ABSTRACT
Aim: Cosmopolitan distributions have classically been explained by Pangean vicariance. However, evidence of recently diverged cosmopolitan groups has re-opened consideration on the processes involved. Our aim is to estimate the processes leading to the worldwide distribution of the kleptoparasitoid genus Ceropales.

Location: Worldwide.

Taxon: Ceropales spider wasps (Pompilidae).

Methods: Data from three molecular markers for 52 specimens of Ceropales and two calibration points from previous analyses were used to reconstruct a dated phylogeny under a relaxed molecular clock. We compared the fit of 12 models using BioGeoBEARS: DEC (subset sympatry, narrow vicariance), DIVALIKE (narrow and wide vicariance), BAYAREALIKE (widespread sympatry), and these same models with an added jump dispersal parameter and constraining dispersal rates among areas. Using the AIC best-fit model (DEC+J), we performed Biogeographic Stochastic Mapping (BSM) to infer biogeographic processes by simulating 200 BSM on the BEAST chronogram.

Results: The origin of crown-group Ceropales was ca. 10.6 Ma (15.7–6.5 95% HPD), and 11 jump-dispersal events explain its distribution. A constrained DEC+J model, allowing adjacent area dispersal was the best-fit AIC model. Dispersals across the Bering land bridge, Isthmus of Panama, Mediterranean Sea, and Sunda Plains took place from the late Miocene to present times.

Main conclusions: Ceropales is a recently diverged group that originated in Eurasia in the Miocene and dispersed to occupy the Americas, Africa, and Australia. Colonization was probably favored by the already diversified hosts (Pompilinae and Pepsinae), which reduced limiting factors such as food resource and nest construction. The evolution of a generalist parasitic lifestyle could facilitate long-distance dispersal. This is the first study addressing the global historical biogeography of a cosmopolitan spider wasp.

KEYWORDS
BioGeoBEARS, Ceropalinae, dispersal, kleptoparasitoid, relaxed molecular clock, vicariance
The processes leading to worldwide distributions have been the subject of long-standing discussion among biogeographers. Early explanations are attributed to Darwin who proposed that widespread taxa dispersed long distance from a single center of origin and geographical barriers fuelled natural selection and induced speciation (Darwin, 1859). This dispersal paradigm was further refined and continued to be supported (Bremer, 1992; Brundin, 1966; Darlington, 1957; Erwin, 1981; Fleagle, 1999; Hennig, 1966; Matthew, 1914; Wallace, 1876). It has nevertheless been widely criticized due to the lack of falsifiable hypotheses (Ball, 1975; Morrone & Crisci, 1995; Nelson & Platnick, 1978) and lack of evidence for possible ways of dispersal such as land bridges (Fichman, 1977; Simpson, 1940; Stankiewicz et al., 2006). The recognition of Earth systems leading to geographical instability (Wegener, 1915; Wilson, 1963) gave rise to an alternative model that incorporated continental drift and sea-level fluctuations to explain the distribution of fossils and living organisms due to dynamism of the planet (Charig, 1971; Colbert, 1973; Cracraft, 1974; Croizat, 1968): the vicariance theory (Croizat, 1958; Schram, 1977). Strictly speaking, vicariance occurs when the formation of a barrier divides an ancestral species’ range and fragments its population, leading to genetic divergence and speciation. Dispersal across such a barrier was assumed to be highly improbable and deemed to be a rare chance event (Ball, 1975; Croizat et al., 1974; Humphries, 2000; Nelson, 1978).

While vicariance biogeography appears to undermine the traditional dispersal paradigm, vicariant explanations are not dependent upon the rejection of dispersal patterns per se (Rosen, 1975; 1978). Platnick and Nelson (1978) proposed that certain kinds of dispersal (i.e., range expansion or ‘diffusion’) actually imply a “hidden” vicariance when a species’ range is enlarged and subsequently divided. These areas can have a secondary overlap of biotas by the collapse of the barrier. The strict definition of dispersal, therefore, is a long-distance dispersal, often over inhospitable habitat (Rosen, 1978). Due to the unlikeliness of dispersal across substantial barriers, many taxa – in particular, cosmopolitan taxa – had been assumed to be of Pangean, Gondwanan, or Laurasian origin (e.g., Craw, 1985; Jaeger & Martin, 1984; Patterson, 1981a; 1981b; Rosen, 1975; Tiffney, 1985; Wiley, 1988). The outcome of such a purely vicariant history underlying tectonic shifts may be represented by sister relationships between taxa from areas that were adjacent before the continental break-up (Figure 1).

