Her (the only taxon with zygomorphic florets) and *Pacourina* Aubl. (the only aquatic member of the tribe) (Keeley and Robinson, 2009). Additionally, the subtribal affinities of some important genera remain unclear (e.g., the Mesoamerican *Eremosis* Gleason, Andean *Critoniopsis* Sch.Bip., *Asian Monosis* DC, Australian *Pleurocarpae* Benth.). There are also some suggested relationships between taxa in the New and Old Worlds based on both morphological and molecular studies, as is the case for the Mesoamerican *Leiboldiae* and the Southeast Asian genera *Strobocalyx* (Blume ex DC) Spach and *Tarlmounia* H. Rob., S. Keeley, J.J. Škvarla & R. Chan (Turner, 1981; Keeley and Jansen, 1994; Keeley et al., 2007; Siniscalchi et al., 2019). Additionally, Robinson proposed a relationship between the Old World genus *Manyonia* H. Rob. and the New World genus *Heterocypelia* H. Rob. and, conversely, placed the New World genera *Telmatophila* Mart. Ex Baker, *Aclepidopsis* H. Rob., and *Mesanthophora* H. Rob. in the African subtribe Erlangeinae (Robinson, 1999a, b).

Regardless of the difficulties in determining relationships within the tribe, the monophyly of the Vernonieae has never been in doubt and was most recently reconfirmed in a phylogenomic study of the family by Mandel et al. (2019). The tribe remains basically as described by Cassini (1819) and Bentham (1873), except for the inclusion of the Moquinieae, which was recently found to be nested in the Vernonieae in molecular studies by Loeuille et al. (2015) and Mandel et al. (2019), although not formally transferred. In addition to being a stable tribe, a basic division of taxa into Old and New World lineages has also remained a key feature. First proposed by Gleason (1906, 1923), this phylogenetic divergence has been confirmed multiple times using molecular and morphological data (Keeley and Turner, 1990; Keeley and Jansen, 1994; Keeley et al., 2007; Keeley and Robinson, 2009; Mandel et al., 2019).

Recent phylogenomic work has added substantially to our understanding of the Vernonieae’s place in the backbone phylogeny of the family (Mandel et al., 2019). They proposed that it should now be placed in its own subfamily (Vernonioideae) with several other tribes that were also traditionally placed in the subfamily Cichorioideae. However, this view is not shared by all workers (H. Robinson, personal communication) and will require further study. Mandel et al. (2019) also shed light on the position of some problematic genera, in particular *Moquinia* DC (as discussed above), *Distephanus* Cass., and *Pseudostiffia* H. Rob., whose tribal affinities have been debated (Funk et al., 2004; Robinson, 2009). Additionally, Siniscalchi et al. (2019) highlighted some areas where further work is needed to resolve relationships within the New World Vernonieae and place problematic genera (i.e., *Stokesia*). The work of Mandel et al. (2019), besides providing a well-resolved family backbone phylogeny, also identified the timing and location of major diversification events for the family and tribes, finding correlations between climate change and increase in open habitats with the radiation of Compositae worldwide.

Despite these new findings, detailed information is lacking about the biogeographic history of the individual tribes. In particular, little is known of the timing and nature of dispersal events, migration pathways, and relationship to environmental factors that impacted tribal radiations.

To gain a better understanding of the evolutionary history and biogeography of the Vernonieae, we undertook a molecular phylogenetic study, including representatives of all subtribes and spanning the geographic range of the tribe. A molecular clock approach was applied to obtain a time-calibrated phylogeny for the tribe, subtribes, major dispersals, and radiation events. We also identified important geographic areas, dispersal, and migration routes with ancestral range estimation analyses. Edaphic specialization was also considered as a factor in the biogeographic spread of the Vernonieae.

**MATERIALS AND METHODS**

**Taxon sampling**

A total of 438 taxa were sampled, including 368 Vernonieae representing all 24 subtribes and 70 outgroup taxa. The latter included Compositae with a fossil record (Barreda et al., 2008), which allowed us to define clades with a fossil record for molecular clocking purposes. A complete list of taxa and GenBank accession numbers are given in Appendix S1. Nomenclature follows
Robinson (1999a, b) and Keeley and Robinson (2009) unless otherwise indicated. Ongoing taxonomic work by Robinson, Loeuille, Dematteis, and others for South and Central American taxa is regularly revealing the existence of new species and genera. Revisionary studies are needed to properly place these, along with previously described taxa at the generic and subtribal levels. Additionally, a revision of the Old World Vernonieae has not yet been completed (H. Robinson, personal communication). Consequently, several Old World species have yet to be formally transferred from *Vernonia* s.l. and thus must retain that genus name here, even though *Vernonia* s.s. is now entirely New World.

**Sequencing and alignment**

Total genomic DNA was obtained from herbarium vouchers or silica dried fresh leaf material. Samples were prepared by hand grinding leaves with liquid N in a mortar and pestle and then processed using DNeasy Plant Mini Kit following the manufacturer's protocols (Qiagen, Valencia, California, USA). For older herbarium specimens, the QiaAmp DNA Stool Mini Kit was used following the manufacturer's protocols, with sample volumes adjusted to 0.3–0.4 g and a lengthened initial incubation period of 2 h at 70°C.

