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From Gondwana to GAARlandia: Evolutionary history and biogeography of ogre-faced spiders (*Deinopis*)

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Abstract

Aim: We explore the evolutionary history of the ogre-faced spiders (*Deinopis*) from their Early Cretaceous origins to present day. Specifically, we investigate how vicariance and dispersal have shaped distribution patterns of this lineage. Within the Caribbean, we test the role of GAARlandia, a hypothesized land bridge that connected South America to the Greater Antilles during the Eocene–Oligocene transition (~35–33 Ma), in the biogeography of *Deinopis*.

Taxon: Araneae: Deinopidae: *Deinopis*.

Location: Caribbean islands, with additional global exemplars.

Methods: Combining standard Sanger sequence data with an Anchored Hybrid Enrichment (AHE) phylogenomic dataset, we use Bayesian inference to estimate the phylogenetic relationships of *Deinopis*. "BioGeoBEARS" is used to test the GAARlandia hypothesis, and to pinpoint major dispersal events in the biogeographic history of *Deinopis*.

Results: The phylogeny supports the nesting of a Caribbean clade within a continental grade. Model comparisons indicate GAARlandia as the best fitting model, and the biogeographic analyses reflect the geologic history within the Caribbean. Ancient and recent overwater dispersal events are also indicated within this lineage. There is also an ancient 113 Ma split into Old and New World clades.

Main Conclusions: The *Deinopis* phylogeny corresponds well with geography. This is reflected in the support for the GAARlandia land bridge hypothesis and the phylogenetic relationships within and among Caribbean islands mirroring nuances of Caribbean geologic history. Overwater dispersal also plays an important role in the biogeographic history of this lineage as implicated in the colonization of the volcanic and sedimentary Lesser Antilles and in a "reverse" colonization of North America. The spider family Deinopidae is an ancient lineage with origins dating back to Gondwana. While overwater dispersal has clearly played a role in the biogeography of the genus, the *Deinopis* phylogeny bears a strong signature of ancient geological events.

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KEYWORDS

Anchored Hybrid Enrichment, Caribbean, GAARlandia, Gondwana, intermediate dispersal model, net-casting spider, phylogenomics, vicariance

1 | INTRODUCTION

Researchers in the field of biogeography continue to explore the relative importance of long-distance dispersal (LDD) and vicariance in shaping biodiversity (Cook & Crisp, 2005; Cowie & Holland, 2006; Yoder & Nowak, 2006). Before the mid 20th century revelation of plate tectonics, LDD (Carlquist, 1981; Darwin, 1859) and often unsubstantiated land bridge hypotheses were the predominant explanations for disjunct biogeographic patterns. Plate tectonics stimulated biogeographers to propose Earth's geologic history as the primary explanation for distribution patterns, rather than stochastic dispersal events (Nelson & Platnick, 1981; Raven & Axelrod, 1974). Today, it is widely accepted that both LDD (Cowie & Holland, 2006; De Queiroz, 2005; Gillespie et al., 2012) and vicariance events (De Boer & Duffels, 1996; Joseph, Moritz, & Hugall, 1995; Trewick, 2000) have fundamentally shaped the evolutionary history of many lineages (Costa, 2010; Gillespie & Roderick, 2002; Gillespie et al., 2012; Weaver, Cruz, Johnson, Dupin, & Weaver, 2016). Islands, especially geologically complex archipelagos, provide excellent canvases for studying these dispersal patterns (Gillespie & Roderick, 2002). The balance between LDD and vicariance depends on both the unique history of each island and the biology of a particular lineage (Agnarsson, Cheng, & Kuntner, 2014; Alonso, Crawford, & Bermingham, 2012; Binford et al., 2008; Crews & Gillespie, 2010; Heinicke, Duellman, & Hedges, 2007). Some islands formed "de novo" through volcanic activities (Darwinian islands), where dispersal must predominate. Other islands are hypothesized to have continental origins, and/or have been connected to the mainland via temporary land bridges (Pindell, 1994; Pitman, 1993). These ancient connections should have provided corridors for biota to disperse and colonize until vicariance events subsequently generated disjunct species distributions.

The Caribbean archipelago is composed of islands with diverse geologic histories (Mann, Schubert, & Burke, 1990; Pindell, 1994; Pindell & Barrett, 1990; Pitman, 1993) and thus an excellent venue for addressing the interplay between dispersal and vicariance in shaping the biogeography of organisms. The Greater Antilles islands, including Cuba, Hispaniola, and Puerto Rico, share geologic histories dating back to the Cretaceous–Paleogene Greater Antilles arc system (Mann et al., 1990; Pindell & Barrett, 1990). A magmatic belt along the northern boundary of the Caribbean plate together with the Aves Ridge formed the Great Caribbean arc (Pindell & Barrett, 1990; Pindell, Kennan, Stanek, Maresch, & Draper, 2006). Relative to the Americas, the arc shifted eastward with the movement of the Caribbean plate, until reaching its present day geography (Iturralde-Vinent, 2006; Iturralde-Vinent & MacPhee, 1999; Mann et al., 1990; Pindell & Barrett, 1990). The volcanic arc is hypothesized to have formed a late-Cretaceous (85–65 Ma) subaerial connection to the Greater Antilles (Iturralde-Vinent, 2006; Nelson & Platnick, 1981; Rosen, 1985); however, the most ancient connections between the continents and the Greater Antilles are not likely biologically relevant. For instance, the Cretaceous–Tertiary boundary meteorite impact on Yucatan, Mexico 65 Ma (Pope, Ocampo, & Duller, 1991) had catastrophic effects, including major tsunamis (Bourgeois, Hansen, Wiberg, & Kauffman, 1988; Hildebrand & Boynton, 1990; Maurasse & Sen, 1991; Smit et al., 1992) that are predicted to have wiped out large fractions of the Caribbean terrestrial biota (Crother & Guyer, 1996; Hedges, Hass, & Maxson, 1992; Iturralde-Vinent, 2006; Iturralde-Vinent & MacPhee, 1999). Furthermore, the volcanic mountain chain did not continuously form emergent islands, but periodically formed suboceanic banks (Iturralde-Vinent, 2006; Pindell, 1994; Pitman, 1993). Geologic evidence suggests continuous land availability in the Caribbean dating back approximately 40 Ma (Iturralde-Vinent, 1982, 2006; Iturralde-Vinent & MacPhee, 1999), ruling out the continental origin of Caribbean biota during the original fragmentation of the continental crusts.

The age of current lineages in the Caribbean is still largely unresolved (Graham, 2003; Hedges, 1996, 2006; Iturralde-Vinent, 2006; Iturralde-Vinent & MacPhee, 1999; MacPhee & Iturralde-Vinent, 1994, 2005). The colonization history, especially of Caribbean biota that are not expected to readily cross oceanic barriers, is of great interest (Heinicke et al., 2007; Ricklefs & Bermingham, 2008). Rare overwater dispersal, for example with vegetation rafts (King, 1962) or during hurricanes (Censky, Hodge, & Dudley 1998), may explain the arrival of some taxa that otherwise do not typically disperse across water. These would be expected to have arrived at different geologic times. Alternatively, the hypothesized GAARlandia (Greater Antilles and Aves Ridge) land bridge predicts the more or less simultaneous colonization of multiple lineages at 35–33 Ma. During the Eocene–Oligocene transition, the Greater Antilles uplift, coupled with low sea levels, exposed portions of Aves Ridge, potentially forming a relatively continuous connection between northern South America and the Greater Antilles (Iturralde-Vinent, 2006; Iturralde-Vinent & MacPhee, 1999). Reaching peak

exposure 35–33 Ma, the causeway would have served as a temporary opportunity for colonization of the Greater Antilles, until being subsequently flooded with rising sea levels (30–24 Ma) (Iturralde-Vinent, 2006). Several prior studies offer support for the GAARlandia colonization route, primarily in the form of dated phylogenies secondarily supporting the hypothesis (Alonso et al., 2012; Říčan, Piálek, Zardoya, Doadrio, & Zrzavy, 2013). However, relatively few studies have explicitly tested the role of GAARlandia (Nieto-Blázquez, Antonelli, & Roncal, 2017; Weaver et al., 2016), and thus its existence remains under active debate (Ali, 2012; Graham, 2003; Hedges, 2006; MacPhee & Iturralde-Vinent, 2005). Furthermore, Neogene–Pliocene overwater dispersal better explains the timing and pattern of Caribbean colonization for many organisms that are not dispersal-limited (Agnarsson et al., 2016; Dávalos, 2004; Hedges, 2001; McHugh, Yablonsky, Binford, & Agnarsson, 2014).

Most biogeographic research in the Caribbean has focused primarily on vertebrates (Dávalos, 2007; Glor, Losos, & Larson, 2005; Hedges et al., 1992; Hrbek, Seckinger, & Meyer, 2007; Murphy & Collier, 1996; Říčan et al., 2013; Sato et al., 2016) and plants (Salzman & Judd, 1995; Santiago-Valentin & Olmstead, 2003; Skean, 1993; Zona, 1990). There have been a few recent studies on invertebrates (Hall, Robbins, & Harvey, 2004; Matos-Maraví et al., 2014; Morrone, 2006; Sourakov & Zakharov, 2011) including spiders (Crews & Gillespie, 2010; Dziki, Binford, Coddington, & Agnarsson, 2015; McHugh et al., 2014) and other arachnids (Cosgrove, Agnarsson, Harvey, & Binford, 2016; Esposito et al., 2015). These studies have found mixed support for vicariance (Chakrabarty, 2006; Dziki et al., 2015; Matos-Maraví et al., 2014; Říčan et al., 2013) and dispersal (Crews & Gillespie, 2010; Glor et al., 2005; McHugh et al., 2014; Sato et al., 2016) depending on the biology and characteristics of each lineage. Old, globally distributed species that do not readily cross barriers are especially attractive because, while LDD may still occur, it is likely not so frequent as to obfuscate reconstruction of biogeographic history. They also present a more powerful test than, for instance, younger, more narrowly distributed taxa or those in which LDD predominates.

Deinopis are large, web-building spiders globally distributed in tropical and warm temperate areas (Asia, Africa, Madagascar, Australia, North and South America, and the Caribbean). *Deinopis* are commonly known as "ogre-faced spiders" due to their enlarged posterior median eye size, or as "net-casting spiders" because they actively cast their specially modified orb webs over prey (Coddington, 1986; Coddington, Kuntner, & Opell, 2012; Coddington & Sobrevila, 1987). The enlarged eyes enable *Deinopis* to hunt at night in low-light conditions (Stafstrom & Hebets, 2016). During the day, these spiders can be found in understorey habitats and typically hang from dried vegetation mimicking dead palm leaves, sticks and twigs, or pine needles (Getty & Coyle, 1996). *Deinopis* is an early diverging spider lineage and geographically widespread, occurring on all of the Gondwanan landmasses (World Spider Catalog) making them an excellent organism for studying ancient biogeographic patterns. The Mesozoic phylogenetic placement of Deinopoidea (Bond et al., 2014; Garrison et al., 2016) and a deinopid fossil known from Lebanese Amber 135–100 Ma (Penney, 2003) suggest that deinopids are an ancient Cretaceous lineage and may have Gondwanan origins (Ruban, Al-husseini, & Iwasaki, 2007). Given the cryptic, sedentary behaviour of these spiders and because they are absent from remote oceanic islands (*sensu* Gillespie & Clague, 2009), we predict that the postulated GAARlandia land bridge was integral to the dispersal of *Deinopis* into the Greater Antilles. Here, we aim to test the biogeographic history of *Deinopis* and the potential role of GAARlandia in the colonization of the Caribbean.

2 | MATERIALS AND METHODS

2.1 | Taxon sample

One hundred and ninety-five *Deinopis* specimens were collected using standard aerial searching and vegetation beating in Cuba, Hispaniola, Jamaica, Puerto Rico, the Lesser Antilles, North America, Central America (Costa Rica), northern South America (French Guyana, Colombia, Ecuador), South Africa, Madagascar, China, Taiwan, and Australia (Figure 1). There are 21 named species in the New World, including four species within the Caribbean. As discussed by Coddington et al. (2012), deinopids are generally rarely collected: only about 300 specimens of 57 species exist in the world's museums (unpubl. data). Our sampling thus represents an extensive effort that vastly increased the number of deinopids in collections. Here, we use *Deinopis* sp. as our operational taxonomic units (OTUs) to refer to the undescribed taxa, or clades with large amounts of polytomies. Specimens were preserved in the field in 95% EtOH. We include 12 outgroup species including near relatives selected based on the most recent phylogenetic analyses of spider families (Bond et al., 2014; Dimitrov et al., 2016; Garrison et al., 2016). See Appendix S1 in Supporting Information for taxon sample information and GPS localities.