Although vicariance analysis provides testable hypotheses, it is limited by the necessity for detailed phylogenies (Weitzman & Weitzman, 1982). With the advent of molecular phylogenetics and divergence time estimation, we can now muster robust phylogenies, but the question arises whether we can falsify vicariance hypotheses using a range of possible ages for processes underlying cladogenic events. Even if the branching pattern of a lineage is congruent with the vicariant fragmentation of an area (i.e., the geological history of continents), the age of the lineage also must be congruent with geology. This is known as pseudo-congruence (Moore & Donoghue, 2003).

While on the one hand recent divergence time estimation analyses have validated vicariance hypotheses (Bakkes et al., 2018; Jerome et al., 2014; Joshi & Edgecombe, 2019; Toussaint et al., 2016), on the other hand it could be shown that they have falsified vicariance explanations in cases showing that dispersals across even large barriers like oceans have taken place (McDowall, 2002; Raxworthy et al., 2002; Schrago & Russo, 2003; Yoder et al., 2003). Furthermore, long-distance dispersal has been demonstrated for certain cosmopolitan taxa with disjunct distributions that diverged only in the Tertiary (Ceccarelli et al., 2016) or that are considered less mobile (Rota et al., 2016; Trewick, 2000; Ward, 2014). Perhaps recent widespread distributions may be more dependent on a species’ ability to colonize new niches than on dispersal ability. For example, generalist species have better dispersal ability because a plastic diet lets them exploit a variety of food resources in new environments (Dennis et al., 2000; Jønsson et al., 2016). The evolution of a generalist parasitic life style could perhaps be a strategy that may facilitate long-distance dispersal (Grégoir et al., 2015).

![Null model under a purely vicariant scenario, with continental drift as the main driver of vicariance. The chronogram depicts cladogenic events corresponding to landmass break-ups based on McIntyre et al. (2017). Branch lengths are proportional to time. [Colour figure can be viewed at wileyonlinelibrary.com)](null)
Pompilidae, or spider wasps, are parasitoids of spiders, which usually paralyze, oviposit, and transport a single host to a nesting site. Pompilidae are generally not obligate parasites of a specific species, but instead parasitize a range of spiders with a particular ecological niche. Being linked to the host’s ecology implies certain limitations to their diversification and their ability to disperse over large distances. For these wasps it has been shown that host switching may provide new niches and is correlated with higher diversification rates (Rodriguez et al., 2016). A few genera within the family have developed the ability to parasitize other spider wasps’ hosts as so-called kleptoparasitoids (Evans, 1953). Within those, Ceropales (Lateille) are unique compared to other pompilid kleptoparasitoids in that they lay their egg in another spider wasp’s host before it is placed in a nesting site, while its being transported (O’Neill, 2001). Compared to other pompilids, kleptoparasitoids may have a higher chance of colonizing new niches and therefore dispersing more rapidly because of a broader niche that does not require them to adapt to the spider’s defense.

For recently diverged taxa such as cosmopolitan Ceropales, the Pangaea vicariance hypothesis can be falsified and long-distance dispersal may be hypothesized. It is intriguing, however, how such small organisms have conquered the globe in such a short period of time. Here, we study the historical biogeography of Ceropales spider wasps using molecular data and divergence time estimation methods. Our aim is to resolve the timing of Ceropales’ diversification, as well as its ancestral range. Most importantly, we aim to reconstruct the dispersal events that led to its current worldwide distribution.

2 | MATERIALS AND METHODS

2.1 | Taxon sampling

We sampled 52 specimens from four subgenera and 49 species from all continents where Ceropales is found. This represents 35% of all known described species. For classification and species identification, we followed Moczar (1986a, 1986b, 1987, 1988, 1989, 1990, 1991). Two species from the sister genus Irenangelus were used as outgroups. All specimens belonged to the Insect Collection of the Department of Biology, Utah State University, Logan, Utah, USA (EMUS), except for two specimens obtained on loan from the Packer Collection at York University, York, Ontario, Canada (PCYU), and Texas A & M University Insect Collection, Kingsville, Texas, USA (TAIU) (see Table S3 in Appendix S1).