Following the work of Keeley et al. (2007), the full nuclear ITS region, chloroplast gene *ndhF*, and the noncoding spacer region *trnL-F* were sequenced and used for the analyses. The ITS region was amplified using the primers ITS4 and ITS5 after Kim et al. (1998). ITS amplifications were performed using an initial denaturing step of 94°C, 120 s; followed by 35 cycles of (94°C, 60 s; 50°C, 60 s; 72°C 120 s), then a final 72°C, 420 s elongation step. Chloroplast region *trnLc-f* intergenic spacer was amplified using primers per Shaw et al. (2005) and, for *ndhF*, those of (Olmstead and Sweere, 1994; Olmstead et al., 2000) and Pfeil et al. (2002). Amplifications for the *trnLc-f* were performed using an initial denaturing step of 94°C, 120 s; followed by 35 cycles of (94°C, 60 s; 54°C, 60 s; 72°C 120 s), then a final 72°C, 420 s elongation step. Amplifications for the *ndhF* region used an initial denaturing step of 94°C, 120 s; followed by 35 cycles of (94°C, 60 s; 51°C, 60 s; 72°C 120 s), then a final 72°C, 420 s elongation step. All PCR reactions were performed with 25 µL of reaction cocktail containing 12.75 µL of sterilized H2O, 2.0 µL of 20 mM dNTPs (Pharmacia Biotech, Piscataway, New Jersey, USA) in an equimolar solution, 2.5 µL of 10X PCR reaction Buffer A (Promega, Madison, Wisconsin, USA), 1.25 µL of 25 mM MgCI2, 0.5 µL 10 mg/ml Bovine Serum Albumin (Sigma-Aldrich, St. Louis, Missouri, USA), 1 µL of 10 mM of each of the two primers, 0.5 Biolase Red Taq DNA polymerase enzyme (Bioline-Thomas Scientific, Swedesboro, New Jersey, USA) and 4 µL of DNA template. The final amount of DNA template, PCR reagents, and Taq was adjusted as necessary to generate sufficient PCR products for DNA sequencing. Samples were purified before sequencing using an Exo-Sap enzymatic PCR product pre-sequencing protocol (USB, Cleveland, Ohio, USA) for 45 min. For sequencing reactions, a final volume of 8.0 µL was used consisting of 1.8 µL of sterilized H2O, 3.2 µL of 1 mM primer, and 3.0 µL of purified DNA template. Sequencing was conducted at the Advanced Studies of Genomics, Proteomics, and Bioinformatics facility at the University of Hawai‘i at Mānoa. Sequences were edited using Sequencher version 3.1.10 (Gene Codes, Ann Arbor, Michigan, USA). Additional sequences were downloaded from GenBank, including sequences from the *rpl32-trnL* intergenic spacer. Sequences were compared against generated reference sequences to check for miscalled or ambiguous bases. Alignments were performed using MAFFT version 7.310 (Katoh et al., 2002). The length of the aligned chloroplast gene, *ndhF*, was 869 bp (233 PIC), the spacer *trnL* region was 1080 bp (219 PIC), the *rpl32-trnL* IGS was 1241 bp (130 PIC), and that of the nuclear ribosomal cistron ITS 1, 5.8S, and ITS 2 was 796 bp (496 PIC).

**Phylogenetic analyses and divergence time estimation**

To test for topological congruence, chloroplast and nuclear regions were analyzed separately and phylogenies compared using “tanglegrams” produced in Dendroscope (Scornavacca et al., 2011; Huson and Scornavacca, 2012) as well as by the partition homogeneity test (ILD) as implemented in PAUP* version 4.0b10 (Swoford, 2002) using 1000 replicates, TBR (tree-bisection reconnection) branch swapping, and MulTrees. Tanglegrams revealed three instances of position change of a taxon to a different subtribe; however, none of these resulted in major changes in topology, biogeography estimates, or calibration. Other differences were changes in placement of taxa within their assigned subtribe, again resulting in no changes in relationships among subtribes (Appendices S2–S4). Phylogenetic resolution from cpDNA sequence is poor when taken alone, which makes it challenging to perform a direct comparison with the nuclear ITS, but adding the cpDNA improves the node support in the concatenated phylogeny estimate (as was previously shown to be the case in the Vernonieae; Keeley et al., 2007). The highest posterior density (HPD) intervals (95%) for node estimates were largely overlapping between cpDNA and ITS (Appendices S5, S6). Given this agreement, a concatenated data set was used for the following analyses (Ronquist et al., 2012).

We used jModelTest (Guindon and Gascuel, 2003; Posada, 2008) to determine the best-fitting models of molecular evolution (GTR+I+G) using the Akaike Information Criterion (AIC) for individual gene regions as well as the concatenated data set. Maximum likelihood phylogeny inference was done in RAxML version 8.2.12 (Stamatakis, 2014) on the RAxML-HPC2 Workflow on XSEDE on the CIPRES Science Gateway (Miller et al., 2010). The tree with the highest log-likelihood from 1000 alternative runs on distinct starting trees was selected, and clade support was calculated from 1000 nonparametric bootstrap replicates.

Joint Bayesian inference (BI) on phylogeny and clade divergence times was implemented in BEAST version 2.6.1 (Bouckaert et al., 2014) on the CIPRES Science Gateway (Miller et al., 2010). The GTR+I+G evolution model was used for the ITS, and combined chloroplast partitions based on AIC results from jModelTest (Guindon and Gascuel, 2003; Posada, 2008). Trees were modeled under a Yule process using a random start tree, with the GTR+I+G substitution model for each partition (ITS, combined plastid markers), and a relaxed clock with a lognormal distribution to account for rate heterogeneity among branches. The analysis was allowed to run for 100 million generations sampled every 5000 generations, and a maximum clade credibility tree was calculated and used as the start tree for analysis of a further 100 million generations. Tracer version 1.6 (Rambaut et al., 2016) was used to assess the burn-in value (40%) before calculating the final maximum clade credibility tree using TreeAnnotator version 2.4. (Bouckaert et al., 2014). Trees were visualized in FigTree version 1.4.3 (Drummond and Rambaut, 2007; Rambaut, 2017).

