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First global molecular phylogeny and biogeographical analysis of two arachnid orders (Schizomida and Uropygi) supports a tropical Pangean origin and mid-Cretaceous diversification

Ronald M. Clouse[1] | Michael G. Branstetter[2,3] | Perry Buenavente[4] | Louise M. Crowley[1] | Jesse Czekanski-Moir[5] | David Emmanuel M. General[6] | Gonzalo Giribet[7] | Mark S. Harvey[8] | Daniel A. Janies[9] | Alma B. Mohagan[10] | Dave P. Mohagan[11] | Prashant P. Sharma[12] | Ward C. Wheeler[1]

[1]Division of Invertebrate Zoology, American Museum of Natural History, New York, NY, USA

[2]Department of Biology, University of Utah, Salt Lake City, UT, USA

[3]Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA

[4]Herpetology Section, Zoology Division, National Museum of the Philippines, Manila, Philippines

[5]Department of Environmental and Forest Biology, State University of New York, College of Environmental Science and Forestry, Syracuse, NY, USA

[6]University of the Philippines Los Baños, Museum of Natural History, Los Baños, Laguna, Philippines

[7]Department of Organismic and Evolutionary Biology, Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA

[8]Department of Terrestrial Zoology, Western Australian Museum, Welshpool DC, WA, Australia

[9]Department of Bioinformatics and Genomics, University of North Carolina at Charlotte, Charlotte, NC, USA

[10]Biology Department, Central Mindanao University, Maramag Bukidnon, Philippines

[11]Center for Biodiversity Research and Extension in Mindanao, Central Mindanao University, Maramag, Bukidnon, Philippines

[12]Department of Integrative Biology, University of Wisconsin-Madison, Madison, WI, USA

Correspondence
Ronald M. Clouse, Division of Invertebrate Zoology, American Museum of Natural History, New York, NY, USA.
Email: rclouse@amnh.org

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Abstract

Aim: We sought to illuminate the history of the arachnid orders Schizomida and Uropygi, neither of which have previously been subjected to global molecular phylogenetic and biogeographical analyses.

Location: Specimens used in this study were collected in all major tropical and subtropical areas where they are presently found, including the Americas, Africa, Australia and the Indo-Pacific region.

Methods: From field-collected specimens, we sequenced two nuclear and two mitochondrial markers, combined these with publicly available data, and conducted multi-gene phylogenetic analyses on 240 Schizomida, 24 Uropygi and 12 other arachnid outgroups. Schizomid specimens included one specimen from the small family Protoschizomidae; other schizomid specimens were in Hubbardiidae, subfamily Hubbardiinae, which holds 289 of the order's 305 named species. We inferred ancestral areas using the Dispersal-Extinction-Cladogenesis model of range evolution, and we used fossil calibrations to estimate divergence times.

Results: We recovered monophyletic Schizomida and Uropygi as each other's sister group, forming the clade Thelyphonida, and terminals from the New World were usually positioned as the earliest diverging lineages. The ancestral area for

schizomids reconstructed unambiguously to the region comprised of Mexico, Southern California and Florida (the xeric New World subtropics). Optimal trees suggested a single colonization of the Indo-Pacific in both orders, although this did not receive bootstrap support. Molecular dating gave an Upper Carboniferous origin for each order, and a mid-Cretaceous expansion of Schizomida, including the origin and initial diversification of those in the Indo-Pacific.

Main conclusions: Ancestral area reconstructions, molecular dating and fossil evidence all support an Upper Carboniferous, tropical Pangean origin for Thelyphonida, Schizomida and perhaps Uropygi. Much of this region became unsuitable habitat for these arachnids during the breakup of Pangea, but they persisted in the area that is now Meso- and South America. From there they then expanded to the Indo-Pacific, where schizomids today display an idiosyncratic combination of microendemism and long-range dispersal.

KEYWORDS

dispersal-extinction-cladogenesis model, historical biogeography, Hubbardiidae, molecular dating, Protoschizomidae, range evolution, short-tailed whip-scorpions, *Stenochrus*, Thelyphonida, whip-scorpions

1 | INTRODUCTION

The arachnid clade Tetrapulmonata represents a major arthropod lineage comprised of four extant orders: Araneae (spiders), Schizomida (short-tailed whip-scorpions, Figure 1a,b), Uropygi (whip-scorpions, vinegaroons, Figure 1c,d) and Amblypygi (whip-spiders). Spiders have diversified into many major lineages and thousands of species on virtually all inhabitable land masses (Wheeler et al., in press), mostly due to their use of venom and silk to immobilize and subdue prey. In contrast, the other three orders currently have only 624 recognized species, and they are nowadays largely restricted to tropical and subtropical bioregions. They have also long been thought to represent a distinct clade—the Pedipalpi—that is supported by numerous molecular and morphological analyses (e.g. Giribet, Edgecombe, Wheeler, & Babbitt, 2002; Pepato, da Rocha, & Dunlop, 2010; Sharma et al., 2014; Shultz, 2007). Pedipalpi are recognized by the elongate first pair of legs (these act as antenniform appendages and are not used as walking legs) and a subchelate distal terminus of the pedipalp. Within the group, Uropygi and Schizomida have been considered sister taxa and are morphologically very similar.

Uropygi are large, robust, heavily sclerotized arachnids with a long, annulated, post-abdominal flagellum. Schizomida are smaller and less heavily sclerotized, also with a post-abdominal flagellum that is modified in males and used during courtship and copulation with females. Extant Uropygi are represented by 111 species in 14 genera and one family (Thelyphonidae), although one Mesozoic and four Palaeozoic genera are unplaced in the order (Rowland & Cooke, 1973). Extant Schizomida are more diverse, with 305 species in 58 genera and two families (Protoschizomidae and Hubbardiidae), and a further three Cenozoic genera are placed in either Hubbardiidae or the extinct family Calcitronidae. Protoschizomids consist of 16 named species that inhabit caves in Mexico and Texas

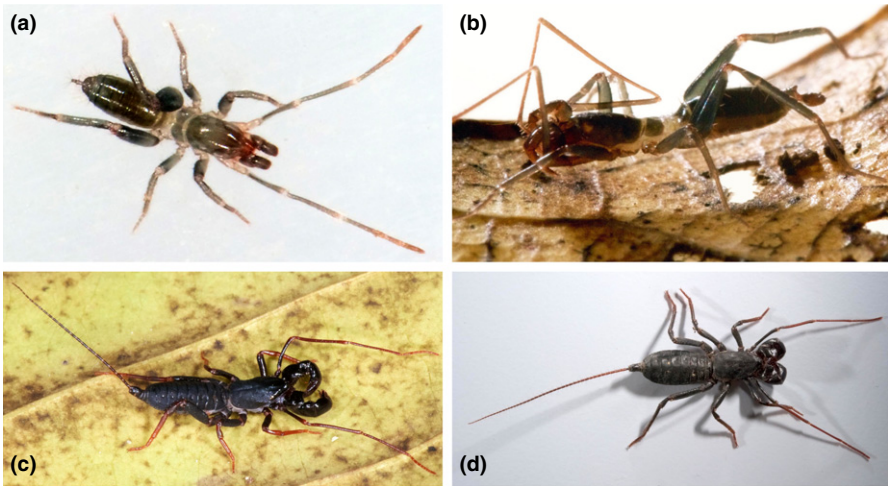

FIGURE 1 Schizomida from (a) Amazonas and (b) Guam; Uropygi: (c) *Thelyphonellus amazonicus* from Amazonas, Brazil (MCZ collection IZ-129084) and (d) *Mastigoproctus giganteus* (MCZ collection IZ-29741) [Colour figure can be viewed at wileyonlinelibrary.com]

(Cokendolpher & Reddell, 1992). Almost all other schizomids are in the hubbardiid subfamily Hubbardiinae, the only exceptions being two species in the subfamily Megaschizominae, which live in eastern South Africa and Mozambique (Reddell & Cokendolpher, 1995).