2.2 | Molecular methods

DNA was extracted from pinned specimens using the Roche DNA Isolation Kit for Cells and Tissues (Roche Molecular Systems, Inc.). The specimen pin was removed and specimens placed in a proteinase K and lysis buffer solution from 24 to 48 h. Further steps of the extraction followed the instruction manual. Amplification and sequencing of long-wavelength rhodopsin (LWRh), and the D2–D3 regions of the 28S ribosomal RNA (28S) followed the methods outlined in Pilgrim and Pitts (2006). Amplification of cytochrome c oxidase I followed the methods in Rodriguez et al. (2014) (for primers used see Table S1 in Appendix S1). Raw sequencing reads were processed and assembled with Sequencher 4.1 (Gene Codes Corp.).

2.3 | Phylogenetic and dating analyses

Alignment of each marker was performed with ClustalW (Thompson et al., 1994) implemented in Geneious 6.1 (created by Biomatters, available at http://www.geneious.com) and manually refined. Introns were removed from the LWRh alignment. All markers were concatenated into a supermatrix and the model of molecular evolution for each marker and codon position (the latter for LWRh and COI) was determined using PartitionFinder 1.01 (Lanfear et al., 2012; http://www.robertlanfear.com/partitionfinder/). The combined data phylogeny was inferred through a Bayesian analysis in MrBayes 3.2 (Huelsenbeck & Ronquist, 2001) by running two independent MCMC (Markov Chain Monte Carlo) for 100,000,000 generations. Chain convergence and ESS (Estimated Sample Size) were assessed in Tracer 1.5 (Rambaut et al., 2003). The first 10% generations were removed as burn-in. Single-gene topologies were also estimated under the best-fit model and visually inspected to detect possible topological incongruencies. An uncorrelated lognormal relaxed-clock model (Drummond et al., 2006; Drummond & Rambaut, 2007) was used for divergence time estimation in BEAST 1.7.5 (Drummond et al., 2012) using the partitioned supermatrix. Substitution models were unlinked among partitions (see Table S2 in Appendix S1), with the underlying clock and trees linked. Because of the lack of fossils in Ceropalinae, we performed a secondary calibration using previously published ages for Ceropalinae and Ceropales (Waichert et al. 2015). Hard minimum ages were placed as priors for the age of crown-group Ceropalinae (lognormal distribution, mean in real space = 8.5, stdev = 1, offset = 13.3) and Ceropales (lognormal distribution, mean in real space = 8.3, SD = 1, offset = 5.3) by setting the offset of the lognormal distribution to the lower bound of the 95% HPD (Highest Posterior Density) reported by Waichert, Rodriguez, et al. (2015). This approach allowed for the highest density of the prior probability to be placed close to the minimum age encountered by Waichert, Rodriguez, et al. (2015), allowing the MCMC to search for older dates at a lower density. The MCMC search was run for 100,000,000 generations. Chain convergence and ESS were assessed with Tracer 1.5. Independent runs were assembled with LogCombiner 1.7.5 (Drummond et al., 2012). The first 10% of the generations were discarded as burn-in.