We used eight clade priors to estimate divergence times, including one secondary calibration, six fossils, and island ages for the crown radiation of the Hawaiian endemic *Hesperomannia* A. Gray
We conducted inference on the biogeographic history of the Vernonieae using the maximum likelihood implementation of the program BioGeoBEARS version 1.1.2 (Matzke, 2013a, b, 2014; Dupin et al., 2016) Ancestral ranges and biogeographic events were inferred using the Bayesian calibrated tree trimmed to include only members of the Vernonieae tribe. The geographic areas of extant taxa were recorded from various sources (Appendix S8). Nine areas were used covering the range of Vernonieae distribution: Asia, Africa, Australia, Hawaii, Andes, Brazilian Shield, North America, Mesoamerica, and the Caribbean. The phylogeny was partitioned into five time-slices (0–10 Ma, 10–20 Ma, 20–30 Ma, 30–40 Ma, 40–50 Ma) to include the period from the estimated date of origin of Kauai and Niihau at 5.1–5.7 Ma (Clague and Dalrymple, 1989; Clague, 1996; Price and Clague, 2002). Uniform node priors were set for each constraint. We followed Mandel et al. (2019) in setting a maximum age for the family and the outgroup taxa of 91.5 Ma, which represents recent estimates of the Apiales/Asterales split (Huang et al., 2016; Panero and Crozier, 2016).

### Historical biogeography

We compared several models, including the DEC model (dispersal-extinction-cladogenesis; Ree et al., 2005; Ree and Smith, 2008) and a DIVALIKE model that uses maximum likelihood (this is where the LIKE suffix comes in) to model the processes included in the parsimony-based DIVA model (dispersal-vicariance analysis; Ronquist, 1997), and a BAYAREALIKE model that also uses maximum likelihood to estimate parameters under the assumptions of the BAYAREA model (Bayesian inference of historical biogeography for discrete areas; Landis et al., 2013). These three base models differ primarily in the types of sympatric and vicariant cladogenetic events allowed (see Van Dam and Matzke, 2016).

To estimate the effect of geographic distance on dispersal, we ran models that added a distance parameter \( x \) to each of the base models (Van Dam and Matzke, 2016). The value \( x \) modifies the geographic distance matrix, acting as a multiplier for each dispersal parameter, effectively estimating dispersal probability as a function of distance. Under the base models, \( x \) is fixed at 0 and distance \( 0 = 1 \) and therefore does not affect the estimate of the dispersal parameters. We constrained the value of \( x \) to be <0.0001, under the assumption that longer geographic distances should not increase the probability of dispersal. We also included models that estimate founder speciation events with the jump parameter \( j \) (Matzke, 2013a, b, 2014) and combined models with a joint estimation of both \( x \) and \( j \).

The best model was selected by comparing the AIC values of all models and by comparing nested models with a likelihood ratio test. After comparing the initial 12 models, the best model (DEC + \( j + x \)) was used to run three additional models. The first limited ancestral areas to physically adjacent areas with the exceptions that Asia and Australia were considered adjacent within the past 10 Ma only and that Africa and the Brazilian Shield were considered adjacent in all time-slices to accommodate extant taxa with ranges that extend across these continents. The second and third models also limited ancestral ranges to adjacent areas but also fixed the root to have a range restricted to either Africa, based on the findings of Mandel et al. (2019), or to the Brazilian Shield, which appeared as an alternate ancestral range in several analyses. We compared all 15 models and conducted 1000 stochastic mapping simulations (Matzke, 2014) on the best two models to estimate the number and types of anagenetic and cladogenetic biogeographic events.

### RESULTS

#### Phylogenetic analyses

Intensive sampling of 368 Vernonieae taxa representing all recognized subtribes, unassigned genera, and two genera of Moquinieae (1) clarifies the relationships among subtribes, (2) identifies taxa in need of reassessment, (3) confirms the inclusion of the Moquinieae in the Vernonieae, and (4) allows for the first model-based assessment of the biogeographic history of the tribe. Bayesian and maximum likelihood analyses produced similar topologies (Appendices S10, S11). Phylogeny estimates recovered subfamilies Barnadesioideae, Mutisioideae, Pertyoideae, Carduoideae, and three tribes of Cichorioideae (Arctotideae + Cichorieae and Liabeae) as successive sister groups to the Vernonieae (Cichorioideae). Within the core Vernonieae (all Vernonieae except Distephanieae), a grade of well-supported Old World clades makes up a series of successive sister groups to the “New World Clade” (Fig. 2). However, few of the currently recognized Old World subtribes are monophyletic. For example, the Linziineae represented by *Linzia, Baccharoides*, and *Pleurocarpaea* form a clade, but Hesperomanniinae (monophyletic) and two genera of a polyphyletic Gymnantheminae (*Gymnanthemum, Decaneuropsis*) are nested within it (Fig. 2; Appendices S10, S11). Further, one species of *Baccharoides* appears outside this clade in the Erlangeineae (*B. lasiopus* (O. Hoffm.) H. Rob.). Similarly, subtribes Erlangeineae and Centrapalinae, together, consist of four well-supported clades, but neither subtribe is monophyletic. The Centrapalinae II clade (Fig. 2) includes members of five genera (*Acilepis* D. Don, *Koyamasia* H. Rob., *Centrapalus* Cass., *Brachythrix* Wild & G.V. Pope, *Cabobanthus* H. Rob.), all currently assigned to Centrapalinae, whereas the Centrapalinae I clade includes two members of...
Centrapalinae, *Camchaya* Gagnep. and *Iodocephalopsis* Thorel ex Gagnep., and one member of Gymnantheminae, *Monosis* DC. Additionally, the combined Centrapalinae/Erlangeinae clade (Fig. 2) includes two genera assigned to Centrapalinae (*Centauropsis* Boj. ex DC and *Hilliardiella* H. Rob.) and three assigned to Erlangeinae (*Cyanthillium* Blume, *Parapolydora* H. Rob., and *Polydora* Fenzl). Labeled as Erlangeinae in Fig. 2, the fourth clade includes members of six genera assigned to Erlangeinae (*Vernoniastrum* H. Rob., *Hoffmannanthus* H. Rob., S. Keeley & Skvarla, *Orbivestus* H. Rob., *Muschleria* S. Moore, *Bothrioclone* Oliver ex. Benth., *Ethulia* L.) along with *Brachythrix* (Centrapalinae), *Baccharoides* (Linziinae), and several Old World taxa of *Vernonia* s.l. Additionally, the position of *Monosis* DC (Gymnantheminae) among them is not well established.