Although the monophyly of Uropygi+Schizomida is uncontroversial (they are often united into a single order, as in Shultz, 2007), only Schizomida—using morphological data and a mixture of generic and species-level terminals—has been subjected to a comprehensive phylogenetic analysis (Cokendolpher & Reddell, 1992; Monjaraz-Ruedas, Francke, & Santibáñez-López, 2017). The few studies that have used molecular data are limited to small regional studies (Harvey, Berry, Edward, & Humphreys, 2008) or to barcoding of individual populations (Zawierucha, Szymkowiak, Dabert, & Harvey, 2013). One result of Cokendolpher and Reddell's (1992) morphological phylogenetic analysis, which focused on Protoschizomidae, was a strengthening of the hypothesis that protoschizomids are distinct from other schizomids, with a morphology that exhibits certain symplesiomorphies; for example protoschizomids lack brushes and true hyaline teeth (serrula) on their chelicerae, both of which character states they share with uropygids.

The paucity of explicit evolutionary hypotheses regarding the relationships of the extant Uropygi and Schizomida hampers our attempts to study the biogeographical origins of their genera or suites of genera. This is unfortunate, as these orders show considerable promise in the study of historical biogeography—most genera are restricted to discrete regions of the world, and, except for a few human-associated (synanthropic) species, they tend to show remarkable geographical fidelity. In addition, the hubbardiine schizomids paint a confusing picture. Clearly, some can disperse great distances, either with human assistance, as exemplified by *Stenochrus portoricensis* Chamberlin, 1922, *Schizomus crassicaudatus* (O. P.-Cambridge, 1872) and *Zomus bagnallii* (Jackson, 1908) (Christophoryová, Šestáková, Krumpál, & Fend'a, 2013), or without, as appears to be the case for the ancestors of endemic species on remote islands (Cokendolpher & Reddell, 1999). However, distributional data show that most species have highly restricted ranges and suggest old in situ origins for many clades (Harvey, 2002; Reddell & Cokendolpher, 1995). This latter characterization is supported by molecular studies of some Western Australian species (Harvey et al., 2008). As currently understood, schizomid ecology offers little insight either: with few exceptions (*i.e.* cave and greenhouse dwellers), they prefer the leaf litter of disturbed habitats in the tropics, but unlike many disturbance-associated species, they are usually not found in great abundance. Moreover, although hubbardiines have 80% more named species in the Neotropics than the Indo-Pacific (168 vs. 93), one place where they are truly abundant is on Pacific islands (RMC, PPS, personal observations).

To test the relationships and biogeographical origins of both Uropygi and Schizomida, we assembled a large collection of specimens, analysing seven of the 17 named genera of Uropygi (note that seven Uropygi genera are mono- or ditypic, and of questionable systematic validity), 14 of the 58 named genera of Schizomida, and a large number of undescribed genera and species in each order, including new schizomid taxa from the poorly known Asian and African faunas. We inferred a multi-locus phylogeny using specimens from nearly every region where they are found, and we reconstructed ancestral areas and divergence time estimates to (1) address the origins of these orders' global distributions and (2) test their putative sister group relationship and reciprocal monophyly (Harvey et al., 2008; Rowland & Cooke, 1973).

2 | MATERIALS AND METHODS

2.1 | Specimen collection and sequencing

We collected schizomids, uropygids and other arachnids during field expeditions, and we borrowed additional specimens preserved for DNA analysis. From these, we sequenced the following markers employing known and newly designed primers (see Appendix S1 in Supporting Information): mitochondrial markers cytochrome *c* oxidase subunit I (largest fragment recovered: 855 bp) and 12S rRNA (489 bp, aligned), and nuclear ribosomal markers 18S rRNA (1,749 bp, aligned) and 28S rRNA (2,287 bp, aligned). The newly generated sequences were deposited in GenBank under the accession numbers KY573074–KY573914 and KY587224–KY587226 (see Appendix S2). We also downloaded publicly available sequences from GenBank (Benson, Karsch-Mizrachi, Lipman, Ostell, & Sayers, 2009) and BOLD (Ratnasingham & Hebert, 2007) (Table 1, Appendix S2); schizomid sequences were downloaded only if accompanied by taxonomic or locality data.

Ribosomal RNA sequences were aligned using MAFFT 7 (Katoh & Standley, 2013) under default parameters. Alignments were prepared for analysis in RAxML 8 (Stamatakis, 2014) by choosing those terminals with at least one nuclear marker sequenced and then trimming the alignments in GBLOCKS 0.91b (Talavera & Castresana, 2007). GBLOCKS settings were such that any position with an indel for up to one half of the terminals was kept, and flanking and conserved positions were set to be equal to at least one half of all terminals. The untrimmed alignments from MAFFT were also used to fragment the data for analysis in POY 5.1.2b (Wheeler, Lucaroni, Hong, Crowley, & Varón, 2015) such that ambiguity in the sequences of unequal length was reduced (see p. 155 of Wheeler et al., 2006 and the program documentation for additional details on POY input data). The alignments from MAFFT in no way constrained the subsequent analysis under direct optimization (DO) in POY, given that gaps in the alignments are removed in POY prior to analysis.

2.2 | Phylogenetic analyses

Our main analyses had 276 terminals with at least one nuclear marker, including 240 schizomids and 24 uropygids from the full geographical range of our collection (Table 1). We also conducted a phylogenetic search using only the marker COI, which included 522 terminals, 175 of which were downloaded from public databases; this allowed the comparison of many of our collected specimens to those examined in previous studies, as well as assistance in species identification. Analyses in RAxML used 500 independent starts, plus

TABLE 1 Total number of specimens sequenced or downloaded from public data sources, then subjected to phylogenetic analyses with all markers combined (COI with 12S, 18S and 28S rRNA) or using COI alone, for each arachnid order included in the study

	Number of museum specimens			Number of public, sequenced specimens			Totals		
Order	Sequenced	In combined tree	In COI tree	Downloaded	In combined tree	In COI tree	Sequences	In combined tree	In COI tree
Schizomida	377	233	330	64	7	59	441	240	389
Uropygi	15	15	14	109	9	108	124	24	122
Amblypygi	2	2	1	1	1	1	3	3	2
Araneae	0	0	0	1	1	1	1	1	1
Opiliones	0	0	0	2	2	2	2	2	2
Pseudoscorpiones	0	0	0	1	1	1	1	1	1
Scorpiones	1	1	1	2	2	2	3	3	3
Solifugae	1	1	1	1	1	1	2	2	2
Total	396	252	347	181	24	175	576	276	522

500 bootstrap resampling replicates. Data were partitioned by gene, and a GTR+Γ model was applied to each partition.