2.4 | Ancestral area estimation

Areas were established as North and Mesoamerica, South America, Eurasia, Africa, and Australia (Figure 2). Because of the young age of Ceropales, areas were established as such to allow for modelling of dispersal across the Isthmus of Panama, North Atlantic Land Bridge, Bering Land Bridge, Mediterranean Sea, and through Southeast Asia. We performed an event-based likelihood ancestral-range estimation implementing three models of range evolution in BioGeoBEARS (Matzke,
versions of these models incorporating jump dispersal for a total of six models. The models evaluated were as follows: (1) DEC, an implementation of Lagrange’s model of dispersal–extinction–cladogenesis (Dispersal Extinction Cladogenesis; Ree & Smith, 2008); (2) DEC+J, includes jump dispersal or allopatric founder-event speciation (Matzke, 2014); (3) a likelihood-based implementation of the process assumptions of dispersal vicariance analysis (DIVA), originally parsimony based (Ronquist, 1996); (4) DIVALIKE+J, including jump dispersal (Matzke, 2014); (5) BAYAREAlike, a likelihood implementation of the process assumptions of BayArea, originally Bayesian (Landis et al., 2013); and (6) BAYAREAlike+J, allowing jump-dispersal (Matzke, 2014). All six models were evaluated under a constrained analysis, where dispersal to non-adjacent areas was not allowed and an unconstrained analysis allowing all possible dispersal events; we therefore evaluated 12 possible scenarios. These constraints were placed mainly because (1) there is a very low probability of interoceanic dispersal, (2) the small ranges of spider wasps are dictated by their limited dispersal ability, and (3) the age of Pompilidae suggests that younger areas do not include disjunct distributions because they have been isolated since the origin of the group (see Rodriguez et al., 2015). The log-likelihood of each pair of nested models (i.e., DEC and DEC+J, DIVALIKE and DIVALIKE+J, BAYAREAlike and BAYAREAlike+J) was compared using a likelihood-ratio test. In addition, the AIC (Akaike Information Criterion, Burnham & Anderson, 1998) was calculated for all models. Using the model with the best AIC score, we performed Biogeographic Stochastic Mapping (BSM) in BioGeoBEARS (Dupin et al., 2017) to simulate possible biogeographic processes. We simulated 200 BSM using the DEC+J model and the consensus tree for the BEAST analysis. Simulated processes were extracted to determine the process with the highest support.

The best partitioning strategy for the combined dataset included six partitions (see Table S2 in Appendix S1). Overall, we recovered high posterior probabilities (PP) for the majority of nodes (PP > 0.95, Figure 2). Subgenera and species groups currently used in Ceropales’s classification (Móczár, 1994) were mostly paraphyletic except for Priesnerius, which was represented by a single species (Figure 1). The taxonomic implications of these results will be discussed elsewhere.

Our results suggested that Ceropales had its origin in the Tortonian, early Miocene (10.6 M, 15.7–6.5 95% HPD), and recovered five major clades including taxa found in shared areas of endemism. These clades originated in the Late Miocene or Pliocene. The Oriental region was the only area not represented by a monophyletic group as the inclusion of the Australian taxa renders it paraphyletic. The mean ages of the nodes and their 95% confidence intervals (CI) for the highest posterior density (HPD) are shown in Figure S1 of Appendix S1.

3 | RESULTS

3.1 | Phylogenetic and dating analyses

The constrained DEC+J analysis produced the highest likelihood scores and the lowest AIC and AICC scores (Table 1, Figure 2). As a conservative approach, and to account for error and missing lineages (extinct or species not sampled), ages for events are reported as an interval of time from the stem-group median age to the crown-group median age, and the 95% HPD are reported as the upper bound 95% HPD from the stem group and the lower bound 95% HPD from the crown group.

The DEC+J analysis recovered an origin for Ceropales in an extensive region composed by North and Mesoamerica and Eurasia, or in Eurasia only. These two ancestral areas were recovered with the same probability (Figure 2). When biogeographic processes allowed in the DEC+J model were simulated onto the phylogeny, the process recovered with the highest probability was subset sympatry from a widespread ancestor found in North and Mesoamerica and Eurasia to a widespread Eurasian ancestor. Despite being the most likely process, it was only recovered in 34% of the simulations. The remaining nodes recovered either narrow sympatry or jump dispersal. Eleven jump dispersal events explain the current distribution of Ceropales (Figure 2, Rodriguez, 2020). From Eurasia, four jump dispersal events to three other areas took place independently. Two separate dispersal events from Eurasia to North Mesoamerica took place from the Tortonian in the late Miocene (12 Ma) to the Gelasion in the Pleistocene (2 Ma). One dispersal from Eurasia to Africa occurred between the Tortonian in the late Miocene (11 Ma) and the Plazecian in the Pliocene (3 Ma) and one dispersal from Eurasia to Australia took place in Calabrian in the Pleistocene (1.1 Ma to 0.3 Ma). Four independent dispersals back from Africa to Eurasia occurred between the Zanclean in the Pliocene (5 Ma) and close to present time. Three dispersal events were recovered from North Mesoamerica to South America between the Messinian in the Late Miocene (7 Ma) and close to present time.

4 | DISCUSSION

With an origin in the Miocene, Ceropales constitutes a young group, whose worldwide distribution cannot be explained by vicariance events caused by continental drift (Figure 1), and its range expansion
is best described by 11 jump dispersal events, most of which took place in the Late Miocene and Pliocene (Figure 2).