The New World Clade is well supported as monophyletic in all analyses and strongly nested within a grade of Old World lineages. Its subtribes are also largely monophyletic as currently circumscribed, albeit with a few notable exceptions.

The first diverging subclade within the larger New World Clade includes the monotypic genera *Pacourina* Aubl. (Pacourininae) and *Acilepidopsis* H. Rob. (Mesanthophorinae) (Fig. 2; Appendices S10, S11). The second diverging clade consists of a mixture of taxa with different subtribal assignments (discussed below): *Strobocalyx* + *Tarlmounia* (Gymnantheminae), *Stokesia* (Stokesiinae), Leiboldiinae, and *Eremosis* (subtribe unassigned). Following these, a third clade includes *Critoniopsis* Sch.Bip. (Piptocarphiinae), sister to a clade consisting of *Cyrtocymura* H. Rob. (Vernoniinae), *Piptocarpa* R. Br. (Piptocarphiinae), *Stilpnopappus* Mart. Ex DC (Lepidaploinae), and another clade consisting of *Rolandra* Rottb. (Rolandrinae), *Trichospira* Kunth (Trichospirinae), and *Stenocephalum* Sch. Bip. (Lepidaploinae) which, in turn, is sister to Elephantopinae. The latter clade (Rolandinae, Trichospirinae, *Stenocephalum* Sch. Bip. (Lepidaploinae) plus Elephantopinae) is sister to Lepidaploinae (Fig. 2). The fourth subclade includes Chrestinae sister to Vernoniinae, with *Heterocypsela* H. Rob. (Dipterocypselineae) and *Tephrothamnus*
The crown node of the Leboldiinae and Eremosis clade was inferred as Mesoamerica, as was Vernoniiinae II, Elephantopinae, Rolandriinae/Trichosyrpinae, Piptocarphinae, Chrestinae, Lepidaploinae II & IV, Vernoniiinae I & IV, and Lycnocephorinae; each had an inferred crown node in the Brazilian Shield. Critioniopsis and Lepidaploinae I & V had an inferred ancestral node range in the Andes, and Lepidaploinae III had an inferred crown node with a geographic range of the Andes plus the Brazilian Shield. The inferred ancestral area of the crown node of Vernoniiinae III was North America (Appendices S10, S11).

The selection of the DEC model over the DIVALIKE and BAYAREALIKE models indicates stronger support for biogeographic patterns consistent with narrow vicariance and subset sympatry rather than widespread sympathy of the BAYAREALIKE model or widespread vicariance of the DIVALIKE model. Support for the DEC model, together with support for restricting ancestral ranges to adjacent areas, indicates a history of range expansions followed by cladogenesis resulting in the unequal splitting of the broader ancestral range into more restricted adjacent sister ranges. Further, the estimation of a nonzero $j$ parameter supports several cases of long-distance dispersal, followed by often rapid cladogenesis responsible for the near-global distribution of the tribe.

Stochastic mapping found, on average, 441 biogeographic events, of which ~21 were founder dispersal events, ~74 were anagenetic dispersal events, ~28 were subset-sympatric speciation events, 304 were narrow sympatric speciation events, and ~14 were cladogenetic vicariance events (Appendix S14). These models are notably bad at estimating range extinction events, and the number of such events was estimated at zero (Matzke, 2014).

Asia was the recipient of nine dispersal events (three cladogenetic and six anagenetic). Eight of these were from Africa, and one was from the Brazilian Shield. Only one dispersal event out of Asia was recorded, consisting of an anagenetic event from Asia to Australia (Appendices S15, S16). In addition to the eight dispersal events from Africa to Asia, additional single dispersal events from Africa to Australia and Hawai‘i, and, on average, about two dispersals to the Brazilian Shield were recorded (Fig. 4). Africa was the recipient of only two dispersal events, with one each recorded from the Brazilian Shield and Asia. Australia received three dispersal events, one from Asia, another from Africa, and one from the Andes (Centratherum australianum) (K. Kirkman) A. R. Bean), but no dispersal events from Australia were recorded. Likewise, Hawai‘i was the recipient of a single dispersal event, but no dispersal events out from Hawaii were recorded (Fig. 4; Appendices S15, S16).

There were 17 anagenetic and two cladogenetic founder dispersal events from the Andes, including nine to the Brazilian shield, eight to Mesoamerica, and three to the Caribbean. The Andes received 30 dispersal events from the Brazilian Shield and one each from Mesoamerica and the Caribbean. Altogether, 46 dispersal events were recorded from the Brazilian Shield while receiving 11 dispersal events from other regions (Appendices S15, S16). North America received four dispersals, two from the Brazilian Shield and Mesoamerica, while also contributing two dispersal events to Mesoamerica. Mesoamerica received ~17 dispersal events and was the source area for four events to the Andes, North America, and the Brazilian Shield. Finally, the Caribbean received 11 dispersal events and contributed one to the Andean region and two to Mesoamerica. Of the 28 subset sympatry events, 12 involved the Andes and the Brazilian Shield, and another six involved a larger range consisting of the Andes and the Brazilian Shield.
FiguRe 3. Calibrated Bayesian phylogeny estimate based on the concatenated data for the ITS, trnL, ndhF, and rpl32 gene regions for 438 taxa. Branch labels indicate the posterior probability support for each clade. Node bars (blue) show the 95% highest probability distribution of node ages. Nodes have been collapsed to show major groupings. An expanded tree is provided in Appendix S10.