Analyses of these datasets were also conducted using dynamic homology (Wheeler, 2001) with the DO method (Wheeler, 1996), as implemented in the parallel version of POY 5.1.2b (Wheeler et al., 2015). Three different searches were done by varying the costs of transformations (transitions and transversions), gaps (indels) and gap openings. In one scheme, we kept all parameters equal to 1, in a second we increased the gap-opening cost to 2, and in the third search we increased only the indel cost to 2. Heuristic searches were performed using the *timed search* function in POY, which combines Wagner builds followed by multiple rounds of TBR branch swapping, parsimony ratchet (Nixon, 1999) and tree fusing (Goloboff, 1996). Two rounds of timed searches were performed, with topologically unique trees or optimal trees being stored in memory following each round. For the terminals with at least one nuclear marker, the maximum search time was 48 hr on 64 processors, and the search on those terminals with just COI ran for 24 hr on 64 processors.

Bremer (Bremer, 1994; Goodman, Olson, Beeber, & Czelusniak, 1982) support values were used to estimate nodal support of the shortest trees found in POY. Bremer values were calculated from the TBR neighbourhood of the "best" trees and are upper-bound values of this NP-Hard support measure [command line: swap(all,visited:"tmp.trees")].

2.3 | Molecular dating

We dated the phylogeny recovered under maximum likelihood (with redundant species representatives removed) using four calibration points. The first one, for the root of our tree (and the crown-group Arachnida), was originally employed by Sharma and Giribet (2014) and was a uniform distribution between 460 and 490 Ma. The next three calibrations used dates 10 Ma before known fossils, each with a normal distribution and standard deviation of 10 Ma. This was based on the assumption that the earliest known fossils of certain lineages are indeed early exemplars of those groups. Fossil arachnid material appears sufficient for this assessment (Dunlop, Penney, Tetlie, & Anderson, 2008), and the assumption is not contradicted by the several dated arachnid phylogenies now available. Thus, the three additional calibration dates we set within Arachnida were as follows: crown-group Opiliones at 410 Ma (based on the Opiliones fossil described in Dunlop, Anderson, Kerp, & Hass, 2004); the split between Uropygi and Schizomida at 329 Ma (based on the Uropygi fossils described and discussed in Tetlie & Dunlop, 2008 and Selden, Dunlop, & Simonetto, 2016); and crown-group Indo-Pacific Schizomida at 110 Ma (based on an unpublished schizomid fossil known from Burmese amber) (Table 2).

We used PATHD8 1.0 (Britton, Anderson, Jacquet, Lundqvist, & Bremer, 2007) to generate preliminary trees for BEAST 1.8.3 (Drummond & Rambaut, 2007), since BEAST requires initial trees to have node depth priors similar to dating calibrations. This avoids an initial tree likelihood of zero, which causes runs to fail. Also, to shorten and stabilize analyses, we constrained the monophyly of certain groups recovered in the ML analysis and previous studies, including all the arachnid orders, Uropygi plus Schizomida (Thelyphonida), Hubbardiidae and the Indo-Pacific Hubbardiinae.

In BEAST, we tested different speciation and clock models, with and without different calibration points, to see which set of priors would produce dating estimates that aligned with known events and had the lowest variance. The random local clock model, especially with a birth-death model of speciation, produced an origin for Uropygi in the Upper Carboniferous (298.9–323.2 Ma), as we would expect from the oldest Uropygi fossil at 319 Ma (Tetlie & Dunlop, 2008). The uncorrelated relaxed clock also produced dates that accommodated fossil evidence, but with more variance. Other clocks resulted in dates too young to accommodate fossils, even when the dates were set as priors. The importance of the clock prior, superiority of the random local clock model, and young crown dates when using the uncorrelated lognormal relaxed clock model have been previously demonstrated (Crisp, Hardy, & Cook, 2014).

Thus we did four runs of 25 million generations each using the random local clock model and a birth-death model of speciation.

TABLE 2 Initial calibrations and resulting dates, with 95% confidence intervals, for key events in the evolution of the arachnid orders Schizomida and Uropygi, as shown in the chronogram in Figure 4

Event	Prior (Ma)	Result ± 95% CI (Ma)	Period
Crown Arachnida	Uniform, 475 ± 15	476.4 ± 14.0	Ordovician
Crown Tetrapulmonata		442.0 ± 38.1	Silurian
Crown Opiliones	Normal, 410 ± 10 *SD*	406.3 ± 18.0	Devonian
Stem (Uropygi+Schizomida)		398.0 ± 30.2	Devonian
Stem Uropygi, stem Schizomida	Normal, 329 ± 10 *SD*	333.0 ± 17.9	Carboniferous
Crown Schizomida		270.0 ± 31.2	Permian
Crown Uropygi		222.8 ± 24.1	Triassic
Stem Indo-Pacific Schizomida		126.9 ± 11.4	Cretaceous
Crown Indo-Pacific Schizomida	Normal, 110 ± 10 *SD*	120.4 ± 11.4	Cretaceous

Stationarity and convergence after a burnin of 10% was checked in the program TRACER 1.6 (Rambaut, Suchard, Xie, & Drummond, 2014), and the maximum clade-credibility tree, using mean dates, was taken from the run that had the best combination of stability and likelihood (MCC trees from each run differed negligibly).

2.4 | Lineage-through-time plots

For the schizomids in the dated tree from Beast, we constructed a lineage-through-time (LTT) plot in the "APE" package (Paradis, Claude, & Strimmer, 2004) in R (R Development Core Team, 2012). We also computed a gamma statistic in R (with the command "2*(1-pnorm (abs(gammaStat(tree))))"), which increases the more an LTT plot differs from one showing a constant rate of growth. In the R package "TREESIM," (by T. Stadler, available at cran.r-project.org/web/packages/TreeSim) we generated trees using different values for speciation and extinction rates, rate changes, extinction events and density-dependent speciation to compare to the LTT plot of schizomids.

2.5 | Ancestral area reconstructions

Three different ancestral area reconstructions were performed using the program RASP 3.1 (Yu, Harris, Blair, & He, 2015) and the Dispersal-Extinction-Cladogenesis (DEC) model of range evolution (Ree, 2005; Ree & Smith, 2008). For the first reconstruction, we started with the best tree recovered under ML, removed the outgroups, and assigned each Uropygi and Schizomida terminal to one of the following area categories (which are limited to 11 total in RASP): Mexico, S. California and Florida (*i.e.* subtropical, xeric, northern New World regions); Central America; South America; synanthropic (used for specimens of *Stenochrus portoricensis* found in Europe, the Canary Is. and S. Florida); West Africa; Mainland Asia & Japan; Philippines; Indonesia; New Guinea & Vanuatu; Micronesia & Palau; and W. Australia. In the second reconstruction, to incorporate topological variation in the analysis, we used the set of trees recovered under parsimony using different cost schemes with the DEC model of range evolution to compute the most likely ancestral range at each node of the first tree recovered under equal costs. Outgroups were removed, trees had parsimony branch lengths and the areas were coded as with the analysis of the maximum likelihood tree. For the third reconstruction we used a random sample of 100 trees from the 23,500 post-burnin trees recovered from the best run in BEAST and the Bayes-DEC model of range evolution. (Using just DEC on a selection of trees in preliminary analyses gave nearly identical results as Bayes-DEC, but with less ambiguity, so we chose the latter to be more conservative.) Outgroups were kept on the trees, and a single area category was used for synanthropic specimens and outgroups.