2.2 | Molecular methods

We applied phylogenetic analyses using a combination of shallow gene coverage with dense specimen sampling (Sanger), and a reduced specimen sampling scheme with deep sequence coverage (Anchored Hybrid Enrichment).

2.3 | Targeted gene methods—full specimen set

DNA was isolated from 190 specimens, with the QIAGEN DNeasy Tissue Kit (Qiagen, Inc., Valencia, CA). We sequenced fragments of one mitochondrial locus (*COI*: Cytochrome c oxidase subunit 1) and three nuclear loci (*18S*, *28S*, *H3*), typically effective phylogenetic markers at shallow taxonomic levels for spiders (Agnarsson, Maddison, & Avilés, 2007; Kuntner & Agnarsson, 2011). We amplified *COI* with the LCO1490 (Folmer, Black, Hoeh, Lutz, & Vrijenhoek, 1994) and C1-N-2776 (Hedin & Maddison, 2001) or with primer pairs of LCO1490 and HCOI2198 (Folmer et al., 1994), *Jerry* (Simon et al., 1994), and C1-N-2776. See Table S1.2 in Appendix S1 for PCR conditions for all four markers. Sanger sequencing of samples from the Caribbean, North America, China, Taiwan, Colombia, and South Africa was done at the University of Arizona Genetics Core.

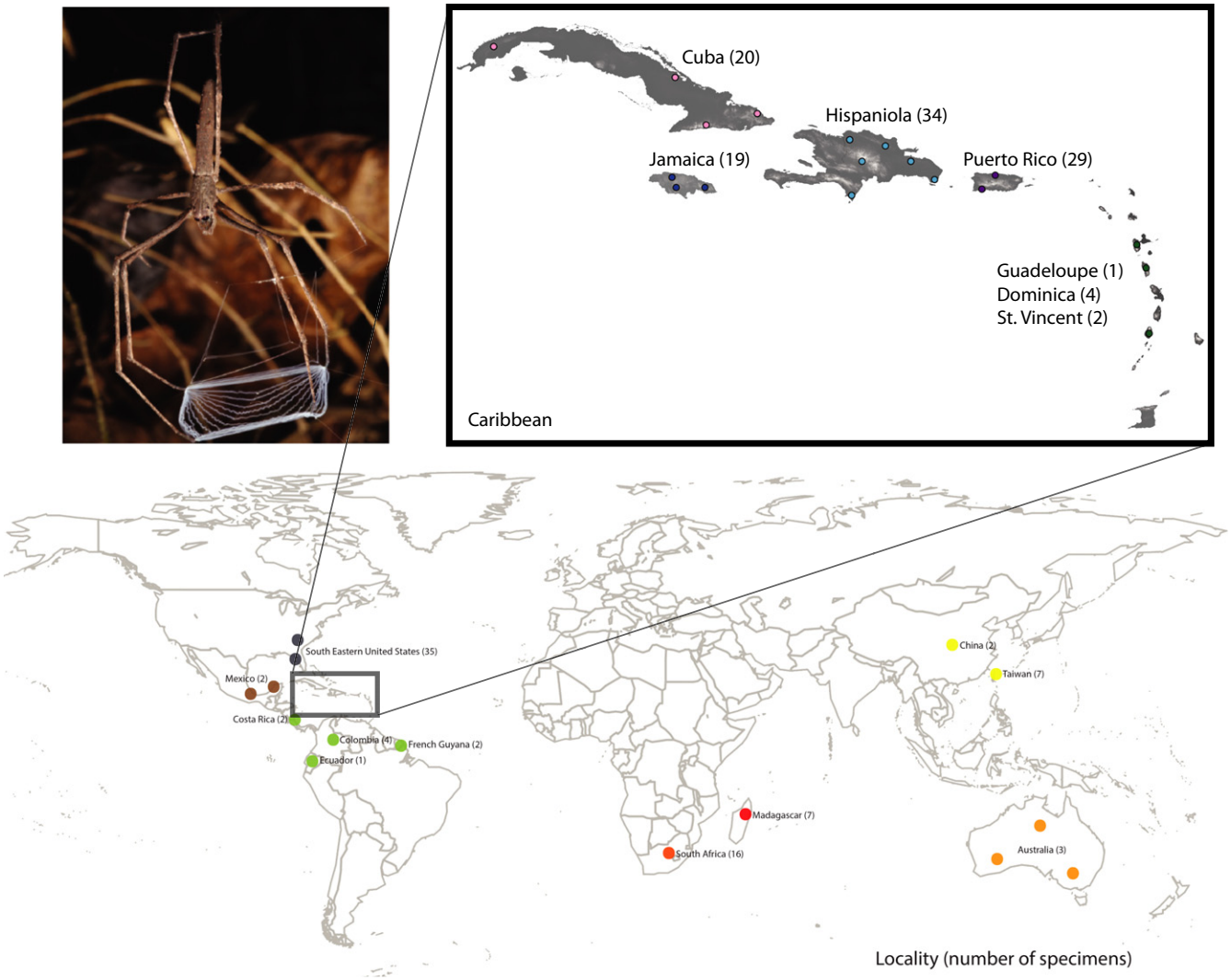

FIGURE 1 Map of collection localities, both globally and locally in the Caribbean. The number of individual specimens that were included in our dataset is shown in parentheses next to each locality. Inset photograph of *Deinopis* in field in Cuba by M. Kuntner [Colour figure can be viewed at wileyonlinelibrary.com]

2.4 | Anchored Hybrid Enrichment—dense genetic sampling with reduced specimen set

The use of Anchored Hybrid Enrichment (AHE) in spiders (Hamilton, Lemmon, Lemmon, & Bond, 2016) is a new phylogenomic approach designed to recover hundreds of unique orthologous loci (i.e., single copy, phylogenetically informative markers) from across the genome. Hamilton et al. (2016) developed the Spider Probe Kit v1 and successfully exhibited the effectiveness of this targeted sequencing approach at resolving both shallow and deep-scale evolutionary relationships within spiders. One drawback of the original paper (Hamilton et al., 2016) was that their taxonomic sampling was biased towards mygalomorph spider taxa. This is the second time AHE has been used in an araneomorph group (Maddison et al., 2017), and the first genus and species-level investigation into relationships within the araneomorphs.

In an attempt to resolve those deeper nodes that were generally weakly supported in the four-locus analysis (<0.95 bootstrap support), we sampled 15 individuals (one per key species). Additionally, we incorporated two individuals from Mexico that were not included in the Sanger dataset. High-quality genomic DNA (≥1 μg) for all specimens was extracted using a Qiagen DNeasy Blood & Tissue kit, drawn from leg tissue that had been preserved using ≥95% EtOH and stored in a −80°C freezer within the Agnarsson lab cryo-collection. DNA concentration was evaluated through agarose gel electrophoresis and spectrophotometry using a NanoDrop ND-1000.

2.5 | Sequence alignment

Sanger sequences were interpreted from chromatograms using PHRED and PHRAP (Green, 2009; Green & Ewing, 2002) within the CHROMASEQ module (Maddison & Maddison, 2011a) in the evolutionary

analysis program MESQUITE 2.75 (Maddison & Maddison, 2011b), with default parameters. The sequences were then proofread by examining chromatograms by eye. Alignments were done in MAFFT (Katoh & Standley, 2013) through the online portal EMBL-EBI, using default settings but increasing the tree rebuilding and maxiterate settings to 100. Gaps were treated as missing characters. Final alignment lengths were: 1,288—*CO1*, 721—*28S*, 812—*18S*, 374—*H3*, for a combined final alignment of 3,195 base pairs (bp).

Anchored Hybrid Enrichment data were generated (library preparation, enrichment, and sequencing) at the Center for Anchored Phylogenomics at Florida State University (www.anchoredphylogeny.com) following the general methods outlined in Lemmon, Emme, & Lemmon (2012) and Hamilton et al. (2016). Sequencing was performed in the Translational Science Laboratory in the College of Medicine at Florida State University. Subsequent bioinformatics (data processing, sequence assembly, quality control, orthology search, alignment) follows the methodology outlined in Hamilton et al. (2016). Following the targeting of the 585 loci in the Spider Probe Kit (Hamilton et al., 2016), 277 loci were recovered from the 17 *Deinopis* specimens (see Appendix S1) investigated herein. Alignments were performed in MAFFT; gaps were treated as missing characters.

2.6 | Phylogenetics

Individual gene trees were estimated using MRBAYES 3.2.2 (Huelsenbeck, Ronquist, Nielsen, & Bollback, 2001; Ronquist & Huelsenbeck, 2003). PARTITIONFINDER 1.1.1 (Lanfear, Calcott, Ho, & Guindon, 2012) was implemented to select the appropriate substitution model using the AIC criterion (Posada & Buckley, 2004). The best model for *COI* was GTR+G+I, for *28S* GTR+G, for *H3* K80+I+G, and for *18S* SYM+I+G. We ran Bayesian inference of all four loci remotely on the CIPRES portal (Miller, Pfeiffer, & Schwartz, 2010) utilizing MRBAYES 3.2.2 with two sets of MCMC and four chains for 30 million generations, sampling the Markov chain every 1,000 generations. Results were examined in TRACER 1.6 (Rambaut & Drummond, 2007) to verify proper mixing of chains and that stationarity had been reached, as well as determine adequate burn-in. For the three nuclear loci, burn-in was set at three million generations, and five million generations for *COI*.

In addition to the "full" dataset (above), where many OTUs were only represented by *COI* sequences, we also ran Bayesian inference on a pruned version of the concatenated alignment—a dataset that included all individuals with at least 65% of the data (3,198 bp), and another dataset that included two "chimeric" taxa representing each *COI* genetic cluster (i.e., mostly eliminated missing character data and allowed for testing the sensitivity of the results to missing data). These analyses were run under the same rates and parameters.

Again, using MRBAYES 3.2.2 on the CIPRES portal for our Bayesian inference, we analysed the 277 loci supermatrix (84,260 bp) recovered from the AHE bioinformatics pipeline (see Hamilton et al., 2016) under default GTR+I+G unpartitioned priors. A coalescence-based species tree approach, ASTRAL (Accurate Species Tree ALgorithm), was used to account for incomplete lineage sorting on our large AHE dataset (Mirarab et al., 2014). RAXML (Stamatakis, 2006, 2014) was used to generate maximum likelihood (ML) gene trees for the ASTRAL analysis, which were replicated with 100 bootstrap replicates (Stamatakis, 2014). The resulting tree was used as a constraint for the four-locus concatenated Bayesian analysis.

2.7 | Divergence time estimations

We used a Bayesian, multi-gene approach with BEAST 1.8.0 (Drummond, Suchard, Xie, & Rambaut, 2012) under a relaxed clock model (Battistuzzi, Billing-Ross, Paliwal, & Kumar, 2011) to estimate divergence times in *Deinopis*. For the Sanger sequencing data, dating and maximum likelihood estimations of ancestral areas were performed with the "chimeric" matrix including all four loci (i.e., low amounts of missing data)—resulting in the smallest taxon sample but most complete gene alignment. In addition, BEAST analyses were run separately on the most taxon-rich dataset (*COI*) as well as on individual nuclear datasets (28S, H3, 18S) and assessed for continuity. A final dating analysis was run on our AHE data, under default GTR+I+G unpartitioned priors, for 30 million generations with a Yule process tree prior.