Mesoamerica, and North America (Appendix S17). The highest number of vicariance events were recorded between the Andes and the Brazilian Shield (4), Africa and Asia (2), and Africa and the Brazilian Shield (Appendix S18).

DiSCUSsion

Phylogenetic progress

As a result of the inclusion of members of all subtribes across the geographic range of the tribe, we were able to establish relationships among the subtribes with strong support, identify areas in need of taxonomic attention, and resolve the positions of several taxa whose hemispheric origins have been debated and those whose subtribal assignments were ambiguous. The Moquinieae are nested within the Vernonieae. Among others of uncertain placement, we resolved the relationships of the Brazilian Acilepidopsis (Mesanthophorinae), North American Stokesia (Stokesiinae), and Southeast Asian Tarlmounia and Strobocalyx (Gymnatheminae). Evolutionary relationships are clarified for Critoniopsis (Pitocarphinae), Eremonis (unassigned), Cyrtocymura (Vernoniinae), Stenocephalum (Lepidaploinae), Stilpnopappus (Lepidaploinae), Tephrothamnus (unassigned), and the Dipterocypselinae. Overall, the taxonomic treatments within the New World accurately reflect most phylogenetic relationships, a credit to the extensive work of Harold Robinson and colleagues over the past 30 years and recent treatments by Benoit Loeuille (Brazil) and Maximiliano DeMatteis (Brazil, Uruguay) and their students.

At the base of the “New World Clade” is a subclade composed of both Mesanthophorinae and Pacourinae. Robinson (1999a, b) suggested a common subtribal relationship between the Mesanthophorinae and Old World Vernonieae based on morphology; however, our results show it firmly within the monophyletic New World Clade and sister to all other New World taxa.

FiGURE 4. Estimation of the worldwide distribution of Vernonieae indicating key biogeographic events. Green areas represent distribution estimated from molecular clock and ancestral range estimation analyses. Light gray areas are approximated shapes of landmasses. Dashed arrows indicate dispersal events (both founder speciation and anagenetic dispersal speciation events; see Appendices S15, S16) inferred with 1000 simulations performed in BioGeoBEARS under the DEC + j + x + adjacent ancestral areas biogeographic model with an unconstrained root. Other arrows indicate inferred range expansion not due to dispersal. Inverted chevrons indicate mountain-building events significant to the evolution of Vernonieae. Maps are modified from Scotese (2014a, b).
The relationship of the monotypic North American genus *Stokesia* (Stokesiinae) to all other Vernonieae has long been problematic (Keeley and Robinson, 2009). It is the only genus in the tribe with heads composed entirely of zygomorphic, near-ligulate florets; and, with only one species, no morphologically based relationships to other taxa were apparent. This changed with molecular work (Keeley et al., 2007) that placed it within the New World Clade, near the Leiboldiinae. This position in the phylogeny is confirmed here. Our findings differ from those of Mandel et al. (2019) and Siniscalchi et al. (2019), which raised questions as to whether *Stokesia* was included in a grade of Old World taxa most closely related to *Centrpalus*, whether it was sister to *Centrpalus + New World Clade* or nested within the New World lineage. If the former Old World relationship prevailed, it was proposed to be the result of an independent dispersal of the most recent common ancestor (MRCA) of *Stokesia* from Africa and not the single one that established the monophyletic New World Clade. By contrast, our results show *Stokesia* nested well within the New World Clade, identifying it as a product of the original New World ancestor (Fig. 2; Appendices S10, S11).

*Tarlmountia* and *Strobocalyx* are of New World origin as reported previously by Keeley et al. (2007), despite their current range in Southeast Asia and Malaysia. They represent the descendants from one of two confirmed dispersals from the New to the Old World (Fig. 4; Appendices S10, S11) (the second is Elephantoptinae from the Brazilian Shield to Africa). The assignment of *Tarlmountia* and *Strobocalyx* to the otherwise entirely Old World subtribe, Gymnantheminae, no longer seems appropriate. These two taxa were not sampled in studies by Mandel et al., 2019 and Siniscalchi et al. [2019], preventing comparison.

The circumscription and relationship of *Eremosis* (subtribe unassigned) to *Critoniopsis* (Piptocarphinae) has been the subject of differing taxonomic interpretations and assignments (Keeley and Robinson, 2009). Briefly, due to similarities in their morphologies and high-elevation habitats (2000–4200 m) in the mountains of Mexico (*Eremosis*) and the Andes (*Critoniopsis*), it was unclear whether they were congener or separate morphologically convergent genera. In a revision of New World Vernonieae (Robinson, 1999a), they were both placed in *Critoniopsis* (Piptocarphinae). However, it later became clear from molecular studies (Keeley et al., 2007) that they were not closely related and were once again given separate generic status (Har–Carrión and Robinson, 2008; Keeley and Robinson, 2009). *Critoniopsis* remained in the South American Piptocarphinae, but *Eremosis* had no apparent affinity and so remained unplaced (Keeley and Robinson, 2009). Here, and in a prior study (Keeley et al., 2007), *Eremosis* is found to be most closely related to the Leiboldiinae with which it shares part of its geographic range (southern Mexico and northern Guatemala) and at least one distinctive morphological character (i.e., basal stylar node; Robinson, 1999a). Additional studies with increased sampling will be required to ascertain whether *Eremosis* would be best recognized by its own subtribe or placed within the Leiboldiinae. *Critoniopsis* forms a natural group requiring a novel subtribe (Fig. 2).

*Cyrtyomura* (Vernoniinae), *Stenoscephalum* (Lepidaploinae), and *Stilpnopappus* (Lepidaploinae) are each on its own branch (Fig. 2), not nested within any other recognized subtribe, and not within the subtribe to which they are currently assigned. Taxonomic changes are needed to recognize their unique positions. On a different note, the unassigned *Tephrothamnus* falls within Vernonieae.