3 | RESULTS

In the likelihood analysis of the dataset having at least one nuclear marker for each taxon, we recovered with high bootstrap support the monophyly of Schizomida (96%) and Uropygi (100%), as well as Schizomida+Uropygi (Thelyphonida, 94%; Figure 2 and Appendix S3, Figure S3.1, in Supporting Information). For each order a New World species was recovered as sister to the remaining lineages (*Thelyphonellus amazonicus* in Uropygi and the protoschizomid *Agastoschizomus lucifer* in Schizomida). In Schizomida, three terminals from the same region formed a grade at the base of the order with high bootstrap support: *A. lucifer* from Mexico plus the remaining species (96%), *Hubbardia pentapeltis* from Southern California plus the remaining species (96%) and *Stenochrus sbordonii* from Mexico plus the remaining species (63%). Within each order we also recovered all Indo-Pacific and Asian terminals in a single clade, albeit without bootstrap support, like most mid-level relationships in the tree. For uropygids, the West African species *Etiennius africanus* placed among Asian terminals (on a long branch and with low support), but for schizomids, West African specimens were recovered with high bootstrap support as a clade among Mesoamerican lineages—although admittedly, Mesoamerica is much better sampled than Africa.

Trees found under parsimony and DO differed from those using maximum likelihood in four key ways (Figure 3 and Appendix S3, Figure S3.2, in Supporting Information). First, the African uropygid *Etiennius africanus* was recovered as sister group to the Brazilian species *T. amazonicus*, both consistently and with high Bremer support. Together these species were recovered as the sister clade to all other Uropygi, again both consistently and with high Bremer

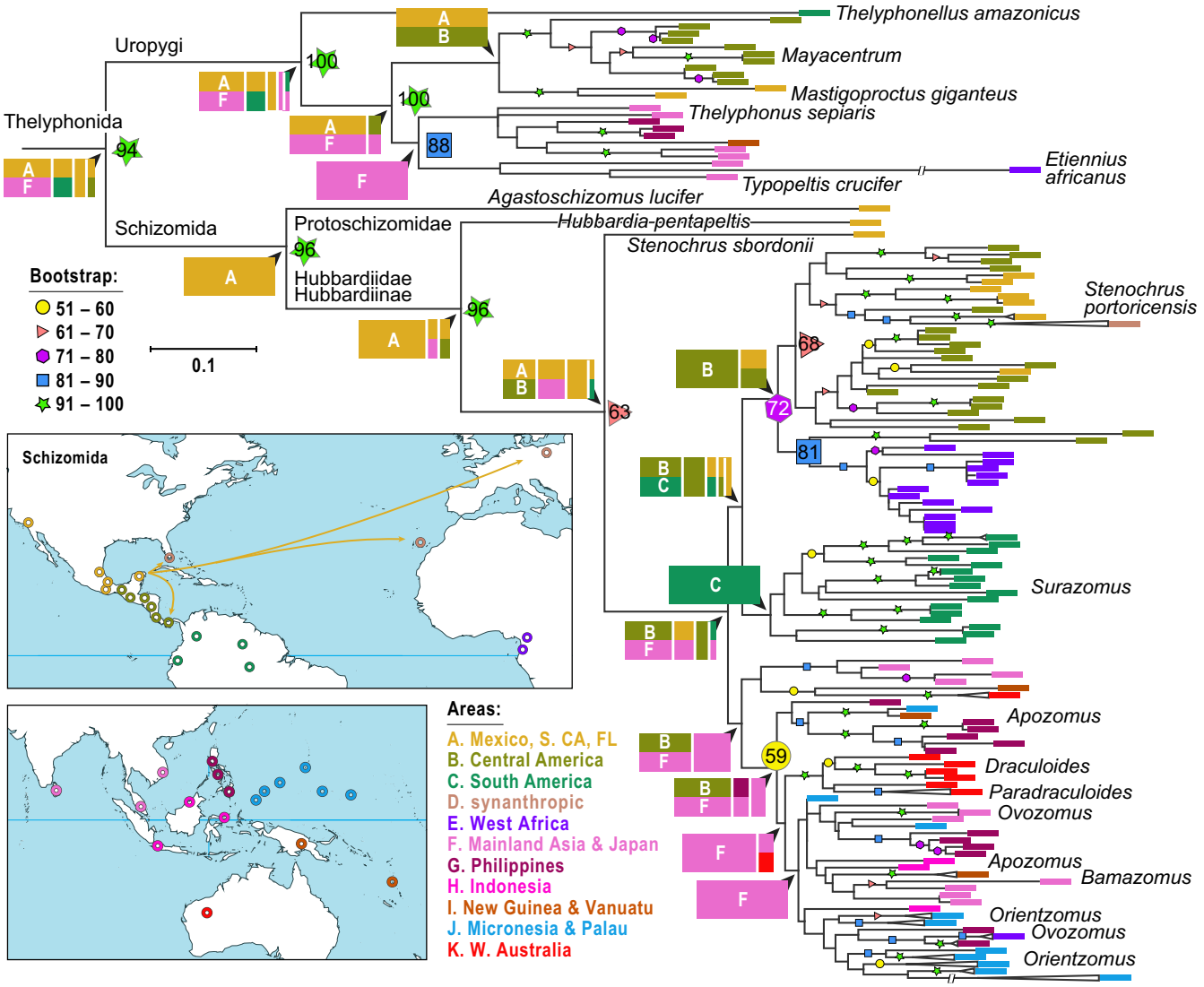

FIGURE 2 The most likely tree found under maximum likelihood (log likelihood = −55036.783997), based on sequences of two nuclear (18S and 28S rRNA) and two mitochondrial (COI and 12S rRNA) markers (outgroups not shown). All terminals have sequence data for at least 18S or 28S rRNA and are represented here by rectangles coloured according to areas of occurrence (full terminal names can be seen in Appendix S3, Figure S3.1, in Supporting Information). Bootstrap supports >50% are shown in increments of 10%, in increasing order, by circles, triangles, hexagons, squares and stars on the relevant nodes (written out for deeper nodes). Ancestral areas, shown for select nodes, were computed using the Dispersal-Extinction-Cladogenesis (DEC) model of range evolution. White breaks in each reconstruction rectangle separate different possible ranges for the hypothetical ancestor, in proportion to their probabilities. Ancestral ranges were allowed to combine two areas, shown by upper and lower boxes, and the most likely ranges have the letters of the areas that correspond to the area list shown. Terminal colours match specimen localities as marked on the inset map [Colour figure can be viewed at wileyonlinelibrary.com]

support. Second, the schizomid from Southern California, *H. pentapeltis*, as well as two terminals from Costa Rica and Nicaragua, were usually recovered as early branches in Schizomida but not stably or with high Bremer support. Third, New World terminals tended to form a paraphyletic grade at the base of Schizomida instead of mostly clustering into one clade. Finally, Indo-Pacific terminals were rendered polyphyletic by the placement of four Malaysian terminals among South American ones, or the placement of the genus "K" from Western Australia among the early schizomid lineages (not shown).