For all dating analyses, the monophyly of Deinopidae was constrained, based on the results of the Bayesian and ML analyses. We utilized the CIPRES online portal to run the BEAST analyses after configuring them locally using BEAUTI (Altekar, Dwarkadas, Huelsenbeck, & Ronquist, 2004; Miller et al., 2010). A fossil calibration, based on the Lebanese amber *Paleomicromenneus*, estimated to be 130–100 Myr (Penney, 2003), was used as a stem with a minimum age of Deinopidae and a uniform distribution offset by 100 with the maximum age that of orbicularian spiders (190 Ma). For the Sanger sequencing dataset, following the results from the phylogenomic study of spiders (Bond et al., 2014), we calibrated the age of orbicularians, in the broadest sense, containing deinopids, using a normal distribution with mean of 190 Ma and 20 standard deviations and the age of the root as 200 ± 20 Ma SD. We also used the *COI* mean and SD substitution rates estimated to be similar across spider lineages, which can be used to estimate divergence times (Bidegaray-Batista & Arnedo, 2011; Kuntner, Arnedo, Trontelj, Lokovsek, & Agnarsson, 2013; McHugh et al., 2014). We set the *COI* mitochondrial substitution rate parameter (ucld.mean) as a normal prior with mean = 0.0112 and *SD* = 0.001. We tested the sensitivity of the results to *a priori* assumptions by conducting and comparing analyses with and without *COI* rate information and with and without constraining Deinopidae monophyly. The Sanger data analyses were run for 30 million generations with a calibrated Yule birth–death tree prior because it can simulate extinction rates over time and is more appropriate if more than one individual represents terminal taxa (Drummond et al., 2012). ESS values for all sets of data were again examined in TRACER 1.6 (Rambaut & Drummond, 2007) to determine burn-in and to check for stationarity. The tree was then assembled in TREEANNOTATOR using a burn-in of three million (five million for our AHE dataset).

2.8 | Biogeography

We used 'BioGeoBEARS' in R (Matzke, 2013) to estimate global and Caribbean ancestral ranges. Maximum range was constrained to two areas. To test global biogeography, the "chimeric" dated phylogeny was used, as topology and divergence times were consistent with AHE tree, yet it had the most complete global taxon sampling. The "prune_specimens_to_species function" was used in R to obtain OTUs. We defined eight geographic regions based on Morrone (2006) as North America (NA), South America (SA), Africa (AF), Southeast Asia east to Wallace's line (AS), Australia (AU), Greater Antilles (GA) and Lesser Antilles (LA). Time slices included the Early Cretaceous split of eastern South America and western Africa (119–105 Ma) (Ali & Aitchison, 2008; Hawkesworth, Kelley, Turner, Le Roex, & Storey, 1999; McLoughlin, 2001; Vidal, Azcolinsky, Cruaud, & Hedges, 2008; Vidal et al., 2010).

To test the GAARlandia model, we applied probabilities to time slices based on historical geology (Iturralde-Vinent, 2006; Iturralde-Vinent & MacPhee, 1999) replicating similar parameters outlined by Weaver et al. (2016). The AHE dated phylogeny was used because node support was 1 for all nodes and error bars were smaller compared to the "chimeric" dated phylogeny. The AHE phylogeny was pruned to include South America and the Greater Antilles; geographic ranges included South America (SA), Hispaniola (HI), Cuba (CU), Jamaica (JA), and Puerto Rico (PR). The GAARlandia model consisted of probabilities of Greater Antilles land connection to South America, as well as inter-island connections from 35–30 Ma. The No GAARlandia model did not include connection from South America to the Greater Antilles, but did share the opening of the Mona Passage (23 Ma) Windward Passage (15 Ma) (Iturralde-Vinent, 2006) (see Table S3.1 in Appendix S3). We also tested the GAARlandia hypothesis with the "chimeric" and *COI* phylogenies under the same model parameters. We applied models Dispersal-Extinction-Cladogenesis DEC and DEC+J, which accounts for founder event speciation. The DEC+J has been criticized as a poor model for founder event speciation by parameterizing the mode but not the rate of speciation and thus creating a tendency towards data explained entirely by cladogenetic events (Ree & Sanmartín, 2018). Here we compare likelihood and AIC values of both the DEC and DEC+J of GAARlandia models to the DEC and DEC+J of No GAARlandia models. The likelihood scores for this GAARlandia analysis were compared to test for significance (a natural log of 2 was considered significant) (Ree & Smith, 2008). Akaike information criterion (AIC) and relative likelihood were used to assess the model probabilities given the data (Table 1).

3 | RESULTS

3.1 | Overview

Fundamental relationships of the entire group were nearly identical in the taxon-rich Sanger and character-rich AHE datasets; the latter with posterior probability support of 1 for every clade. Combined, they yield a robustly supported phylogeny with most nodes having >0.95 posterior probability (Figure 2) (Huelsenbeck & Rannala, 2004). The phylogeny supports a fundamental separation between New and Old World clades, as well as the nesting of Caribbean clades within a continental grade. Within the Caribbean clade, we find a number of deep divergences as well as evidence for higher diversity in the region than previously explained by morphology alone. The biogeographic analyses indicate vicariance in addition to several implied LDD events.

3.2 | GAARlandia vicariance

Within the New World clade, we tested whether GAARlandia vicariance or LDD overwater hypotheses could explain the colonization of the Caribbean. Results suggest that the Greater Antilles were colonized once, from South America (Figures 2–5) and that the timing of the event is consistent with the GAARlandia land bridge. Accordingly, results from AIC model comparison supported GAARlandia, both DEC and DEC+J were better fitting models than both No GAARlandia DEC and DEC+J models (Table 1). Furthermore, genetic structure within the Caribbean reflects patterns consistent with our current understanding of historical island connectivity (Iturralde-Vinent, 2006). The Western Hispaniola clade is sister to the rest of the Greater Antilles and North America. A second clade consists of individuals from Eastern Hispaniola, Southern Hispaniola (Rabo de Gato), and Puerto Rico (Figure 2). At a finer scale, the phylogenetic structure within the Greater Antilles clade also matches the within-island geologic history (Figures 2 and 4). Our sampling captures deep and diverse genetic histories (divergence times 20–5 Ma) within Hispaniola and Cuba. Neither island is monophyletic, but both include apparently old lineages that are separated by mountain ranges (Figures 2 and 4). The two Cuba species coincide with the isolated mountain ranges of Turquino and Cubitas, and two Hispaniola species are separated by the Cordillera Central (Mann, Draper, & Lewis, 1991) (Figures 2 and 3). While the Puerto Rico lineage is monophyletic, it has two strongly supported clades containing northern and southern individuals on either side of the Cordillera Central mountain range.

3.3 | Overwater dispersal

Several overwater dispersal events are proposed including relatively recent (<10 Ma) and short-distance colonizations of (a) North America from Cuba, (b) the Lesser Antilles from South America, and (c) between Lesser Antilles islands (Guadeloupe, Dominica and St. Vincent) (Figure 5). Our molecular dating analyses indicate overwater dispersal to the Lesser Antilles after 32 Ma (Figure 3), consistent with the uplift of the volcanic and sedimentary Lesser Antilles Middle Eocene in the north (Guadeloupe and Dominica) and Oligocene in the south (St. Vincent) (Pindell, 1994; Pindell & Barrett, 1990). Overwater dispersal may also be indicated in the Old World, but the data are sparse at this point.

TABLE 1 'BioGeoBEARS' relative model probabilities. Two models, Dispersal-extinction-cladogenesis (DEC) and (DEC+J), the (+J) allowing for founder event speciation were used to test dispersal data with and without GAARlandia. (LnL) log-likelihood; (*d*) rate of dispersal; (*e*) rate of extinction; (*j*) relative probability of founder event speciation at cladogenesis; (AIC) Akaike's information criterion; (ΔAIC) AIC-min(AIC); (AIC weight) normalized relative model likelihood; (relative LL) model relative likelihood.

Model	Ln*L*	Number of parameters	*d*	*e*	*j*	AICc	ΔAIC	AICc_wt	Relative LL
DEC GAARlandia	−17.07	2	0.7878	0.0156	0	40.15	0	0.7653	1
DEC+J GAARlandia	−16.12	3	1.2016	0.0195	0.4598	43.02	2.87	0.1824	0.2384
DEC No GAARlandia	−20.48	2	0.1609	0.0266	0	46.97	6.82	0.0253	0.0331
DEC+J No GAARlandia	−18.02	3	0.7250	0.0292	0.3755	46.84	6.69	0.0269	0.0352

3.4 | Gondwanan origin

All analyses split the Deinopidae into two major clades, a predominantly Old World one containing species from Africa, Madagascar, Asia, and Australia (including the Old World tropical genus *Menneus*), and an exclusively New World group containing *Deinopis* from the Caribbean, and North, Central, and South America. AHE analyses, place a single individual from Mexico (individual not sampled in Sanger sequencing) nested within the Old World clade (Figure 3), see Discussion for details. This specimen possesses abdominal humps—a trait that characterizes part of the Old World clade. Thus, its morphology is consistent with its unexpected placement as sister to specimens from South Africa. Our AHE BEAST analysis dates the divergence between Old and New World Deinopidae at 113.84 Ma (130.09–98.80 95% highest posterior density [HPD]), timing that is consistent among "chimeric" and individual gene BEAST analyses (Figure 3 and Fig. S2.3). This split coincides with the timing of a continental break up that isolated eastern South America from western Africa during the Early Cretaceous period (119–105 Ma) (Ali & Aitchison, 2008; Hawkesworth et al., 1999; McLoughlin, 2001; Vidal et al., 2008, 2010). Furthermore, a global biogeographic analysis estimates the most recent common ancestor of Old and New World clades possessed an ancestral range within Africa and South America (Figure 5).

4 | DISCUSSION

Our study used a combination of AHE and Sanger sequencing data paired with taxon sampling focusing on the Caribbean and the New World to reveal the biogeography and evolutionary history of the poorly known ogre-faced spiders. The biogeographic data suggest that *Deinopis* colonized the Greater Antilles once (Figures 4 and 5). The split between South America and Caribbean lineages occurred prior to the existence of GAARlandia, while the first split within the Caribbean occurs a few million years after its submergence. Colonizations within the Greater Antilles occurred sometime in the interim and biogeographic analyses support a role of the postulated GAARlandia land bridge in this colonization (Table 1), as well as inter-island connectedness until 15 Ma when Cuba separated from Hispaniola (Iturralde-Vinent, 2006).

GAARlandia-mediated dispersal from South America to the Caribbean has been subject to critique and debate (Ali, 2012; Hedges, 1996, 2006). Our study adds to the growing number of lineages where the postulated land bridge is expected to have aided dispersal into the Greater Antilles, including other spiders (Binford et al., 2008; Crews & Gillespie, 2010; McHugh et al., 2014), frogs (Alonso et al., 2012), and freshwater fish (Říčan et al., 2013; Weaver et al., 2016). Many studies that exclusively compare clade age to the age of GAARlandia also support alternative hypotheses of earlier dispersals to the proto-Antilles islands, where land may have existed 5–10 Ma prior (Iturralde-Vinent, 2006), or more recent overwater dispersal events. Here, however, we find support for GAARlandia-mediated dispersal through likelihood-ratio hypothesis testing.

High levels of endemism among and within islands suggest, following a single colonization, *Deinopis* subsequently diversified in response to the separation of islands, and geological barriers (mountain ranges) within islands. Indeed, the biogeographic analyses reflect the many nuances of the complex geological history of the Caribbean including the interconnectedness of the Greater Antilles. For example, the sister relationship between eastern Hispaniola including Puerto Rico is consistent with the hypothesis that these regions had a relatively recent land connection until the opening of the Mona Passage (30–22 Ma) (Iturralde-Vinent, 2006). Furthermore, within multiple islands, we find genetically unique clades that are separated by barriers such as mountain ranges (Figure 3). Similar patterns of high interspecific genetic divergence have been found in dispersal-limited lineages of spiders, including Mesothelae (Liphistiidae) spiders as well as mygalomorphs (Hamilton, Formanowicz, & Bond, 2011; Hamilton, Hendrixson, Brewer, & Bond, 2014; Xu, Liu, Chen, Li, & Kuntner, 2015; Xu, Liu, Chen, Ono, et al., 2015; Xu, Liu, Cheng, et al., 2015; Xu et al., 2016). These finding provides an additional context in which to explore the origin and age of Caribbean taxa, including the potential impact of geology on phylogeny.