Pompilinae and Pepsinae, the two most diverse groups in Pompilidae, began to diversify during the late Eocene (38.6 Mya, HPD = 65.1–19.4) (Waichert, Rodriguez, et al., 2015). Suitable hosts were already widespread throughout the continents when Ceropales began to diversify. Colonization was probably favored by the already diversified hosts, which reduced limiting factors such as food resource and nest construction.

4.1 The origin of Old World–New World disjunct distributions

The classic vicariance model explains disjunct distributions between the Palaearctic and Nearctic as the result of a widespread Laurasian ancestor. The expected phylogenetic pattern is a sister relationship between Eurasia and the Nearctic (Figure 1). Our results show at least two sister relationships fitting this expected pattern, but with divergence times more than 30 million years younger than the breakup of Laurasia in the Eocene (McIntyre et al., 2017).

With the increasing use of molecular divergence time estimation methods, examples of disjunct faunas much younger than a Laurasian split have come to light, as have possible pathways for dispersal. For dispersal between the Palaearctic and Nearctic and vice versa, two possible pathways have been postulated: the Bering Land Bridge (BLB) and the North Atlantic Land Bridge (NALB). Global pattern analyses recover a greater frequency through the BLB (Sanmartín et al., 2001). According to our analyses, the Old World–New World disjunct distributions in Ceropales are the product of two separate dispersal events from the Palaearctic to the Nearctic through the BLB in the Late Miocene and Pliocene, when this route was available for dispersal (Rodriguez et al., 2015). This route was also consistent with the historical biogeographic analysis of another spider wasp group (genus Aporus), which dispersed in the opposite direction in the Early Miocene, more than 10 million years earlier (Rodriguez et al., 2015).

4.2 Dispersal routes between North Mesoamerica and South America

Four independent dispersal events to South America were obtained through our analyses. These events are inferred to be younger than had been obtained for other pompilids (Rodriguez et al., 2015; Waichert, Rodriguez, et al., 2015), where dispersal occurred between 18 and 5 Ma. The date obtained by these previous studies agrees with the recent discovery that the Isthmus of Panama may have formed earlier than about 15 Ma (Montes et al., 2012). The dates recovered here, however, also overlap with the classic age of formation of the Isthmus of Panama (ca. 3 Ma). There are examples of other Hymenoptera that dispersed from North to South America after the classic age of formation of the Isthmus of Panama (ca. 3 Ma) (Martins & Melo, 2015; Ramírez et al., 2010), but there are examples where dispersal took place within 15 to 20 Ma (Wilson et al., 2014).

4.3 Dispersal to the Ethiopian region

The presence of worldwide-distributed taxa in the Ethiopian region has classically been explained by vicariance events that split a widespread Gondwanan population. The expected phylogenetic pattern for such event is a sister relationship between Ethiopian and Neotropical clades (Figure 1). The African Ceropales, however, are closely related to Eurasian Hymenoptera that dispersed from North to South America after the classic age of formation of the Isthmus (ca. 3 Ma) (Martins & Melo, 2015; Ramírez et al., 2010), but there are examples where dispersal took place earlier than about 15 Mya (Montes et al., 2012). The dates recovered here, however, also overlap with the classic age of formation of the Isthmus of Panama (ca. 3 Ma). There are examples of other Hymenoptera that dispersed from North to South America after the classic age of formation of the Isthmus of Panama (ca. 3 Ma) (Martins & Melo, 2015; Ramírez et al., 2010), but there are examples where dispersal took place within 15 to 20 Ma (Wilson et al., 2014).