Trees recovered using only the marker COI tended to recover similar relationships as the trees using all markers, including monophyly of Schizomida, early New World lineages and a close relationship among Indo-Pacific species. The resulting trees (one from maximum likelihood and three strict consensus trees from each cost scheme under parsimony) are found in Appendix S3, Figures S3.3–6, in Supporting Information.

Using the DEC model on the single best tree recovered from maximum likelihood analysis or Bayes-DEC on a selection of trees from the BEAST runs resulted in a high probability for the ancestral range of Thelyphonida, Uropygi and Schizomida as the northern arid New World subtropics (Mexico, Southern California, and, for some specimens of the uropygid *Mastigoproctus giganteus*, Florida; Figures 2 & 4). This result was especially clear for schizomids, where it

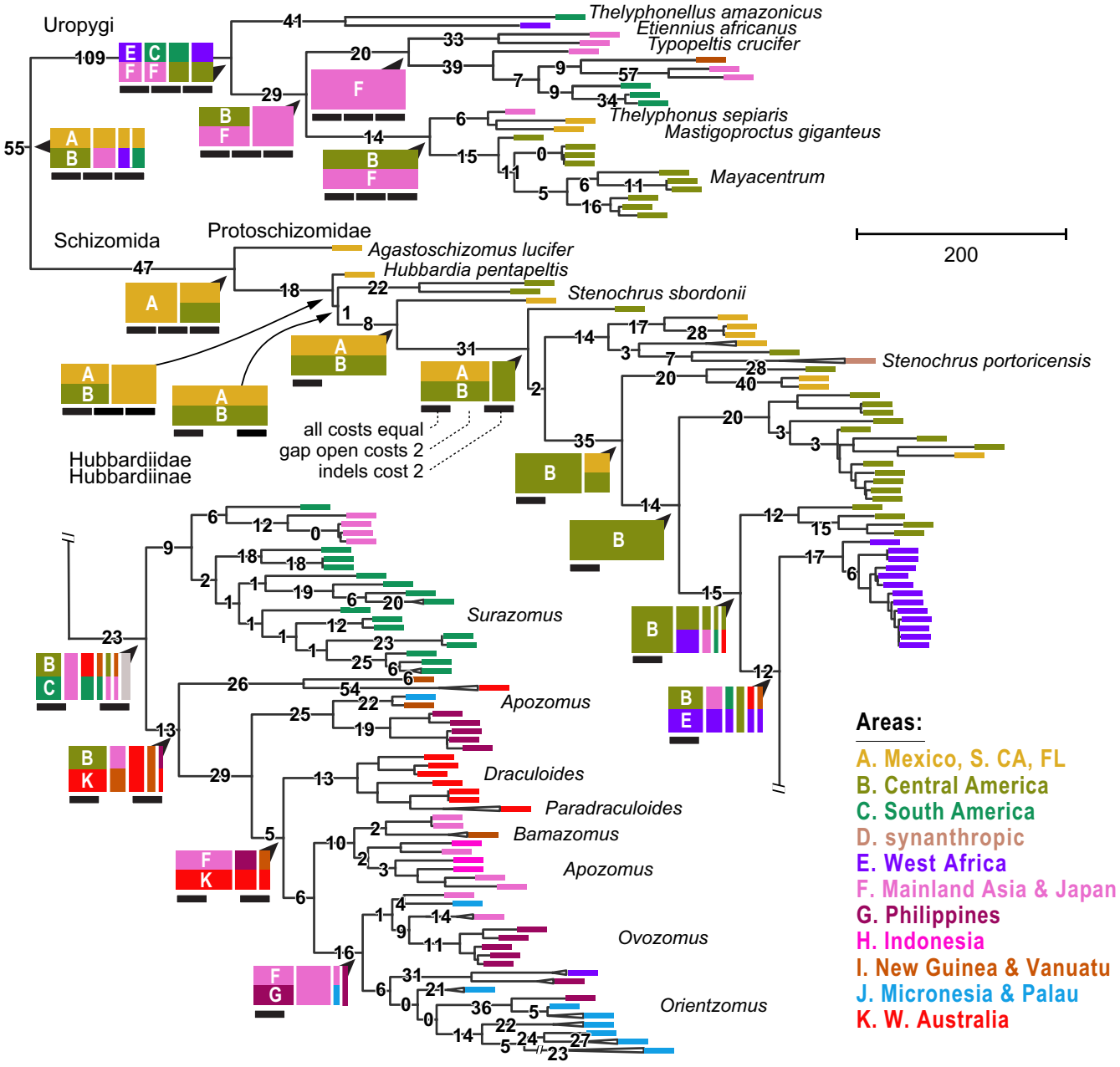

FIGURE 3 One of two shortest trees (length 15,383 steps) found using direct optimization under the parsimony criterion and equal costs for transformations (transitions and transversions), gaps (indels) and gap openings. Data and terminals used are the same as for the tree found under maximum likelihood in Figure 2 (all four markers for those with at least one nuclear marker), although not aligned before tree-searching nor trimmed in GBLOCKS. Terminals are represented here by rectangles coloured according to areas of occurrence (full terminal names can be seen in Appendix S3, Figure S3.2, in Supporting Information). Ancestral area reconstructions, found using the DEC model of range expansion on the set of all seven trees found under parsimony under different cost schemes, are displayed under nodes of interest as in Figure 2. Bremer supports for selected nodes are shown and were obtained using a static alignment implied by the shortest tree. The other tree recovered using equal costs (which differed mostly in rearrangements among conspecifics), as well as trees recovered using different cost schemes were checked for the presence of clades in the tree shown, and the results are shown in the three rectangles below the ancestral area reconstructions; black denotes a clade found in all other trees, and white indicates clades found in no other trees (partial discoveries did not occur among clades shown) [Colour figure can be viewed at wileyonlinelibrary.com]

was reconstructed at 100%. Using the DEC model on the set of trees recovered under parsimony gave a highly ambiguous ancestral range for Uropygi but still returned the New World as the most likely home to the ancestor of thelyphonids and schizomids (Figure 3). Within schizomids, the lack of the Southern African hubbardiid subfamily Megaschizominae in our analyses makes the ancestral range of Hubbaridiidae less certain, but the other subfamily, Hubbardiinae, appears to have also originated in what is today the dry subtropics of the New World, namely the region that encompasses most of Mexico and parts of the southern US.