Within the Caribbean, we find evidence for multiple overwater dispersal events including a "reverse colonization" from island to continent—the colonization of North America via northern Cuba (northern GAARlandia). The same pattern is found, e.g., in the *Loxosceles* and *Sicarius* spiders (Binford et al., 2008). Reverse colonization has also been documented in various biotas on a global scale, including the *Anolis carolinesis* lizard from Cuba to North America (Bellemain & Ricklefs, 2008; Glor et al., 2005). The classic biogeographic view indicates that islands mainly serve as sinks for continental taxa (Agnarsson & Kuntner, 2012; Bellemain, Bermingham, & Ricklefs, 2008; Sturge, Jacobsen, Rosensteel, Neale, & Omland,

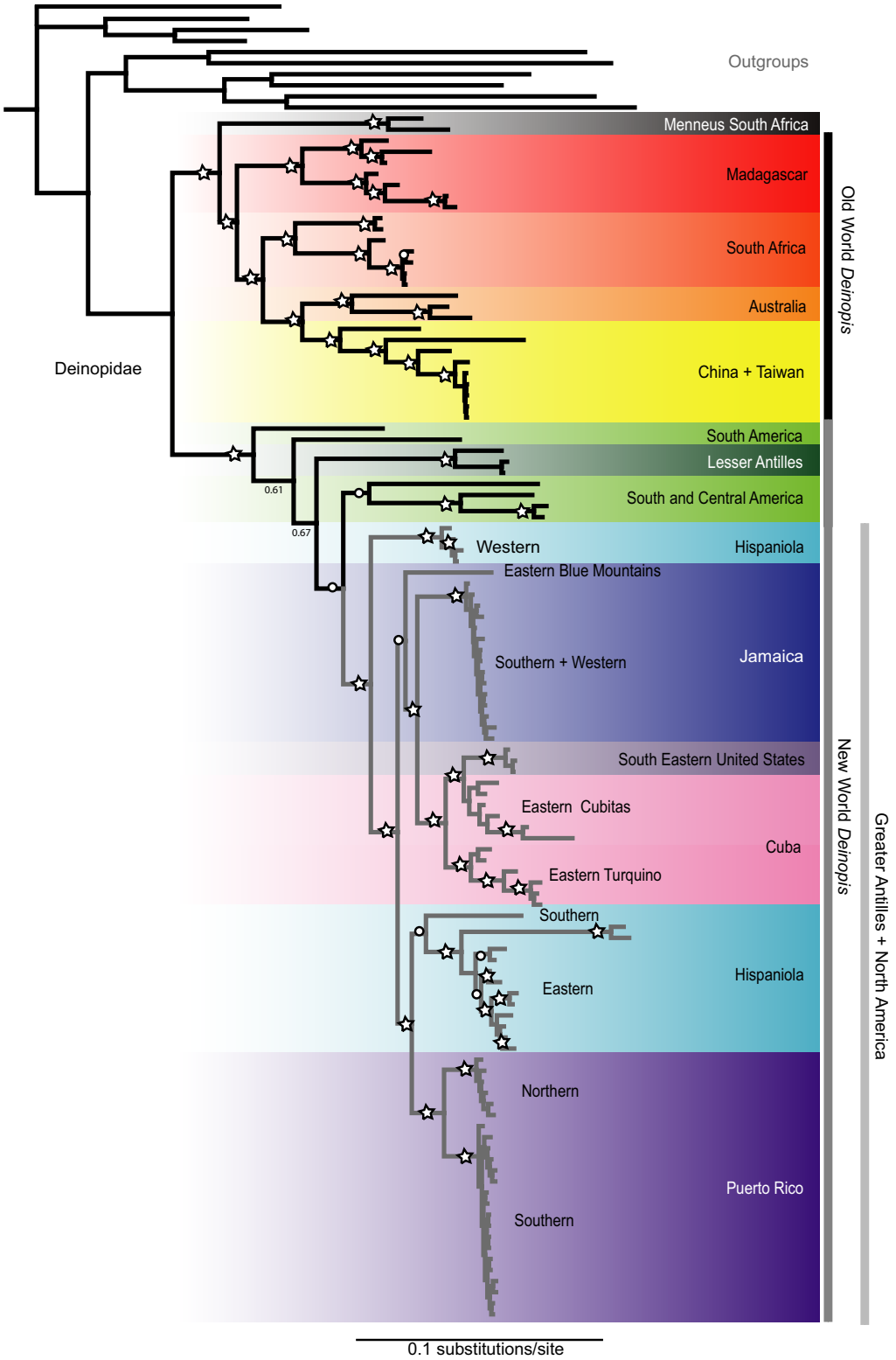

FIGURE 2 Bayesian inference phylogeny of the concatenated supermatrix alignment with 45% missing data. The Bayesian inference tree obtained from the AHE analysis was used as a constraint tree. Open stars indicate posterior probability support of >0.95. Open circles indicate posterior probability support of 0.75–0.95. Clades are coloured by general geographic region. Scale bar on lower left is 0.1 expected substitutions per site. For unedited version with tip labels see Appendix S2. [Colour figure can be viewed at wileyonlinelibrary.com]

2009); however, these dispersal probabilities are dependent on the interplay between the size and distance of the island to the mainland as well as the dispersal ability of the taxa. We also find evidence of relatively short-distance overwater dispersal to and between the Lesser Antilles, logically as these are volcanic and sedimentary islands never connected to the mainland. Interestingly, this overwater

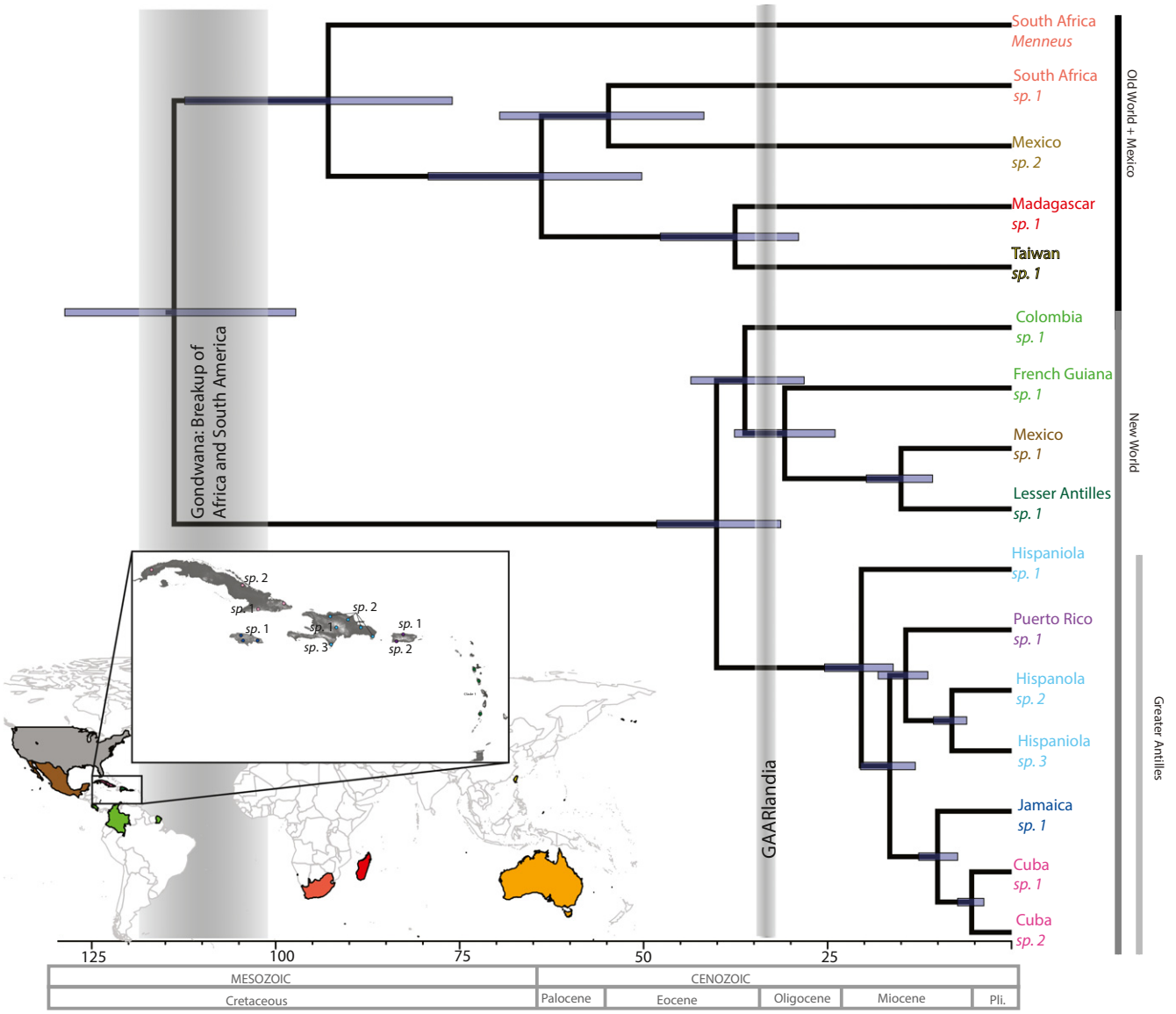

FIGURE 3 Beast divergence time estimations of Anchored Hybrid Enrichment data. Scale shows millions of years. Grey error bars show margins of error around specific Beast divergences. See Appendix S2 for tip labels. [Colour figure can be viewed at wileyonlinelibrary.com]

dispersal occurred soon after the emergence of these islands, suggesting that perhaps conditions during the emergence of these islands were favourable to dispersal.

4.1 | Global implications

In sum, we find correspondences between phylogeny and geologic events spanning over 100 Myr. Few studies to date have placed Caribbean biogeography in a global context (Gamble, Bauer, Greenbaum, & Jackman, 2008; Longrich, Vinther, Pyron, Pisani, & Gauthier, 2015; Pramuk, Robertson, Sites, & Noonan, 2008; Pyron, 2014), consequently limiting ancestral ranges of West Indies biota to the Americas. Trade winds can bring flora and fauna from Africa to the Neotropics through trans-Atlantic sweepstakes dispersal (Heinicke et al., 2007; Raxworthy, Forstner, & Nussbaum, 2002; Vidal et al., 2008; Voelker, Rohwer, Outlaw, & Bowie, 2009). Results from the dated phylogeny (Figure 3) are consistent with the argument that *Deinopis* was present on Gondwana before diverging into Old World and New World clades following the breakup of the supercontinent. There have been similar findings with other ancient spiders such as sicariids (Binford et al., 2008) and archaeids (Wood, Matzke, Gillespie, & Griswold, 2013). Still, it is clear *Deinopis* spiders have diversified through both vicariance and LDD events. Our analyses reveal several intriguing examples of overwater dispersal events, both ancient and recent, and short and long distance. The global dataset, though limited, suggests possible dispersal to Madagascar, and Australia, from Africa. The colonization of Madagascar is dated at 80–60 Ma, significantly after the separation of Madagascar from Africa (Figures 3 and 5). Overwater dispersal from Africa is a hypothesis supported by the majority of Malagasy lineages studied to date (Agnarsson & Kuntner, 2005). Furthermore, while the