The status of the Dipterocypselinae is also questionable. We found *Heterocypsela* H. Rob. (Dipterocyselinae) to be nested within Vernonieae in a subclade that also includes *Quechualia* H. Rob. and *Dasyantha* H. Rob. (both assigned to Vernonieae). The Chrestinae, Vernoniiinae, and Lychnophorinae are each monophyletic (except for the taxa noted above). The latter subtribe is also strongly supported as sister to a clade consisting of Vernoniiinae + Chrestinae, as found previously by Keeley et al. (2007) and Louelle et al. (2015). However, our findings differ from those of Siniscalchi et al. (2019), who reported Lychnophorinae + *Allocephalus* J. Bringel, J. N. Nakaj. and H. Rob (Dipterocypselinae) to be the sister group to all other New World taxa. As Siniscalchi et al. (2019) did not include either of these latter two taxa in their analyses, it is challenging to compare our results. However, they do provide a common message: The subtribal status of the Dipterocyselinae should be reassessed and perhaps sunk into the Vernonieae.

In contrast to the well-executed taxonomies of the New World subtribes, relationships among the Old World subtribes cannot be resolved at present given their pervasive polyphylly. Subtribal circumscription and species assignments require a thorough revision. This includes a complete overhaul of the Centrpalinae, with its geographically discrete Asian and African clades, and the Erlangeinae. Current assignments place members in several subtribes. Similarly, the Linziinae now includes the monophyletic Hawaiian endemic Hesperomanninae and the Australian genus *Pleurocarpae*. Further, the Gymnantheminae now includes *Strobocalyx* and *Tephrothamnus*, both New World taxa that dispersed to Southeast Asia and are not related to the Old World taxa with which they currently share subtribal assignment, and *Monosis* remains unplaced. Additional samples are especially needed from Madagascar and India. There are numerous endemic Vernonieae reported from both countries, and they were once physically connected. Their separation and movements across the Indian Ocean could have provided an important pathway for dispersal. Our phylogeny can serve as a base for the much-needed total revision of Old World subtribes.

**Biogeographic history**

The traditional hypothesis of an African origin of the Vernonieae, along with the majority of tribes in the Cichorioideae (summarized in Funk et al., 2009), was supported in the family-wide phylogenomic study of the Compositae by Mandel et al. (2019) and tribal study by Siniscalchi et al. (2019). However, with the Moquinieae now found to be nested within the Vernonieae, a broader ancestral area for the tribe must be considered. In our study, the best model (DEC+ j + x + adjacent ancestral areas) inferred a combined ancestral range of Africa plus the Brazilian Shield (Fig. 4). When the Moquinieae are excluded from the analyses, Vernonieae ancestry of the New World Clade is once again strongly supported as African (Figs. 2 and 4; Appendices S10, S11).

Interestingly, there is a difference in the position of the Moquinieae between the chloroplast and nuclear DNA analysis. The Moquinieae consistently nested in the Distephaninae in ITS but are sister to Distephaninae or sister to the remaining Vernonieae in the chloroplast analyses. These differing positions are mirrored in the conflicting results from the phylogenomic data sets used by Siniscalchi et al. (2019), where Moquinieae were found to be sister to *Distephanus ambongensis* (Humbert) H. Rob. In Mandel et al. (2019), the Moquinieae were sister to the core Vernonieae, as found in our combined data set. When we conducted a taxon
removal analysis, we found that when *D. ambongensis* was removed but all other *Distephanus* species retained, Moquinieae are strongly supported in a position sister to the “core Vernonieae.” Further clarification of early tribal divergences will require the inclusion of more gene regions and perhaps more comprehensive sampling of *Distephanus* species.

For the entirely Old World lineages diverging after the Moquinieae, there is a pattern of repeated splits between entirely African and entirely Asian clades. This is inferred to have occurred at least six times in the Old World grade from the Eocene to recent times (Figs. 2–4). This pattern can best be explained by ancestral areas composed of a combined African + Asian range. Once split, each of these Old World clades has strong biogeographic fidelity. Distephaniniae, Linzia, Erlangeiniae, and subclades within Gymnantheminiae, Centrapalini II, and the Centrapalini/ Erlangeiniae combined clade each have members that are entirely African, whereas Centrapalini I and subclades within Centrapalini II and Gymnantheminiae have entirely Asian members (Fig. 2; Appendices SS, S6).

The New World Clade is monophyletic, as discussed above, with a number of adaptive geographically localized radiations. From initial establishment on the Brazilian Shield, the largest two subtribes, Vernonini and Lepidaploiniae (~200 species each), have gradually expanded, largely via dispersals, but also via range expansions. The latter likely included episodes of sympatry and local extinctions created by rearrangements in size and location of suitable habitat areas that resulted from the extensive geotectonic, topographic, and climatic changes that occurred across the Americas over the past 40 Ma. *Vernonanthura* H. Rob. (Vernonini) and *Lessingianthus* H. Rob. (Lepidaploinae) occur widely across grasslands, cerrado, campos rupestre, and caatinga habitats in eastern Brazil and Argentina. There are additional localized radiations in *Chrestinae* (~20 spp.), *Piptocarphinae* (*Piptocarpha* ~50 spp.), and *Lychnophorinae* (~65 spp.). Others, such as *Lepidaplout* (~150 spp.), moved along the Andes and expanded into Central America, Mexico, and via long-distance dispersal to the Caribbean. *Criticonepis* (~60 spp.) also spread northward along the slopes of the Andes at 2000–4200 m elevation (notably in Ecuador and Colombia). Moving farther north, *Eremosis* (~30 spp.) is found in higher-elevation volcanic mountains in Central America and Mexico; the Leiboldiniae (~12 spp.) are restricted to volcanic mountains of southern Mexico and northern Guatemala; and in eastern North America, *Vernonia* s.s. (~25 spp.) represents a recent radiation into a temperate climate. Some of the major factors that influenced this movement from South to North America are discussed below.