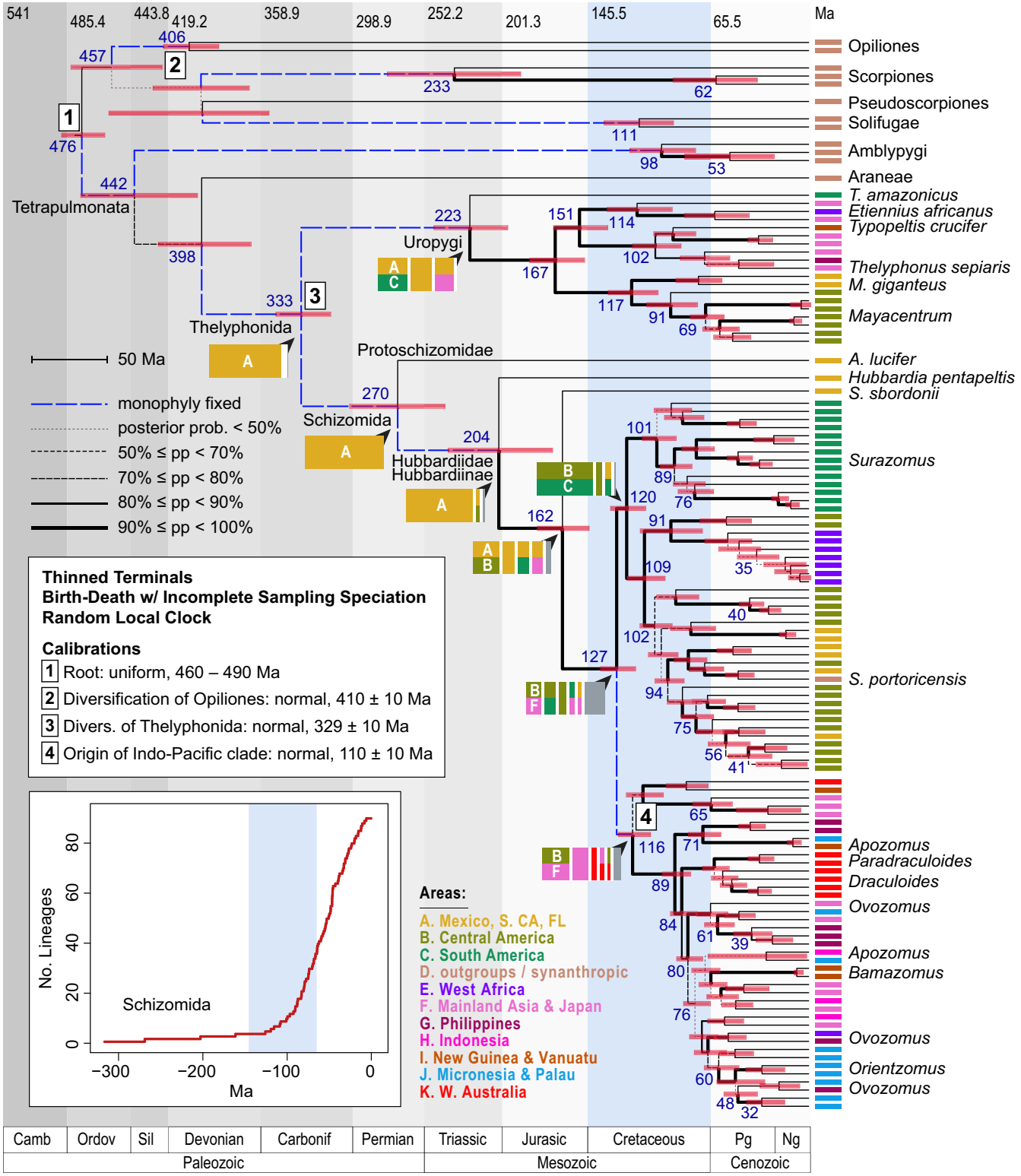

FIGURE 4 Maximum clade credibility tree with mean dates, using the tree shown in Figure 2 as a starting tree (with redundant specimens of putative species removed) and constraining the monophyly of certain clades (shown as long-dashed, blue branches). Terminals are represented here by rectangles coloured according to areas of occurrence (full terminal names can be seen in Appendix S3, Figure S3.7, in Supporting Information). Posterior probabilities are indicated by line type and thickness. MCMC runs in BEAST used a birth-death model of speciation with incomplete sampling and a random local clock model. The tree was calibrated with fossil-based data listed and shown on the tree as boxed numbers 1–4. Dates in millions of years are written in blue next to selected nodes, as are ancestral area reconstructions made using the Bayes-Lagrange Statistical DEC method (depicted in the same style as in Figure 2). The lower inset shows a lineages-through-time plot for the schizomid terminals [Colour figure can be viewed at wileyonlinelibrary.com]

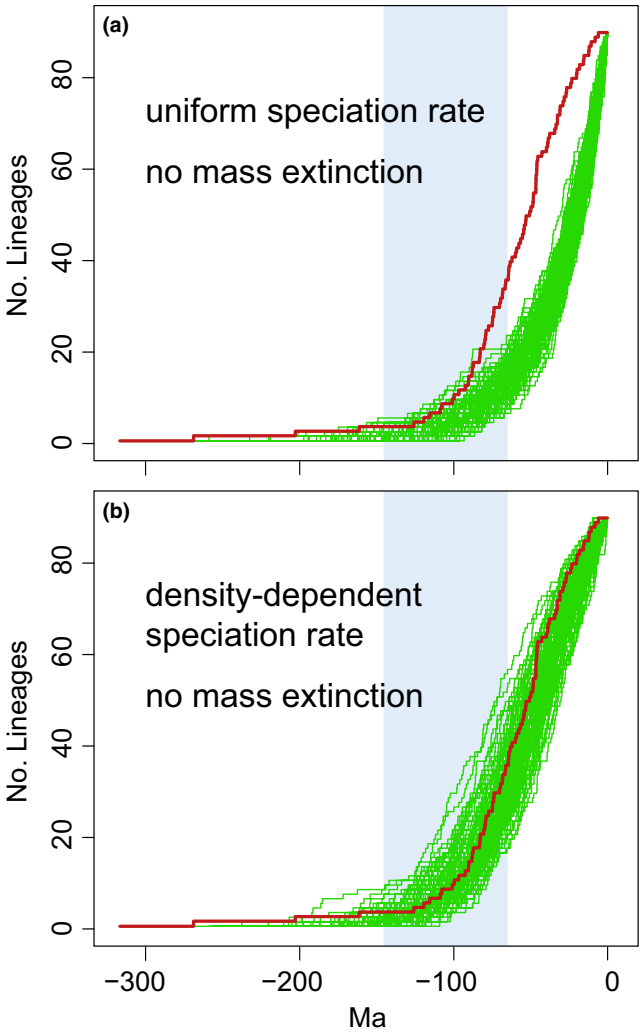

FIGURE 5 A comparison of the lineage-through-time plot for Schzomida terminals shown in Figure 4 to 100 simulated trees (green) generated using only a uniform speciation rate (a) or a density-dependent speciation rate (b). Trees with only a uniform speciation rate (a) were computed using the following code in the R package TREESIM: sim.rateshift.taxa(90, 100, c(1,1),c(0,0),c(1,1),c(0,0), complete = FALSE, K = 0, norm = TRUE). Trees with a density-dependent speciation rate (b) were computed using the following code: sim.rateshift.taxa(90, 100, c(1.5,1.5),c(0,0),c(1,1),c(0,0), complete = FALSE, K = 110, norm = TRUE) [Colour figure can be viewed at wileyonlinelibrary.com]

BEAST runs stabilized quickly, usually after 10 million trees, and the only dates not to achieve effective sample size (ESS) values above 200 were for the origins of Scorpiones and Solifugae in the outgroups, the relationships for which BEAST had difficulty resolving. We found a Carboniferous origin for Schizomida and a moderate increase in lineage accumulation until the mid-Cretaceous, when the number of lineages increased rapidly, and schizomids expanded to the then contiguous Africa and the Indo-Pacific region (Figure 4 and Appendix S3, Figure S3.7, in Supporting Information). Our gamma statistic (5.05×10^{-7}) indicated that this increase was expected from a constant rate of speciation, and indeed, using a speciation model that used a constant rate slowed by an increase in species (density dependence), LTT plots of simulated trees closely resembled that of schizomids in our dated tree (Figure 5). Our final chronogram gave some Micronesian dates that appear too old, such as the split between *Orientzomus* sp. "Chuuk" and *Orientzomus* sp. "Pohnpei 2" at 31.9 Ma, as Pohnpei is believed to be not older than 8.7 Ma (Craig, Currie, & Joy, 2001; Rehman, Nakaya, & Kawai, 2013). However, species such as *Orientzomus* sp. "Pohnpei 3," found on Pohnpei and Palau, 2,500 km away, demonstrate that similarly aged Indo-Pacific species can have wide distributions, and closely related haplotypes can be found on different islands.