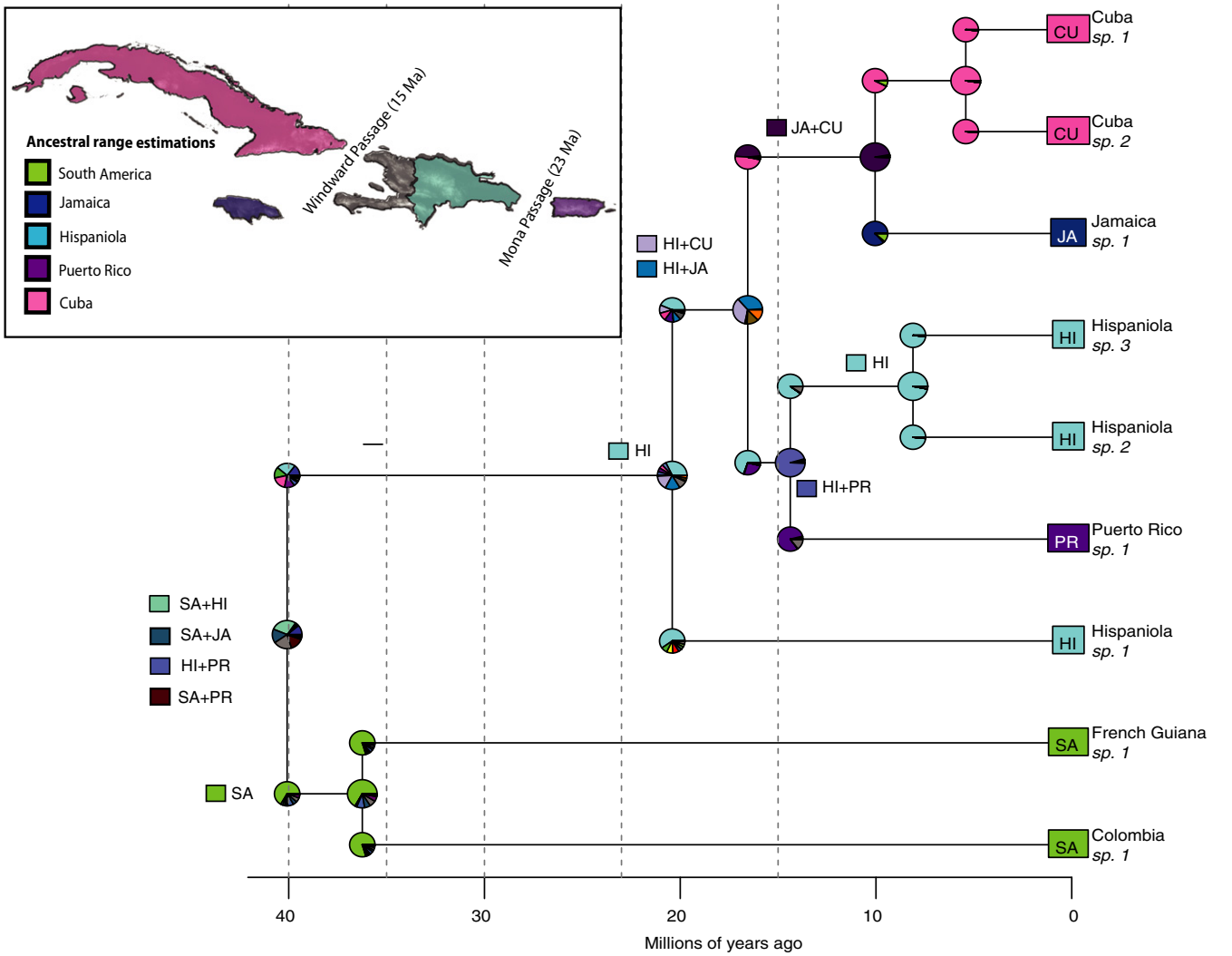

FIGURE 4 'BioGeoBEARS' ancestral range estimation of the GAARlandia DEC+J model. Coloured squares indicate the most probable range of the most recent common ancestor. Tip labels are coloured by species areas (islands and mainland). [Colour figure can be viewed at wileyonlinelibrary.com]

Australia clade is grouped with the rest of the Old World, historically the continent was connected to South America through Antarctica around 60–50 Ma (Sanmartín & Ronquist, 2004), almost 100 Ma after separating from India and Africa (Hawkesworth et al., 1999; McLoughlin, 2001). Thus LDD from South Africa or a possible ancient land bridge connecting Eurasia to Australia must be invoked to explain the nesting of Australian specimens within the clade from Africa instead of purely Gondwanan vicariance. More extensive global sampling is necessary to address these biogeographic questions. Unexpectedly, we find the placement of one of the two Mexico specimens within an otherwise purely Old World clade (Figures 3 and 5). While surprising, the shared traits otherwise restricted to Old World species (i.e., abdominal hump morphology) independently support this finding. Barring further evidence, relatively recent LDD must thus be invoked to explain the presence of *D. diabolica* (Kraus, 1956), which shares these Old World morphological features, in the Americas. Further testing from a much more broad global taxonomic sampling effort is required to resolve these evolutionary relationships.

4.2 | Mitochondrial DNA phylogeography

Notably, the single-locus mtDNA *COI* analysis corresponds closely to geography and alone supported the GAARlandia hypothesis (Fig. S2.5). Single-marker analyses are prone to insufficient resolution and/or large error, often due to deep mitochondrial divergences or introgression events that obscure the true evolutionary past (Capesius & Bopp, 1997; Gontcharov, Marin, & Melkonian, 2004; Hoef-Emden, Marin, & Melkonian, 2002; Nei, Kumar, & Takahashi, 1998; Nickrent, Parkinson, Palmer, & Duff, 2000; Poe & Swofford, 1999). In this case, *COI* appears to capture the major events in the history of this ancient lineage. Generally, the individual nuclear Sanger data correspond to geology to a much lesser degree. This may reflect the lower substitution rates of nuclear data, thus less informative characters. Additionally, it could also indicate population dynamics such as male biased dispersal that would lead to different evolutionary histories between the maternal and paternal genetic lines (Aars & Ims, 2000; Doums, Cabrera, & Peeters, 2008; Knight et al., 1999; Pusey,

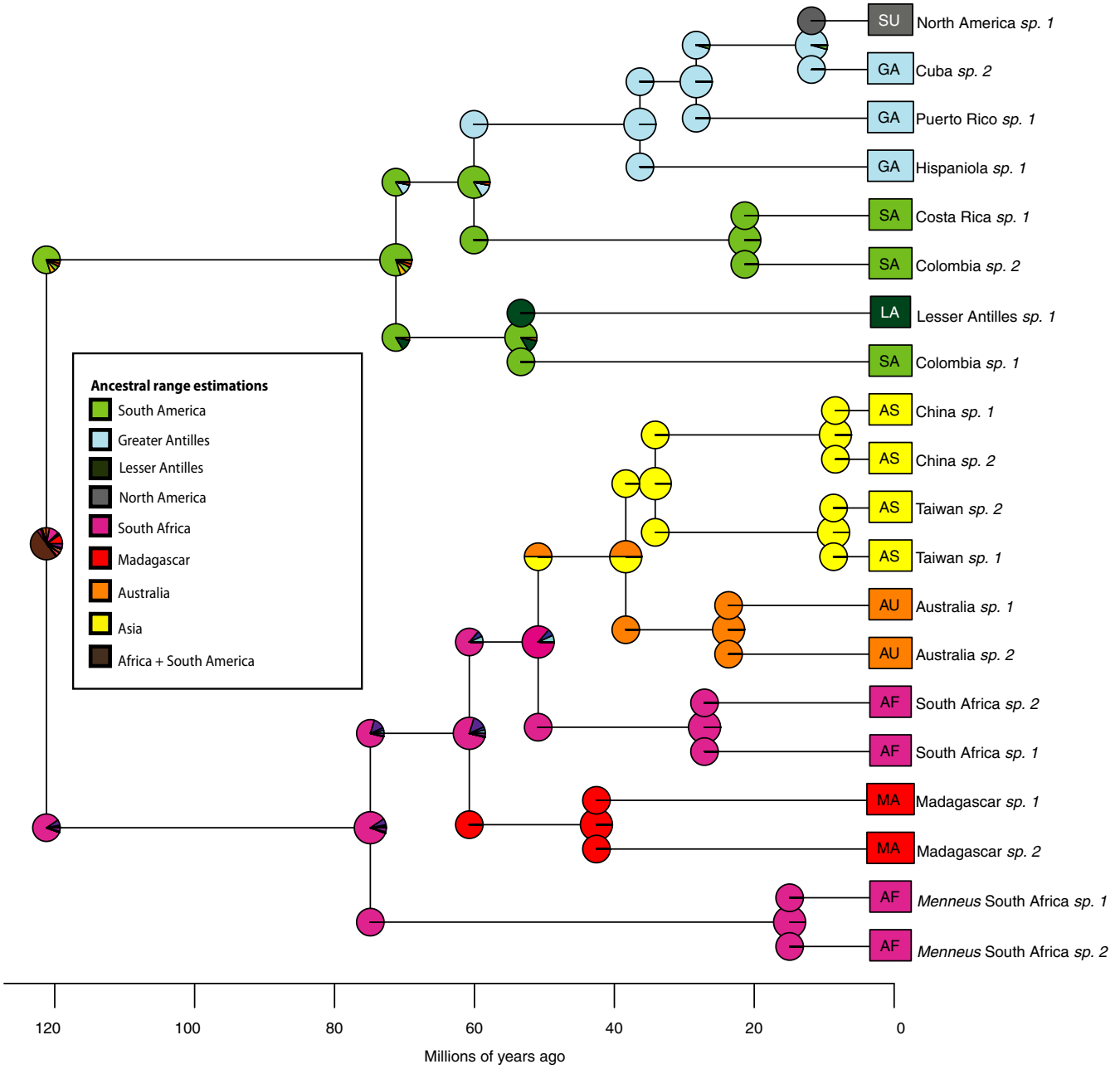

FIGURE 5 'BioGeoBEARS' global ancestral range estimation of the DEC+J model. Coloured squares indicate the most probable range of the most recent common ancestor. Corresponding dated phylogeny with nodal support and full tip labels in Supplementary Material. Tip labels are coloured by species areas (islands and mainland). [Colour figure can be viewed at wileyonlinelibrary.com]

1987). The results from the AHE data (Hamilton et al., 2016), consistent with the *COI* results, indicate the former: that single-locus nuclear marker (standard Sanger sequencing data) may be positively misleading due to limited variation, and possibly other processes. These results are consistent with the long-celebrated success of mitochondrial data in phylogeography (Avise, 2000).

4.3 | Secondary loss of highly derived eyes?

Another surprising result that this study has uncovered is the non-monophyly of *Deinopis*. *Menneus* is nested within the genus (*contra* [Coddington et al., 2012]), which ignites intriguing morphological, evolutionary, and biogeographic questions. Did *Menneus* disperse overwater or vicariantly through Eurasia from Africa to Australia and then go extinct elsewhere, or did the morphology (secondarily reduced eye size and abdominal humps) evolve separately on both continents? Future studies may address the intriguing hypothesis that in *Menneus* the size of the uniquely large posterior median eyes (characteristic of *Deinopis*) has been secondarily reduced. Yet, with a very small sample of *Menneus* in this dataset, further taxon sampling is necessary to untangle the phylogenetic and biogeographic relationships within Old World Deinopidae. With a family level

molecular phylogenetic revision, future studies can assess whether *Menneus* is monophyletic and begin to untangle the unexpected and complex evolutionary history within this lineage of spiders. Our study suggests there are future venues for investigating the evolution of eye size and function in this fascinating group.

5 | CONCLUSION

Ogre-faced spiders represent a global lineage that champions the fundamental importance of both vicariance and dispersal. This lineage surfaces as an excellent biogeographic tool that despite its rarity, offers great promise for further, more detailed global studies. Multiple LDD events within this group reveal potential good dispersal abilities. Future studies can test dispersal ability and other factors such as priority related effects possibly underlying these colonization patterns. Furthermore, the origin, and putative secondary loss, of a highly unique visual system, suggests promising venues for research outside the realm of biogeography.

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COMPETING INTERESTS

The authors have declared that no competing interests exist.

DATA ACCESSIBILITY

The concatenated alignment and phylogenetic trees will be available from Dryad.

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REFERENCES

Aars, J., & Ims, R. A. (2000). Population dynamics and genetic consequences of spatial density-dependent dispersal in patchy populations. *The American Naturalist*, *155*, 252–265. https://doi.org/10.1086/303317

Agnarsson, I., Cheng, R. C., & Kuntner, M. (2014). A multi-clade test supports the intermediate dispersal model of biogeography. *PLoS ONE*, *9*, 1–5. https://doi.org/10.1371/journal.pone.0086780

Agnarsson, I., & Kuntner, M. (2005). Madagascar: An unexpected hotspot of social *Anelosimus* spider diversity (Araneae: Theridiidae). *Systematic Entomology*, *30*(4), 575–592. https://doi.org/10.1111/j.1365-3113.2005.00289.x

Agnarsson, I., & Kuntner, M. (2012). The generation of a biodiversity hotspot: Biogeography and phylogeography of the Western Indian Ocean Islands. In *Current topics in phylogenetics and phylogeography of terrestrial and aquatic systems*. InTech. https://doi.org/10.5772/38958

Agnarsson, I., LeQuier, S. M., Kuntner, M., Cheng, R. C., Coddington, J. A., & Binford, G. (2016). Phylogeography of a good Caribbean disperser: *Argiope argentata* (Araneae, Araneidae) and a new "cryptic" species from Cuba. *ZooKeys*, *2016*(625), 25–44. https://doi.org/10.3897/zookeys.625.8729

Agnarsson, I., Maddison, W. P., & Avilés, L. (2007). The phylogeny of the social Anelosimus spiders (Araneae : Theridiidae) inferred from six molecular loci and morphology. *Molecular Phylogenetics and Evolution*, *43*(3), 833–851. https://doi.org/10.1016/j.ympev.2006.09.011

Ali, J. R. (2012). Colonizing the Caribbean: Is the GAARlandia land-bridge hypothesis gaining a foothold? *Journal of Biogeography*, *39*, 431–433. https://doi.org/10.1111/j.1365-2699.2011.02674.x

Ali, J. R., & Aitchison, J. C. (2008). Gondwana to Asia: Plate tectonics, paleogeography and the biological connectivity to the Indian sub-continents from the Middle Jurassic through the latest Eocene (166-35 Ma). *Earth Science Reviews*, *88*, 145–166. https://doi.org/10.1016/j.earscirev.2008.01.007

Alonso, R., Crawford, A. J., & Bermingham, E. (2012). Molecular phylogeny of an endemic radiation of Cuban toads (Bufonidae:Peltophryne) based on mitochondrial and nuclear genes. *Journal of Biogeography*, *39*, 434–451. https://doi.org/10.1111/j.1365-2699.2011.02594.x

Altekar, G., Dwarkadas, S., Huelsenbeck, J. P., & Ronquist, F. (2004). Parallel metropolis coupled Markov chain Monte Carlo for Bayesian phylogenetic inference. *Bioinformatics*, *20*, 407–415. https://doi.org/10.1093/bioinformatics/btg427

Avise, J. C. (2000). *Phylogeography: The history and formation of species*. Cambridge, MA: Harvard University Press.