**Importance of long-distance dispersal** —The Vernonieae achieved a near-global range initially by long-distance dispersal (Fig. 4). Their range now includes much of the Americas, sub-Saharan and eastern Africa, Southeast Asia, Australia, Malaysia, and islands in the remote Pacific. The most significant of these events was long-distance dispersal across the Atlantic from Africa to the Brazilian Shield ~40 mya. This resulted in the founding of a second center of diversity for the tribe, resulting in the New World Clade, which now includes over half the taxa in the tribe. These dispersals all occurred within a 10–20 Ma period from the time of the tribe’s origin (Figs. 2–4). This timing of major dispersal events correlates with the findings of Mandel et al. (2019) of an explosive radiation of the Compositae worldwide in the middle Eocene along with the increase in speciation rate for the Vernonieae lineage noted in their study.

**Other factors influencing the biogeographic spread of the tribe**

Once established near the southern tips of continents in both the Old and New Worlds, Vernonieae gradually extended northward, eventually reaching the Himalayas in the Old World and up to the Canadian border in eastern North America in the New World, respectively. These parallel range expansions are correlated with two intertwined factors: (1) the availability of extensive corridors of suitable mid- to high-elevation habitat running linearly south to north in both Africa and the Americas that existed for an extended period (from ~40 to ~3 mya), and (2) edaphic specialization on volcanic, iron-rich and iconically extreme soils. In addition, climate change over the past 65 Ma (Zachos et al., 2001; Holstein et al., 2011) resulted in a drier and more seasonal climate than existed previously altering the size and distribution of ecosystems worldwide (Bowen et al., 2002; Wing et al., 2005; Jaramillo et al., 2010). In Africa and South America in particular, vast expanses of tropical forests were replaced by savannas and shrublands characterized by extended dry periods (Retallack, 2001; Strömberg, 2011). These kinds of open habitats are the preferred home of all but a few of the 25,000–30,000 members of the Compositae. The increase in the area of open habitats worldwide has been an important factor in the global spread of the family (Mandel et al., 2019). Also aiding their wide geographic range extension, the Vernonieae, like most members of the Compositae, produce seeds that are modified for wind dispersal using the pappus, a circular calyx of feathery bristles attached to the achene. In Vernonieae, most species have from 10 to 100+ flowers per head and dozens to hundreds of heads seasonally generating immense quantities of seeds. Additionally, many species are perennials, contributing to the seed pool year after year. Also important to the range expansion of the Vernonieae is the tribe’s ability not only to tolerate but to specialize in habitats unavailable to other plants (discussed below). Rapid species formation and adaptive radiations are stimulated when new opportunities and resources become available (Schurr et al., 2012; Linder et al., 2013, 2014). The Vernonieae are ideally suited to thrive when geotectonic events upset existing vegetation types, presenting them with newly available opportunities.

**Edaphic specialization** —Edaphic tolerance is second only to climate in determining the specific niche to which a plant is adapted (Bradshaw, 1984; Rajakaruna, 2004, and references therein). For the Vernonieae, this is an important part of the tribe’s phylogenetic niche and an important factor in colonizing new landscapes in Africa and South America. In the eastern United States, a common name for *Vernonia*, the type genus, is “ironweed,” referring to its preference for iron-containing soil. However, in addition to being rich in iron, volcanic soils have unique properties due to a mixture of elements. These derive principally from the pedogenic formation of Al/Fe humus complexes (allophane, imogolite, ferrihydrate) and accumulated organic carbon, making them distinct from soils derived from other parent materials (Dahlgren et al., 2004). Adding to this, the Vernonieae are also highly tolerant of other ultramafic and ionically extreme soils (serpentine, bauxite, dolomite, limestone, etc.) that appear at and near the Earth’s surface due to geotectonic shifts and weathering processes such as those that affected the topography and environments of both Africa and South America (e.g., plate collisions, uplift of crustal materials, submergence and reemergence of coastlines, volcanism). Serpentine-, limestone-, and metal-containing soils are toxic to the vast majority of plant species
(Kruckeberg, 1951) but are also associated with endemic radiations for those taxa that can tolerate them (Rajakaruna et al., 2003; Dillenberger and Kaderett, 2013). While tolerance to ultramafic and ionically extreme soils is known to occur in other Compositae tribes (e.g., Smith et al., 2001), to the best of our knowledge and that of colleagues (V. Funk, personal communication), the Vernonieae is the only tribe that is nearly obligate to soils high in Fe, Al, Mg, and Ca, typically and most widely seen in volcanic areas.

While the extent to which the obligate nature of this relationship exists is not yet known (a hypothesis that remains to be tested), the distribution of Vernonieae closely follows that of past and present areas of volcanic activity (Fig. 4). This can be seen in the northward movement along parallel volcanic mountain chains in Africa and South America as they were created between 3 and 40 mya on both continents. These were corridors for migration that allowed the Vernonieae to extend its range in a nearly continuous line from Brazil to eastern North America (Ferrari et al., 1999; Gregory-Wodzicki, 2000; Marshall and Liebherr, 2000; Antonelli et al., 2009; Morrone, 2010) and over 6000 km in East Africa (Cowling et al., 2009; Sepulchre et al., 2009; Tolley et al., 2011). Donoghue (2008) noted the importance of suitable geographic corridors for the movement of species with a given set of traits when environmental change occurs. With changing climate that favored sun-loving species and continuous availability of the preferred substrate, there was little to interfere with the tribe's northward progress (especially since most other plants could not survive on these soils). The northward movement of the New World Vernonieae following Andean uplift is a biogeographic pattern found in several other Compositae (e.g., *Perezia* Lag., Barnadesioideae (Gruenstaeudl et al., 2009), as well as members of the Solanaceae (Särkinen et al., 2013) and Apiales (Nicolas and Plunkett, 2014) and a variety of animals (Dupin et al., 2016). When the mountain ranges of Central America and Mexico were joined to the Andes (~3 mya; Ferrari et al., 1999; Marshall, 2007; Morrone, 2010), the habitats most favored by the Vernonieae extended nearly continuously for ~10,000 km. Volcanic soils also exist in eastern North America, where the much-weathered remnants of ancient volcanic activity remain visible in some areas today (i.e., the Appalachians). The tribe's current range overlaps that of an ancient and now largely invisible chain of volcanoes that stretched from Texas to New York (Clark, 2001). Similarly, in the Old World there are many ancient volcanoes in India and surrounding countries of Southeast Asia, Tibet, China, and Malaysia (Siebert and Simkin, 2002–present) where Vernonieae can be found.