4 | DISCUSSION

4.1 | Ancestral areas

Thelyphonida and its two constituent orders, Uropygi and Schizomida, appear to have descended from ancestors in the Americas. The primary caveat to this conclusion is the more ambiguous reconstruction for the ancestral range of Uropygi; aspects of the tree topologies that push the reconstruction towards a New World location are the unambiguous New World origin for schizomids and the deep placement of the Amazonian uropygid *T. amazonicus*, but the clustering of Asian and New World Uropygi into two clades, the placement of the Indian uropygid *Thelyphonus sepiaris* among New World terminals in parsimony trees, and the sister group relationship of the African uropygid *E. africanus* with *T. amazonicus* in parsimony trees all make the uropygid ancestral range unclear. All ancestral range reconstructions suggest that after originating in what is today the region comprised of the northern, New World subtropics, hubbardiine schizomids dispersed to Central America, from there to South America and Africa, and then to the Indo-Pacific, with remote Pacific islands being the most recent regions colonized.

Our analyses suggest that expansion to Asia and the Pacific may have started through a single colonization event. This result was recovered in our optimal tree found under maximum likelihood, but without bootstrap support and not under parsimony; regardless, what was consistently recovered, and with low resampling support, was the monophyly of the bulk of Indo-Pacific specimens, and it seems reasonable to conclude that schizomid and uropygid range expansions or colonizations from the New World into this region were rare.

Contrary to this scenario, however, putative stem-group Uropygi and Schizomida fossils are from eastern North America and Europe (Dunlop & Horrocks, 1996; Selden et al., 2016; Tetlie & Dunlop, 2008). Given the primitive morphologies of these fossils and our lack of molecular dating evidence that the orders originated much before them (Upper Carboniferous), palaeontological evidence indicates that the actual ancestral area of each order is what is today temperate North American and Europe.

The most parsimonious reconciliation between our ancestral area reconstructions and the fossil evidence is that thelyphonids originated in the area between what is today North America, South America, Africa and Europe, which was a tropical, geologically dynamic, terrestrial region through the centre of the Pangea

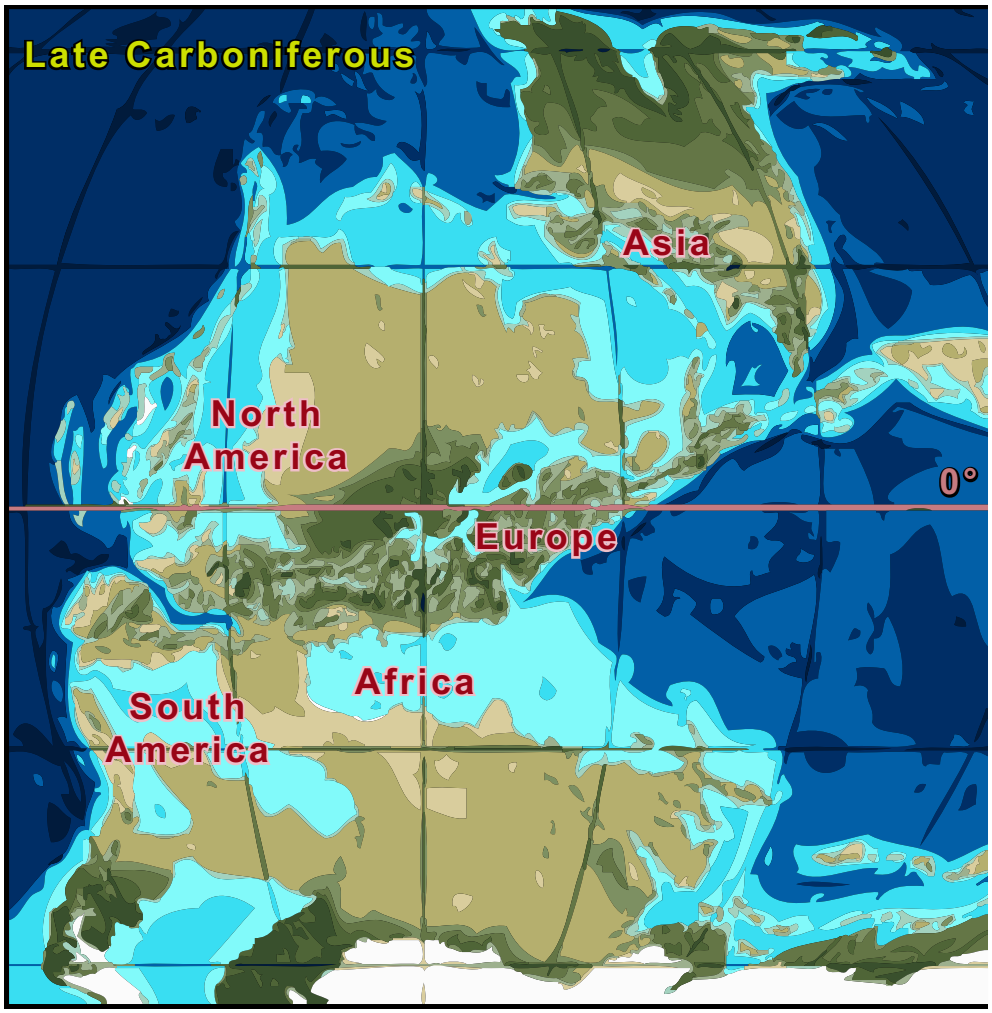

FIGURE 6 Landmass configuration in the Late Carboniferous (323–299 Ma), shown here at approximately 306 Ma (modified from publicly available PALAEOMAP Project images at www.scotese.com) [Colour figure can be viewed at wileyonlinelibrary.com]

supercontinent during the time of their origin (Figure 6). Much of this zone has become unsuitable for these arachnids—Europe and eastern North America are now colder and drier, North Africa is arid, and much of the exposed land has been submerged by various marine incursions due to the opening of the Atlantic Ocean. However, the far western end, which today extends from northern South America to the southern USA, remained warm and in most places moist, and lineages there gave rise to the present-day global diversity in each order.