Battistuzzi, F. U., Billing-Ross, P., Paliwal, A., & Kumar, S. (2011). Fast and slow implementations of relaxed-clock methods show similar patterns of accuracy in estimating divergence times. *Molecular Biology and Evolution*, *28*(9), 2439–2442. https://doi.org/10.1093/molbev/msr100

Bellemain, E., Bermingham, E., & Ricklefs, R. E. (2008). The dynamic evolutionary history of the bananaquit (*Coereba flaveola*) in the Caribbean revealed by a multigene analysis. *BMC Evolutionary Biology*, *8*, 240. https://doi.org/10.1186/1471-2148-8-240

Bellemain, E., & Ricklefs, R. E. (2008). Are islands the end of the colonization road? *Trends in Ecology & Evolution*, *23*(8), 461–468. https://doi.org/10.1016/j.tree.2008.05.001

Bidegaray-Batista, L., & Arnedo, M. A. (2011). Gone with the plate: The opening of the Western Mediterranean basin drove the

diversification of ground-dweller spiders. *Bio Med Central Evolutionary Biology*, *11*, 317. https://doi.org/10.1186/1471-2148-11-317

Binford, G. J., Callahan, M. S., Bodner, M. R., Rynerson, M. R., Núñez, P. B., Ellison, C. E., & Duncan, R. P. (2008). Phylogenetic relationships of *Loxosceles* and *Sicarius* spiders are consistent with Western Gondwanan vicariance. *Molecular Phylogenetics and Evolution*, *49*(2), 538–553. https://doi.org/10.1016/j.ympev.2008.08.003

Bond, J. E., Garrison, N. L., Hamilton, C. A., Godwin, R. L., Hedin, M. C., & Agnarsson, I. (2014). Phylogenomics resolves a spider backbone phylogeny and rejects a prevailing paradigm for orb web evolution. *Current Biology*, *24*, 1–6. https://doi.org/10.1016/j.cub.2014.06.034

Bourgeois, J., Hansen, T. A., Wiberg, P. L., & Kauffman, E. G. (1988). A tsunami deposit at the Cretaceous-Tertiary boundary in Texas. *Science*, *241*(4865), 567–570. https://doi.org/10.1126/science.241.4865.567

Capesius, I., & Bopp, M. (1997). New classification of liverworts based on molecular and morphological data. *Plant Systematics and Evolution*, *207*(1–2), 87–97. https://doi.org/10.1007/BF00985210

Carlquist, S. (1981). Chance dispersal: Long-distance dispersal of organisms, widely accepted as a major cause of distribution patterns, poses challenging problems of analysis. *American Scientist*, *69*, 509–516.

Censky, E. J., Hodge, K., & Dudley, J. (1998). Over-water dispersal of lizards due to hurricanes. *Nature*, *395*(6702), 556. https://doi.org/10.1038/26886

Chakrabarty, P. (2006). Systematics and historical biogeography of Greater Antillean Cichlidae. *Molecular Phylogenetics and Evolution*, *39*(3), 619–627. https://doi.org/10.1016/j.ympev.2006.01.014

Coddington, J. A. (1986). Orb webs in "Non-orb Weaving" ogre-faced spiders (Araneae:Dinopidae): A question of genealogy. *Cladistics*, *2*(1), 53–67. https://doi.org/10.1111/j.1096-0031.1986.tb00442.x

Coddington, J. A., Kuntner, M., & Opell, B. D. (2012). Systematics of the spider family Deinopidae with a revision of the genus *Menneus*. *Smithsonian Contributions to Zoology*, *636*, 1–61. https://doi.org/10.5479/si.00810282.636.1

Coddington, J. A., & Sobrevila, C. (1987). Web manipulation and two stereotyped attack behaviors in the ogre-faced spider *Deinopis spinosus* Marx (Araneae, Deinopidae). *Journal of Arachnology*, *15*(2), 213–225.

Cook, L. G., & Crisp, M. D. (2005). Directional asymmetry of long-distance dispersal and colonization could mislead reconstructions of biogeography. *Journal of Biogeography*, *32*(5), 741–754. https://doi.org/10.1111/j.1365-2699.2005.01261.x

Cosgrove, J. G., Agnarsson, I., Harvey, M. S., & Binford, G. J. (2016). Pseudoscorpion diversity and distribution in the West Indies: Sequence data confirm single island endemism for some clades, but not others. *Journal of Arachnology*, *44*(3), 257–271. https://doi.org/10.1636/R15-80.1

Costa, W. J. E. M. (2010). Historical biogeography of cynolebiasine annual killifishes inferred from dispersal-vicariance analysis. *Journal of Biogeography*, *37*(10), 1995–2004. https://doi.org/10.1111/j.1365-2699.2010.02339.x

Cowie, R. H., & Holland, B. S. (2006). Dispersal is fundamental to biogeography and the evolution of biodiversity on oceanic islands. *Journal of Biogeography*, *33*(2), 193–198. https://doi.org/10.1111/j.1365-2699.2005.01383.x

Crews, S. C., & Gillespie, R. G. (2010). Molecular systematics of Selenops spiders (Araneae: Selenopidae) from North and Central America: Implications for Caribbean biogeography. *Environmental Sciences*, *101*(2), 288–322. https://doi.org/10.1111/j.1095-8312.2010.01494.x

Crother, B. I., & Guyer, C. (1996). Caribbean historical biogeography: Was the dispersal-vicariance debate eliminated by an extraterrestrial bolide? *Herpetologica*, *52*(3), 440–465.

Darwin, C. (1859). *On the origin of species by means of natural selection or the preservation of favoured races in the struggle for life*. London: John Murray.

Dávalos, L. M. (2004). Phylogeny and biogeography of Caribbean mammals. *Biological Journal of the Linnean Society*, *81*(3), 373–394. https://doi.org/10.1111/j.1095-8312.2003.00302.x

Dávalos, L. M. (2007). Short-faced bats (Phyllostomidae: Stenodermatina): A Caribbean radiation of strict frugivores. *Journal of Biogeography*, *34*(2), 364–375. https://doi.org/10.1111/j.1365-2699.2006.01610.x

De Boer, A. J., & Duffels, J. P. (1996). Historical biogeography of the cicadas of Wallacea, New Guinea and the West Pacific: A geotectonic explanation. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *124*(1–2), 153–177. https://doi.org/10.1016/0031-0182(96)00007-7

De Queiroz, A. (2005). The resurrection of oceanic dispersal in historical biogeography. *Trends in Ecology & Evolution*, *20*(2), 68–73. https://doi.org/10.1016/j.tree.2004.11.006

Dimitrov, D., Benavides, L. R., Arnedo, M. A., Giribet, G., Griswold, C. E., Scharff, N., & Hormiga, G. (2016). Rounding up the usual suspects: A standard target-gene approach for resolving the interfamilial phylogenetic relationships of ecribellate orb-weaving spiders with a new family-rank classification (Araneae, Araneoidea). *Cladistics*, *33*, 221–250. https://doi.org/10.1111/cla.12165

Doums, C., Cabrera, H., & Peeters, C. (2008). Population genetic structure and male-biased dispersal in the queenless ant *Diacamma cyaneiventre*. *Molecular Ecology*, *11*(11), 2251–2264. https://doi.org/10.1046/j.1365-294X.2002.01619.x

Drummond, A. J., Suchard, M. A., Xie, D., & Rambaut, A. (2012). Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, *29*, 1969–1973. https://doi.org/10.1093/molbev/mss075

Dziki, A., Binford, G. J., Coddington, J. A., & Agnarsson, I. (2015). Spintharus flavidus in the Caribbean—a 30 million year biogeographical history and radiation of a "widespread species". *PeerJ*, *3*, e1422. https://doi.org/10.7717/peerj.1422

Esposito, L. A., Bloom, T., Caicedo-Quiroga, L., Alicea-Serrano, A. M., Sánchez-Ruíz, J. A., May-Collado, L. J., … Agnarsson, I. (2015). Islands within islands: Diversification of tailless whip spiders (Amblypygi, *Phrynus*) in Caribbean caves. *Molecular Phylogenetics and Evolution*, *93*, 107–117. https://doi.org/10.1016/j.ympev.2015.07.005

Folmer, O., Black, M., Hoeh, W., Lutz, R., & Vrijenhoek, R. (1994). DNA primers for amplification of mitochondrial cytochrome oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, *3*(5), 294–299.

Gamble, T., Bauer, A. M., Greenbaum, E., & Jackman, T. R. (2008). Evidence for Gondwanan vicariance in an ancient clade of gecko lizards. *Journal of Biogeography*, *35*(1), 88–104. https://doi.org/10.1111/j.1365-2699.2007.01770.x

Garrison, N. L., Rodriguez, J., Agnarsson, I., Coddington, J. A., Griswold, C. E., Hamilton, C. A., … Bond, J. E. (2016). Spider phylogenomics: Untangling the Spider Tree of Life. *PeerJ*, *4*, e1719. https://doi.org/10.7717/peerj.1719

Getty, R. M., & Coyle, F. A. (1996). American Arachnological Society Observations on prey capture and anti-predator behaviors of ogre-faced spiders. *The Journal of Arachnology*, *24*(2), 93–100.

Gillespie, R. G., Baldwin, B. G., Waters, J. M., Fraser, C. I., Nikula, R., & Roderick, G. K. (2012). Long-distance dispersal: A framework for hypothesis testing. *Trends in Ecology and Evolution*, *27*(1), 47–55. https://doi.org/10.1016/j.tree.2011.08.009

Gillespie, R. G., & Clague, D. A. (2009). *Encyclopedia of islands*. Berkeley, CA: University of California Press.

Gillespie, R. G., & Roderick, G. K. (2002). Arthropods on islands: Colonization, speciation, and conservation. *Annual Review of Entomology*, *47*(1), 595–632. https://doi.org/10.1146/annurev.ento.47.091201.145244

Glor, R. E., Losos, J. B., & Larson, A. (2005). Out of Cuba: Overwater dispersal and speciation among lizards in the *Anolis carolinensis* subgroup. *Molecular Ecology*, *14*(8), 2419–2432. https://doi.org/10.1111/j.1365-294X.2005.02550.x

Gontcharov, A. A., Marin, B., & Melkonian, M. (2004). Are combined analyses better than single gene phylogenies? A case study using SSU rDNA and rbcL sequence comparisons in the Zygnematophyceae (Streptophyta). *Molecular Biology and Evolution*, *21*(3), 612–624. https://doi.org/10.1093/molbev/msh052

Graham, A. (2003). Historical phytogeography of the Greater Antilles. *Brittonia*, *55*(4), 357–383. https://doi.org/10.1663/0007-196X(2003)055%5B0357:HPOTGA%5D2.0.CO;2

Green, P. (2009). Phrap 1.090518. Retrieved from http://phrap.org

Green, P., & Ewing, B. (2002). Phred. version 0.020425c *Computer program and documentation available at www.phrap.org*.