|                  | LnL  | AIC  | △AIC | AICc  | AICc weight | △AICc | AICc weight |
|------------------|------|------|------|-------|-------------|-------|-------------|
| DEC+J Constrained| -37.37 | 80.74 | 0    | 0.45  | 81.24       | 0     | 0.45        |
| DIVALIKE+J Constrained| -37.51 | 81.03 | 0.29 | 0.39  | 81.53       | 0.29  | 0.39        |
| BAYAREALIKE+J Constrained| -38.37 | 82.74 | 2    | 0.16  | 83.24       | 2     | 0.16        |
| DEC+J Unconstrained| -46.08 | 98.16 | 17.42 | 0.59  | 98.66       | 17.42 | 0.59        |
| DIVALIKE+J Unconstrained| -46.85 | 99.71 | 18.97 | 0.27  | 100.2       | 18.96 | 0.27        |
| BAYAREALIKE+J Unconstrained| -47.54 | 101.1 | 20.36 | 0.14  | 101.6       | 20.36 | 0.14        |
| DEC Constrained| -48.76 | 101.5 | 20.76 | 1.40E–05 | 101.8 | 20.56   | 1.60E–05 |
| DIVALIKE Constrained| -49.6  | 103.2 | 22.46 | 5.90E–06 | 103.4 | 22.16   | 6.70E–06 |
| DEC Unconstrained| -52.96 | 109.9 | 29.16 | 0.0017 | 110.2 | 28.96   | 0.0019    |
| DIVALIKE Unconstrained| -57.5  | 119   | 38.26 | 1.80E–05 | 119.2 | 37.96   | 2.00E–05 |
| BAYAREALIKE Constrained| -70.61 | 145.2 | 64.46 | 4.40E–15 | 145.5 | 64.26   | 5.00E–15 |
| BAYAREALIKE Unconstrained| -72.74 | 149.5 | 68.76 | 4.20E–12 | 149.7 | 68.46   | 4.80E–12 |
Three dispersal events from Africa to Eurasia took place later in the history of Ceropales, which coincide with Pleistocene glacial cycles and lower sea levels in the Mediterranean. Despite the absence of land connections after the MSC (Ricci et al., 2017), the Pleistocene has been a highly reported time for dispersal between the Ethiopian and Palaearctic regions (Frajman & Schönswetter, 2017) for a number of terrestrial invertebrates, such as spiders, land snails, and hoverflies (Opatova et al., 2016; Sherpa et al., 2018; Ståhls et al., 2016).

4.4 | Dispersal to the Australian region

Our results show a sister relationship between taxa from the Eurasian and Australian regions, with a recent divergence in the Pleistocene (Figure 2). The observed pattern is incongruent with the expected. The Eurasian region has classically been observed as sister to North America as a result of the break-up of Laurasia (Figure 1). Under this same scenario, the Australian insect fauna is a mix between relictual and disjunct elements (Yeates & Cassis, 2017), with origins from Gondwanan break-up, dispersal through temporary land bridges or long-distance dispersal (Figure 1). Recent divergences as a result of dispersal in the Pleistocene are consistent with the drying of extensive areas, such as the Sunda Plains, during glacial cycles (Lohman et al., 2011). These large, exposed areas may have served as land bridges for dispersal between the Oriental and Australian regions. This route has been proposed as the main dispersal path used by humans ca. 65,000 years ago, thousands of years before the last glacial maximum (De Deckker et al., 2019). In the Pliocene–Pleistocene, this route of dispersal has been documented for invertebrate groups such as land snails (Köhler & Criscione, 2013) and moths (Spitsyn et al., 2018).

5 | CONCLUSIONS

This is the first study to address the biogeographical processes that produced the current distributions of a cosmopolitan pompilid lineage. In general, our results fit previously suggested hypotheses for the processes underlying these distributions. The kleptoparasitic Ceropales is a young lineage of spider wasps (crown-group age 10.6 Ma) in which dispersal over a BLB land bridge in the Late Miocene and Pliocene best fits our results for the Old World–New World distribution. The North Mesoamerica–South America distribution is explained by dispersal through the Isthmus of Panama. Dispersal from the Palaearctic to the Ethiopian region coincides with the Messinian Salinity Crisis and is best explained by dispersal through land bridges facilitated by this event. Finally, range expansion to Australia from the Oriental region took place in the Pleistocene, when the drying of the Sunda plains produced land bridges that allowed faunal movement.

Ceropales is the youngest widespread genus within Pompilidae (Waichert, Rodríguez, et al., 2015). Females exhibit kleptoparasitoid behavior, where adults oviposit on spiders already paralyzed by other pompilids. This behavior could be advantageous by reducing limiting colonization factors, for example, adaption to the spider's defenses. This could result in an expanded niche and allowed the group to colonize, which may have facilitated dispersal through all continents in a short period of time.