An alternative hypothesis reduces the emphasis on the tropical juncture between the constituent landmasses of Pangea and simply postulates a Laurasian range for the ancestor to Thelyphonida. This is consistent with the fossil evidence, but it does require additional steps to be aligned with today's representatives of the group. First, thelyphonids today show a clear preference for tropical habitats, and as most of Laurasia was temperate, becoming increasingly so during the Mesozoic, their ancestor would likely come from the most southern regions of Laurasia. Indeed, this is where fossil stem-group forms have been found. Second, the deep placement of a South American species in the uropygid phylogeny—along with the West African species in trees from the parsimony analyses—suggests an origin for modern Uropygi that was closer to the tropical seam between South America, Africa and Laurasia than for Schizomida. If the origin of Uropygi were further north, with the extinction of early lineages due to habitat changes, we would expect *M. giganteus*, which is from North American arid subtropics, to be sister group to the remaining uropygids.

A significant outcome of the schizomid ancestral area reconstructions was the subset of areas that were never reconstructed as ancestral ranges, or if so, with very low probability. The Indo-Malay region, Pacific Islands and Australia had little influence on deep ancestral area reconstructions, despite having a significant schizomid fauna, and our West African specimens were always recovered as closely related to, but more derived than, certain New World lineages. Further collections may reveal old lineages in large places such as New Guinea and the Philippines, and whole regions of Africa and Asia remain poorly collected for schizomids. Still, we predict that the oldest lineages in each order will be from regions that were once part of tropical Pangea.

4.2 | Dating

Our estimate of an Upper Carboniferous origin for both Uropygi and Schizomida is consistent with their earliest known fossil representatives and the great antiquity of the major arachnid lineages (Dunlop, 2010). Our analyses (Figure 5) suggest that a mid-Cretaceous expansion of schizomids is the result of a constant speciation rate, perhaps tempered by density dependence. This latter assumption is reasonable, given that many present-day species appear to have resulted from ancient colonization of isolated habitats, such as small Pacific islands, which, once occupied, would not readily add new schizomid species.

4.3 | Dispersal

Stenochrus portoricensis and *Orientzomus* sp. "Pohnpei 3" demonstrate the ability of some species to maintain gene flow across large ranges, and they can clearly undergo long-distance dispersal, as demonstrated by the presence of this species of *Orientzomus* on remote Pacific islands. The fact that different islands in the Pacific Ocean have distinct species indicates that this ability to disperse is not necessarily mediated by human movements, perhaps representing another iconic taxon to exemplify Wilson's (1961) taxon cycles. Nonetheless, our collections on Pohnpei Island in Micronesia demonstrate that descendant lineages can quickly become restricted to small areas. *Orientzomus* sp. "Pohnpei 2" is genetically distinct on different sides of the island, despite these areas being only a few kilometres apart and connected by continuous forest (Appendix S3, Figure S3.8, in Supporting Information), and *O.* sp. "Pohnpei 3" is restricted to a reef island, just offshore from the high island.

This strange pattern of long-distance dispersal and restricted ranges, along with their remarkable abundance on Pacific islands, are consistent with two characteristics of schizomids: a common preference for disturbed habitats (e.g. Moreno-González, Delgado-Santa, & De Armas, 2014) and the frequent absence of males (suggesting parthenogenesis; Reddell & Cokendolpher, 1995). Schizomids could have quickly colonized emerging Pacific islands, and as their populations grew, further colonization attempts failed. For Pohnpei and many other islands, the only areas that would have offered new disturbed habitat for new colonists would be reef islets, which can become inundated during large storms.

4.4 | Contrasting patterns on Palau

Not counting Guam, for which we have limited collections, patterns of schizomid diversity in Micronesia roughly followed what would be expected from island sizes and proximity to major landmasses (Craig et al., 2001). The main islands of Palau (Appendix S3, Figure S3.8) have four species, and they also constitute the largest island group in the region after Guam (466 km^2) and are the closest group of Micronesian islands to the major landmasses of the Malay Archipelago. Islands which are more remote than Palau (Chuuk, 47 km^2 and around 1,500 km from New Guinea), or closer to large landmasses but very small (Merir, about 450 km from Indonesia but 1 km^2) have only one species. Yap and Pohnpei each have two species; the former is smaller than Palau but closer to major landmasses than Pohnpei, and the latter is nearly as large as Palau but even more remote than Chuuk.

Palau is not only closer to large landmasses and among the larger Micronesian islands, but at 30–40 Ma it is also 3–4 times older (except for Guam). Moreover, at the last glacial maximum (approximately 14,000 years ago), most of the archipelago would have been consolidated into a single island with 3–4 times the total land area of the contemporary archipelago (Appendix S3, Figure S3.8). Patterns of genetic diversity on Palau also contrast sharply with those on Pohnpei, with no discernable congruence between relatedness and locality on Palau. If the populations on Palau underwent allopatric divergence, as appears to be happening now on Pohnpei, any trace of that is now erased, as closely related sequences are often quite distant geographically. Palau's schizomids actually appear to have colonized the islands in multiple events, and perhaps their ancestral ranges included (or still include) the vast forests of New Guinea to the south or Mindanao to the west. Such a wide distribution is found in Palau today with *Orientzomus* sp. "Pohnpei 3," which appears to be a coastline, coralline and karst specialist throughout Micronesia.

4.5 | Future directions

We see four exciting new avenues of inquiry with Schizomida and Uropygi. First, our phylogenetic analyses can guide future taxonomic work and test hypotheses of morphological evolution. For example our analyses of just COI (Appendix S3), which include a large number of specimens for certain species, recover species as clades in most cases; however, genera were not always recovered as monophyletic (e.g. *Draculoides* and *Surazomus*), and certain specimens (e.g. *D. julianneae* specimens T63313 and T63314) do not appear to be closely related to most other specimens with the same identification. In addition, a key morphological question to pursue is determining what features of *S. sbordonii* led to its historical placement in *Stenochrus*, when it in fact appears to be more closely allied with *Agastoschizomus* and *Hubbardia* as one of the earliest diverging lineages in the order.

Second, the historical hypotheses for Schizomida and Uropygi presented here—not only the phylogenies but also their implied ancestral ranges and dates of origin and diversification—should be revisited in the future as more specimens with preserved DNA are acquired. On one hand, our sample here includes multiple specimens from nearly all of the regions where these animals are found, but on the other hand we did not sample the majority of named genera in each order. The number of new species and genera uncovered in our sample indicates the work still needed to capture the true scale of thelyphonid diversity in a phylogenetic analysis, and new lineages discovered in the future could easily change the scenario suggested by our analyses here.

Third, in line with the aforementioned goal of improving taxon sampling, the Megaschizominae should be placed in a molecular phylogeny as soon as specimens become available. The schizomid

biogeographical scenario resulting from our analyses is unlikely to change dramatically, due to the placement of Protoschizomidae and the early lineages of Hubbardiidae, but a key pending question is whether the megaschizomines are simply derived from Hubbardiinae.

Finally, despite schizomids enjoying considerable success in colonizing the Indo-Pacific, was this truly the result of a single migration from the New World? What were the routes they took to colonize the region, and how does this compare to the history of Asian uropygids? Large genomic datasets from carefully selected terminals, using our results here as a guide, should bring further clarity to the history of these often neglected but biogeographically interesting arachnids.

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BIOSKETCH

Ronald Clouse is interested in the histories of various leaf-litter arthropods, especially in the Indo-Pacific.

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SUPPORTING INFORMATION

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