Hall, J. P. W., Robbins, R. K., & Harvey, D. J. (2004). Extinction and biogeography in the Caribbean: New evidence from a fossil riodinid butterfly in Dominican amber. *Proceedings. Biological Sciences/The Royal Society*, *271*(1541), 797–801. https://doi.org/10.1098/rspb.2004.2691

Hamilton, C. A., Formanowicz, D. R., & Bond, J. E. (2011). Species delimitation and phylogeography of *Aphonopelma hentzi* (araneae, mygalomorphae, theraphosidae): Cryptic diversity in North American tarantulas. *PLoS ONE*, *6*(10), e26207. https://doi.org/10.1371/journal.pone.0026207

Hamilton, C. A., Hendrixson, B. E., Brewer, M. S., & Bond, J. E. (2014). An evaluation of sampling effects on multiple DNA barcoding methods leads to an integrative approach for delimiting species: A case study of the North American tarantula genus *Aphonopelma* (Araneae, Mygalomorphae, Theraphosidae). *Molecular Phylogenetics and Evolution*, *71*(1), 79–93. https://doi.org/10.1016/j.ympev.2013.11.007

Hamilton, C. A., Lemmon, A. R., Lemmon, E. M., & Bond, J. E. (2016). Expanding anchored hybrid enrichment to resolve both deep and shallow relationships within the spider tree of life. *BMC Evolutionary Biology*, *16*(1), 212. https://doi.org/10.1186/s12862-016-0769-y

Hawkesworth, C., Kelley, S., Turner, S., Le Roex, A., & Storey, B. (1999). Mantle processes during Gondwana break-up and dispersal. *Journal of African Earth Sciences*, *28*, 239–261. https://doi.org/10.1016/s0899-5362(99)00026-3

Hedges, S. B. (1996). Historical biogeography of West Indian vertebrates. *Annual Review of Ecology and Systematics*, *27*(1), 163–196. https://doi.org/10.1146/annurev.ecolsys.27.1.163

Hedges, S. B. (2001). Biogeography of the West Indies: An overview. In C. A. Woods, & F. E. Sergile (Eds.), *Biogeography of the West Indies: Patterns and Perspectives* (pp. 15–33). Boca Raton: CRC Press. https://doi.org/10.1201/9781420039481

Hedges, S. B. (2006). Paleogeography of the Antilles and origin of West Indian terrestrial vertebrates. *Annals of the Missouri Botanical Garden*, *93*(2), 231–244. https://doi.org/10.3417/0026-6493(2006)93[231:POTAAO]2.0.CO;2

Hedges, S. B., Hass, C. A., & Maxson, L. R. (1992). Caribbean biogeography: Molecular evidence for dispersal in West Indian terrestrial vertebrates. *Proceedings of the National Academy of Sciences of the United States of America*, *89*(5), 1909–1913. https://doi.org/10.1073/pnas.89.5.1909

Hedin, M. C., & Maddison, W. P. (2001). A combined molecular approach to phylogeny of the jumping spider subfamily Dendryphantinae (Araneae: Salticidae). *Molecular Phylogenetics and Evolution*, *18*(3), 386–403. https://doi.org/10.1006/mpev.2000.0883

Heinicke, M. P., Duellman, W. E., & Hedges, S. B. (2007). Major Caribbean and Central American frog faunas originated by ancient oceanic dispersal. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(24), 10092–10097. https://doi.org/10.1073/pnas.0611051104

Hildebrand, A. R., & Boynton, W. V. (1990). Proximal Cretaceous-Tertiary boundary impact deposits in the Caribbean. *Science*, *248*(4957), 843–847. https://doi.org/10.1126/science.248.4957.843

Hoef-Emden, K., Marin, B., & Melkonian, M. (2002). Nuclear and nucleomorph SSU rDNA phylogeny in the cryptophyta and the evolution of cryptophyte diversity. *Journal of Molecular Evolution*, *55*(2), 161–179. https://doi.org/10.1007/s00239-002-2313-5

Hrbek, T., Seckinger, J., & Meyer, A. (2007). A phylogenetic and biogeographic perspective on the evolution of poeciliid fishes. *Molecular Phylogenetics and Evolution*, *43*(3), 986–998. https://doi.org/10.1016/j.ympev.2006.06.009

Huelsenbeck, J. P., & Rannala, B. (2004). Frequentist properties of bayesian posterior probabilities of phylogenetic trees under simple and complex substitution models. *Systematic Biology*, *53*(6), 904–913. https://doi.org/10.1080/10635150490522629

Huelsenbeck, J. P., Ronquist, F., Nielsen, R., & Bollback, J. P. (2001). Bayesian inference of phylogeny and its impact on evolutionary biology. *Science*, *294*(5550), 2310–2314. https://doi.org/10.1126/science.1065889

Iturralde-Vinent, M. A. (1982). Aspectos geológicos de la biogeografia de Cuba. *Ciencias de La Tierra Y El Espacio*, *5*, 85–100.

Iturralde-Vinent, M. A. (2006). Meso-Cenozoic Caribbean Paleogeography: Implications for the historical biogeography of the region. *International Geology Review*, *48*(9), 791–827. https://doi.org/10.2747/0020-6814.48.9.791

Iturralde-Vinent, M. A., & MacPhee, R. D. E. (1999). Paleogeography of the Caribbean: Implications for Cenozoic biogeography. *Bulletin of the American Museum of Natural History*, *238*, 1–95.

Joseph, L., Moritz, C., & Hugall, A. (1995). Molecular support for vicariance as a source of diversity in rainforest. *Proceedings of the Royal Society B: Biological Sciences*, *260*(1358), 177–182. https://doi.org/10.1098/rspb.1995.0077

Katoh, K., & Standley, D. M. (2013). MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. *Molecular Biology and Evolution*, *30*(4), 772–780. https://doi.org/10.1093/molbev/mst010.

King, W. (1962). The occurrence of rafts for dispersal of land animals into the West Indies. *Quarterly Journal of the Florida Academy of Sciences*, *25*(1), 45–52.

Knight, M. E., van Oppen, M. J. H., Smith, H. L., Rico, C., Hewitt, G. M., & Turner, G. F. (1999). Evidence for male-based dispersal in Lake Malawi cichlids from microsatellites. *Molecular Ecology*, *8*(9), 1521–1527. https://doi.org/10.1046/j.1365-294x.1999.00740.x

Kraus, O. (1956). Eine neue Deinopidae aus El Salvador. *Senckenbergiana Biologica*, *37*, 167–170.

Kuntner, M., & Agnarsson, I. (2011). Biogeography and diversification of hermit spiders on Indian Ocean islands (Nephilidae: *Nephilengys*). *Molecular Phylogenetics and Evolution*, *59*(2), 477–488. https://doi.org/10.1016/j.ympev.2011.02.002

Kuntner, M., Arnedo, M. A., Trontelj, P., Lokovsek, T., & Agnarsson, I. (2013). A molecular phylogeny of nephilid spiders: Evolutionary history of a model lineage. *Molecular Phylogenetics and Evolution*, *69*(3), 961–979. https://doi.org/10.1016/j.ympev.2013.06.008

Lanfear, R., Calcott, B., Ho, S. Y. W., & Guindon, S. (2012). PartitionFinder: Combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, *29*(6), 1695–1701. https://doi.org/10.1093/molbev/mss020

Lemmon, A. R., Emme, S. A., & Lemmon, E. M. (2012). Anchored hybrid enrichment for massively high-throughput phylogenomics. *Systematic biology*, *61*(5), 727–744. https://doi.org/10.1093/molbev/mss020

Longrich, N. R., Vinther, J., Pyron, R. A., Pisani, D., & Gauthier, J. A. (2015). Biogeography of worm lizards (*Amphisbaenia*) driven by end-Cretaceous mass extinction. *Proceedings of the Royal Society of London B: Biological Sciences*, *282*(1806), 20143034. https://doi.org/10.1098/rspb.2014.3034

MacPhee, R. D. E., & Iturralde-Vinent, M. A. (1994). First tertiary land mammal from Greater Antilles: An early Miocene Sloth (Xenarthra, Megalonychidae) from Cuba: 2 Tables. *American Museum of Natural History 3094*, 13 pp.

MacPhee, R. D. E., & Iturralde-Vinent, M. A. (2005). The interpretation of Caribbean paleogeography: Reply to Hedges. *Insular Vertebrate Evolution*, *12*, 175–184. Retrieved from http://www.redciencia.cu/cdorigen/arca/paper/mcitu.pdf

Maddison, W. P., Evans, S. C., Hamilton, C. A., Bond, J. E., Lemmon, A. R., & Lemmon, E. M. (2017). A genome-wide phylogeny of jumping spiders (Araneae, Salticidae), using anchored hybrid enrichment. *ZooKeys*, *695*, 89–101. https://doi.org/10.3897/zookeys.695.13852

Maddison, D. R., & Maddison, W. P. (2011a). Chromaseq 1.0: A Mesquite package for analyzing sequence chromatograms. Retrieved from http://mesquiteproject. org/packages/chromaseq.

Maddison, W. P., & Maddison, D. R. (2011b). Mesquite 2.75: a modular system for evolutionary analysis. Retrieved from mesquiteproject.org/mesquite/download/download.html.

Mann, P., Draper, G., & Lewis, J. F. (Eds.). (1991). An overview of the geologic and tectonic development of Hispaniola. Geologic and Tectonic Development of the North America-Caribbean Plate Boundary in Hispaniola. *Geological Society of America Special Paper*, *262*, 1–28.

Mann, P., Schubert, C., & Burke, K. (1990). Review of Caribbean neotectonics. In *The geology of North America. Vol. H-The Caribbean region*. Boulder, CO: Geological Society of America, Vol. 1990, 307–338. Research supported by University of Texas, CONICIT, and Universidad de Los Andes.

Matos-Maraví, P., Núñez Águila, R., Peña, C., Miller, J. Y., Sourakov, A., & Wahlberg, N. (2014). Causes of endemic radiation in the Caribbean: Evidence from the historical biogeography and diversification of the butterfly genus *Calisto* (Nymphalidae: Satyrinae: Satyrini). *BMC Evolutionary Biology*, *14*(1), 199. https://doi.org/10.1186/s12862-014-0199-7

Matzke, N. J. (2013). BioGeoBEARS: BioGeography with Bayesian (and likelihood) evolutionary analysis in R Scripts. R Package, Version 0.2, 1, 2013.

Maurasse, J.-M. R., & Sen, G. (1991). Impacts, tsunamis, and the Haitian Cretaceous-Tertiary boundary layer. *Science*, *252*(5013), 1690–1693. https://doi.org/10.1126/science.252.5013.1690

McHugh, A., Yablonsky, C., Binford, G., & Agnarsson, I. (2014). Molecular phylogenetics of Caribbean Micrathena (Araneae:Araneidae) suggests multiple colonisation events and single island endemism. *Invertebrate Systematics*, *28*(4), 337–349. https://doi.org/10.1071/IS13051

McLoughlin, S. (2001). The breakup history of Gondwana and its impact on pre-Cenozoic floristic provincialism. *Australian Journal of Botany*, *49*(3), 271–300. https://doi.org/10.1071/BT01054

Miller, M. A., Pfeiffer, W., & Schwartz, T. (2010). Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In *Proceedings of the gateway computing environments workshop (GCE)* (pp. 1–8). New Orleans, LA.

Mirarab, S., Reaz, R., Bayzid, M. S., Zimmermann, T., Swenson, M. S., & Warnow, T. (2014). ASTRAL: Genome-scale coalescent-based species tree estimation. *Bioinformatics*, *30*(17), 541–548. https://doi.org/10.1093/bioinformatics/btu462

Morrone, J. J. (2006). Biogeographic areas and transition zones of Latin America and the Caribbean islands based on panbiogeographic and cladistic analyses of the entomofauna. *Annual Review of Entomology*, *51*(125), 467–494. https://doi.org/10.1146/annurev.ento.50.071803.130447

Murphy, W. J., & Collier, G. E. (1996). Phylogenetic relationships within the aplocheiloid fish genus *Rivulus* (Cyprinodontiformes, Rivulidae): Implications for Caribbean and Central American biogeography. *Molecular Biology and Evolution*, *13*(5), 642–649. https://doi.org/10.1093/oxfordjournals.molbev.a025624

Nei, M., Kumar, S., & Takahashi, K. (1998). The optimization principle in phylogenetic analysis tends to give incorrect topologies when the number of nucleotides or amino acids used is small. *Proceedings of the National Academy of Sciences*, *95*(21), 12390–12397. https://doi.org/10.1073/pnas.95.21.12390

Nelson, G. J., & Platnick, N. I. (1981). *Systematics and biogeography: Cladistics and vicariance*. New York: Columbia University Press.