In addition to following the iron-rich soils produced by successive volcanism, the Vernonieae were also able to colonize vast expanses of South America in the cerrado, chapada, and caatinga of Brazil and the plateaus of southern and eastern Africa. These areas also have soils high in iron and aluminum, similar to the composition of volcanic zones. In the cerrado of Brazil, where soil composition has been studied extensively, the majority of soils have a high content of iron and aluminum oxides at all depths, and the iron oxide content is substantially higher in the surface horizons there than in almost any of the soils in Europe or the United States (Buol, 2009). The savannas of East Africa, also species-rich areas for Vernonieae, have similar underlying latosols/ferrosols (Eswaran et al., 1993; Neall, 2009) with a high content of iron/aluminum/magnesium.

Our robust phylogeny includes taxa in multiple subtribes, allowing us to see the importance of soil type in adaptive radiations across hemispheres. For example, additional areas of endemism and adaptive radiations among Vernonieae occur on limestone and serpentine in the West Indies (Lepidaploinae); on volcanic soil in the Eastern Arc of Africa greystone belt (Centrapalinae, Erlangeinae); on limestone in Thailand (*Camchaya, Acilepis*); on dolomite and bauxite (*Lychnophorinae*) and on kaolinite (*Piptocarpinae*) in Brazil; in high-elevation volcanic mountain ranges in the Andes (*Critioniopsis*), Mexico (*Eremosis*), and Mesoamerica (*Leiboldiinae*); and in eastern North America (*Vernonia*). There are likely other endemic radiations as well, in parts of Africa and India that are edaphically correlated, although we have much less information for those regions. The ability to tolerate ultramafic and ionically extreme soil types is known in a variety of Compositae tribes and also likely represents a phylogenetically conserved ability within the family, although not typically exercised to the extent seen in the Vernonieae.

**CONCLUSIONS**

In terms of reaching a global distribution and the total number of species, the “evil tribe” is one of the most successful in the sunflower family. Through the inclusion of all Vernonieae subtribes in our analyses, the biogeography of the tribe is realized in the most comprehensive molecularly based investigation of the tribe to date. Not only is it clear that specific long-distance dispersals were key to initially establishing its near-global distribution, but also that the specialization of the tribe on soils rich in iron and other metals, primarily made available by volcanic mountain-chain building from ~3 to ~40 mya, created corridors for species range expansions north from southern Africa to Southeast Asia and beyond and from the Brazilian Shield to eastern North America. This occurred within an extended period of climate and geotectonic change that favored the sun-loving, drought-tolerant Compositae.

The highly dispersible Vernonieae were in the right place(s), originating and establishing near the tips of immense Southern Hemisphere continents with a great deal of room for radiation, at the right time, when global climate change swept away tropical forests and created increasingly large areas of open and dry landscapes across the Southern Hemisphere with continuous corridors for dispersal when geotectonic forces united to create mountain chains extending the length of Africa and South America and beyond, and with the right genetic makeup to take advantage of the metal-rich Fe, Al, and Mg soils that are toxic to most other plants and were produced by the volcanoes that formed the mountains. There has also been plenty of time during the past ~50 Ma for speciation, radiation across the continents, and dispersal multiple times from multiple places—including to the most distant island archipelago of any continent, the Hawaiian Islands, and to islands in the Caribbean formed by volcanoes rising from the ocean floor. It is hard to beat having the right genetic makeup to specialize on a particular soil type being created in an ever-expanding line, at the right time and at the right place(s) to take advantage of new opportunities. The Vernonieae has a near worldwide range and is the sixth-largest tribe in the Compositae, the largest and most widespread plant family in the world. Not so bad for an “evil tribe.”

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AUTHOR CONTRIBUTIONS

S.C.K. initiated the project, provided phylogenetic interpretation, and wrote the paper. J.T.C. and T.J.G. equally collected and analyzed the data, produced figures and tables, and contributed insights throughout; coauthorship is alphabetical.

DATA AVAILABILITY

Raw, demultiplexed sequence data produced for the current study have been deposited with links to BioProject accession number PRJNA485502 in the NCBI BioProject database (https://www.ncbi.nlm.nih.gov/bioproject/). Biosample accession numbers are listed in Appendix S1. The sample data spreadsheet, including geographic characters, sequence alignments for each of the 427 loci and the concatenated sequence matrix, and trees are available from the Dryad Digital Repository: https://10.5061/dryad.6wpzgmtp (White et al., 2008).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

APPENDIX S1. Taxa sampled, GenBank records.

APPENDIX S2. Tanglegram agreement between ITS and trnL.

APPENDIX S3. Tanglegram agreement between ITS and rpl32.

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APPENDIX S5. Clade support HPD values for all taxa and selected clades with nuclear ITS compared to cpDNA.

APPENDIX S6. Clade support HPD values for all taxa and selected clades with all DNA regions combined.

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APPENDIX S18. Average number of vicariance events estimated from 1000 simulations of the data.

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