ACKNOWLEDGMENTS

This work was supported by a Center for Women and Gender graduate student grant to J.R., by National Science Foundation award DEB-0743763 to J.P.P. and C.D.v.D. CW thanks CNPq (National Counsel of Technological and Scientific Development), award #249917/2013-0 and grant #435045/2018-0; and FAPES (Fundação de Âmargo à Pesquisa e Inovação do Espírito Santo)/CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior) for #71026436 and #85320846. We thank Nicholas Matzke (The University of Auckland) and an anonymous reviewer for significantly improving this manuscript. We also thank Jaime Florez (ANIC, CSIRO) for assistance with R script development. Specimens used for this study were sampled from the existing EMUS collection. Information on specimen date and place of collection as well as who collected them can be found with the Dryad dataset at https://doi.org/10.5061/dryad.c59zw3r5f.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad, https://doi.org/10.5061/dryad.c59zw3r5f.

ORCID

Juanita Rodríguez https://orcid.org/0000-0001-9922-1978

REFERENCES

Bakkes, D. K., Mansell, M. W., & Sole, C. L. (2018). Phylogeny and historical biogeography of silky lacewings (Neuroptera: Psychopsidae). *Systematic Entomology*, 43, 43–55.

Ball, I. R. (1975). Nature and formulation of biogeographical hypotheses. *Systematic Biology*, 24, 407–430.

Bremer, K. (1992). Ancestral areas: A cladistic reinterpretation of the center of origin concept. *Systematic Biology*, 41, 436–445.

Brundin, L. (1966). Transantarctic relationships and their significance, as evidenced by chironomid midges with a monograph of the subfamilies Podonominae and Aphroteniinae and the austral Heptagyiae. *Kongliga Svenska Vetenskapssocietens Handlingar*, 4, 1–472.

Burnham, K. P., & Anderson, D. R. (1998). *Model selection and multi-model inference: A practical information-theoretic approach*. Springer. https://doi.org/10.1007/b97636.

Cecarelli, F. S., Opell, B. D., Haddad, C. R., Raven, R. J., Soto, E. M., & Ramirez, M. J. (2016). Around the world in eight million years: Historical biogeography and evolution of the spray zone spider amauroides (Araneae: Anyphaenidae). *PLoS One*, 11, e0163740.

Charig, A. J. (1971). Faunal provinces on land: evidence based on the distribution of fossil tetrapods, with especial reference to the reptiles of the Permain and Mesozoic. In F. A. Middlemiss, P. F. Rawson, & G. Newall (Eds.), *Faunal provinces in space and time* (pp. 111–128). Seel House Press.

Colbert, E. (1973). Continental drift and the distributions of fossil reptiles. In D. H. Tailing, & S. K. Runcorn (Eds.), *Implications of continental drift for the Earth sciences* (pp. 395–412). Academic Press.

Cracraft, J. (1974). Continental drift and vertebrate distribution. *Annual Review of Ecology and Systematics*, 5, 215–261.

Craw, R. C. (1985). Classic problems of southern hemisphere biogeography re-examined. *Panbiogeographic analysis of the New...
BIOSKETCH

Juanita Rodriguez is a research scientist at the Australian National Insect Collection. She is interested in the application of molecular phylogenetic methods to the study of systematics, macroevolutionary processes, and biogeography. Sarah Bank is a PhD student at University of Göttingen. Her research interests are evolution, phylogenetics, systematics, biogeography, and biodiversity. Cecilia Waichert is a professor at Universidade Vila Velha. Her research focuses on systematics, biogeography, evolution, and natural history of wasps (Hymenoptera). James Pitts is a professor at Utah State University. His research interests include the evolution of behavior, wasp systematics, and North American desert biogeography. Carol von Dohlen is a professor in the Department of Biology, Utah State University. Her research focuses on insect molecular phylogenetics and its applications for understanding evolutionary patterns and processes.

Author Contributions: J.R. and J.P.P. conceived the ideas; J.R. analyzed the data and led the writing; S.B. and C.W. contributed to writing and figure elaboration. C.v.D. provided support for data collection, analysis, and writing.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Rodriguez J, Bank S, Waichert C, von Dohlen CD, Pitts JP. Around the world in 10 million years: Rapid dispersal of a kleptoparasitoid spider wasp (Pompilidae: Ceropales). J Biogeogr. 2021;48:1669–1678. https://doi.org/10.1111/jbi.14103