Nickrent, D. L., Parkinson, C. L., Palmer, J. H., & Duff, R. J. (2000). Multigene phylogeny of land plants with special reference to bryophytes and the earlist land plants. *Molecular Biology and Evolution*, *17*(12), 1885–1895. https://doi.org/10.1093/oxfordjournals.molbev.a026290

Nieto-Blázquez, M. E., Antonelli, A., & Roncal, J. (2017). Historical Biogeography of endemic seed plant genera in the Caribbean: Did GAARlandia play a role? *Ecology and Evolution*, *7*(23), 10158–10174. https://doi.org/10.1002/ece3.3521

Penney, D. (2003). A new deinopid spider from Cretaceous Lebanese amber. *Acta Palaeontologica Polonica*, *48*(4), 569–574.

Pindell, J. L. (1994). Evolution of the Gulf of Mexico and the Caribbean. In S. K. Denovan & T. A. Jackson (Eds.), *Caribbean geology: An introduction* (pp. 13–39). Kingston, Jamaica: University of West Indies Publishers' Association.

Pindell, J. L., & Barrett, S. F. (1990). Geological evolution of the Caribbean region: A plate tectonic perspective. In G. Dengo & J. E. Case (Eds.), *The Caribbean Region: Geological society of America*. The Geology of North America pp. 405–432.

Pindell, J., Kennan, L., Stanek, K. P., Maresch, W. V., & Draper, G. (2006). Foundations of Gulf of Mexico and Caribbean evolution: Eight controversies resolved. *Geologica Acta: An International Earth Science Journal*, *4*(1–2).

Pitman, W. C. III (1993). Fragmentation of Gondwana: The separation of Africa from South America. In P. Goldblatt (Ed.), *Biological relationships between Africa and South America* (pp. 15–34). New Haven and London: Yale University Press. https://doi.org/10.2307/j.ctt22726mc

Poe, S., & Swofford, D. L. (1999). Rings of single-walled carbon nanotubes. *Nature*, *398*(6725), 299–299. https://doi.org/10.1038/18589

Pope, K. O., Ocampo, A. C., & Duller, C. E. (1991). Mexican site for K/T impact crater? *Nature*, *351*(6322), 105–105. https://doi.org/10.1038/351105a0

Posada, D., & Buckley, T. R. (2004). Model selection and model averaging in phylogenetics: Advantages of Akaike information criterion and Bayesian approaches over likelihood ratio tests. *Systematic Biology*, *53*(5), 793–808. https://doi.org/10.1080/10635150490522304

Pramuk, J. B., Robertson, T., Sites, J. W., & Noonan, B. P. (2008). Around the world in 10 million years: Biogeography of the nearly cosmopolitan true toads (Anura: Bufonidae). *Global Ecology and Biogeography*, *17*(1), 72–83. https://doi.org/10.1111/j.1466-8238.2007.00348.x

Pusey, A. E. (1987). Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends in Ecology & Evolution*, *2*, 295–299. https://doi.org/10.1016/0169-5347(87)90081-4

Pyron, R. A. (2014). Biogeographic analysis reveals ancient continental vicariance and recent oceanic dispersal in amphibians. *Systematic Biology*, *63*(5), 779–797. https://doi.org/10.1093/sysbio/syu042

Rambaut, A., & Drummond, A. J. (2007). Tracer 1.4. Retrieved from http://tree.bio.ed.ac. uk/software/tracer.

Raven, P. H., & Axelrod, D. I. (1974). Angiosperm biogeography and past continental movements. *Annals of the Missouri Botanical Society*, *61*(3), 539–673. https://doi.org/10.2307/2395021

Raxworthy, C. J., Forstner, M. R. J., & Nussbaum, R. A. (2002). Chameleon radiation by oceanic dispersal. *Nature*, *415*(6873), 784–787. https://doi.org/10.1038/415784a

Ree, R. H., & Sanmartín, I. (2018). Conceptual and statistical problems with the DEC+J model of founder-event speciation and its comparison with DEC via model selection. *Journal of Biogeography*, *45*, 741–749. https://doi.org/10.1111/jbi.13173

Ree, R. H., & Smith, S. A. (2008). Maximum likelihood inference of geographic range evolution by dispersal, local extinction and cladogenesis. *Systematic Biology*, *57*(1), 4–14. https://doi.org/10.1080/10635150701883881

Říčan, O., Piálek, L., Zardoya, R., Doadrio, I., & Zrzavy, J. (2013). Biogeography of the Mesoamerican Cichlidae (Teleostei:Heroini): Colonization through the GAARlandia land bridge and early diversification. *Journal of Biogeography*, *40*(3), 579–593. https://doi.org/10.1111/jbi.12023

Ricklefs, R., & Bermingham, E. (2008). The West Indies as a laboratory of biogeography and evolution. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *363*(1502), 2393–2413. https://doi.org/10.1098/rstb.2007.2068

Ronquist, F., & Huelsenbeck, J. P. (2003). MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, *19*, 1572–1574. https://doi.org/10.1093/bioinformatics/btg180

Rosen, D. E. (1985). Geological hierarchies and biogeographic congruence in the Caribbean. *Annals of the Missouri Botanical Garden*, *72*(4), 636–659. https://doi.org/10.2307/2399218

Ruban, D. A., Al-husseini, M. I., & Iwasaki, Y. (2007). Review of Middle East Paleozoic plate tectonics. *GEOARABIA-MANAMA-*, *12*(3), 35–56.

Salzman, V. T., & Judd, W. S. (1995). A revision of the greater Antillean species of *Bactris* (Bactridinae: Arecaceae). *New York Botanical Garden Press*, *47*(4), 345–371. https://doi.org/10.2307/2807563

Sanmartín, I., & Ronquist, F. (2004). Southern hemisphere biogeography inferred by event-based models: Plant versus animal patterns. *Systematic Biology*, *53*(2), 216–243. https://doi.org/10.1080/10635150490423430

Santiago-Valentin, E., & Olmstead, R. G. (2003). Phylogenetics of the Antillean Goetzeoideae (Solanaceae) and their relationships within the Solanaceae based on chloroplast and ITS DNA sequence data. *American Society of Plant Taxonomists*, *28*(2), 452–460. https://doi.org/10.1043/0363-6445-28.2.452

Sato, J. J., Ohdachi, S. D., Echenique-Diaz, L. M., Borroto-Páez, R., Begué-Quiala, G., Delgado-Labañino, J. L., … Kita, M. (2016). Molecular phylogenetic analysis of nuclear genes suggests a Cenozoic over-water dispersal origin for the Cuban solenodon. *Scientific Reports*, *6*, 31173. https://doi.org/10.1038/srep31173

Simon, C., Frati, F., Beckenback, A., Crespi, B., Liu, H., & Flook, P. (1994). Evolution, weighting and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. *Annals of the Entomological Society of America*, *87*(1), 651–701. https://doi.org/10.1093/aesa/87.6.651

Skean, J. D. (1993). Monograph of *Mecranium* (Melastomataceae-Miconieae). *American Society of Plant Taxonomists*, *39*, 1–116.

Smit, J., Montanari, A., Swinburne, N. H., Alvarez, W., Hildebrand, A. R., Margolis, S. V., … Asaro, F. (1992). Tektite-bearing, deep-water clastic unit at the Cretaceous-Tertiary boundary in northeastern Mexico. *Geology*, *20*(2), 99–103. https://doi.org/10.1130/0091-7613(1992)020<0099:TBDWCU>2.3.CO;2

Sourakov, A., & Zakharov, E. V. (2011). "Darwin's butterflies"? DNA barcoding and the radiation of the endemic Caribbean butterfly genus *Calisto* (Lepidoptera, Nymphalidae, Satyrinae). *Comparative Cytogenetics*, *5*(3), 191–210. https://doi.org/10.3897/compcytogen.v5i3.1730

Stafstrom, J. A., & Hebets, E. A. (2016). Nocturnal foraging enhanced by enlarged secondary eyes in a net-casting spider. *Biology Letters*, *12*(5), 20160152. https://doi.org/10.1098/rsbl.2016.0152

Stamatakis, A. (2006). RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, *22*(21), 2688–2690. https://doi.org/10.1093/bioinformatics/btl446

Stamatakis, A. (2014). RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, *30*(9), 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Sturge, R. J., Jacobsen, F., Rosensteel, B. B., Neale, R. J., & Omland, K. E. (2009). Colonization of South America from Caribbean Islands confirmed by molecular phylogeny with increased taxon sampling. *The Condor*, *111*, 575–579. https://doi.org/10.1525/cond.2009.080048

Trewick, S. A. (2000). Molecular evidence for dispersal rather than vicariance as the origin of flightless insect species on the Chatham Islands, New Zealand. *Journal of Biogeography*, *27*(5), 1189–1200. https://doi.org/10.1046/j.1365-2699.2000.00492.x

Vidal, N., Azcolinsky, A., Cruaud, C., & Hedges, S. B. (2008). Origin of tropical American burrowning reptiles by transatlantic rafting. *Biology Letters*, *4*, 115–118. https://doi.org/10.1098/rsbl.2007.0531

Vidal, N., Marin, J., Morini, M., Donnellan, S., Branch, W. R., Thomas, R., … Hedges, S. B. (2010). Blindsnake evolutionary tree reveals long history on Gondwana. *Biology Letters*, *6*, 558–561. https://doi.org/10.1098/rsbl.2010.0220

Voelker, G., Rohwer, S., Outlaw, D. C., & Bowie, R. C. K. (2009). Repeated trans-Atlantic dispersal catalysed a global songbird radiation. *Global Ecology and Biogeography*, *18*(1), 41–49. https://doi.org/10.1111/j.1466-8238.2008.00423.x

Weaver, P. F., Cruz, A., Johnson, S., Dupin, J., & Weaver, K. F. (2016). Colonizing the Caribbean: Biogeography and evolution of livebearing fishes of the genus *Limia* (Poeciliidae). *Journal of Biogeography*, *43*(9), 1808–1819. https://doi.org/10.1111/jbi.12798

Wood, H. M., Matzke, N. J., Gillespie, R. G., & Griswold, C. E. (2013). Treating fossils as terminal taxa in divergence time estimation reveals ancient vicariance patterns in the palpimanoid spiders. *Systematic Biology*, *62*(2), 264–284. https://doi.org/10.1093/sysbio/sys092

Xu, X., Liu, F., Chen, J., Li, D., & Kuntner, M. (2015). Integrative taxonomy of the primitively segmented spider genus *Ganthela* (Araneae: Mesothelae: Liphistiidae): DNA barcoding gap agrees with morphology. *Zoological Journal of the Linnean Society*, *175*(2), 288–306. https://doi.org/10.1111/zoj.12280

Xu, X., Liu, F., Chen, J., Ono, H., Agnarsson, I., Li, D., & Kuntner, M. (2016). Pre-Pleistocene geological events shaping diversification and distribution of primitively segmented spiders on East Asian margins. *Journal of Biogeography*, *43*(5), 1004–1019. https://doi.org/10.1111/jbi.12687

Xu, X., Liu, F., Chen, J., Ono, H., Li, D., & Kuntner, M. (2015). A genus-level taxonomic review of primitively segmented spiders (Mesothelae, Liphistiidae). *ZooKeys*, *488*, 121–151. https://doi.org/10.3897/zookeys.488.8726

Xu, X., Liu, F., Cheng, R.-C., Chen, J., Xu, X., Zhang, Z., … Kuntner, M. (2015). Extant primitively segmented spiders have recently diversified from an ancient lineage. *Proceedings. Biological Sciences / The Royal Society*, *282*(1808), 1–10. https://doi.org/10.1098/rspb.2014.2486

Yoder, A. D., & Nowak, M. D. (2006). Has vicariance or dispersal been the predominant biogeographic force in Madagascar? Only time will tell. *Annual Review of Ecology Evolution and Systematics*, *37*, 405–431. https://doi.org/10.1146/annurev.ecolsys.37.091305.110239

Zona, S. (1990). A Monograph of *Sabal* (Arecaceae: Coryphoideae). *Aliso*, *12*(4), 583–666. https://doi.org/10.5642/aliso.19901204.02

BIOSKETCH

Lisa Chamberland is a PhD student at the University of Vermont studying the interplay between long-distance dispersal and vicariance in shaping the evolutionary history and biogeography of Deinopidae, the net-casting spiders.

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SUPPORTING INFORMATION

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

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