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Historical biogeography and the evolution of habitat preference in the North American camel spider family, Eremobatidae (Arachnida:Solifugae)

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ABSTRACT

Abiotic variables can influence species distributions, often restricting taxa to an acquired climatic signature or conversely, related species are conserved in the same ecological space over millions of years. An investigation into how abiotic change has shaped geographic distributions of taxa may be key to understanding diversification of lineages, and in the absence of reliable morphological characteristics, such information may support taxonomic units at multiple scales.

Here, we examine the historical biogeography and patterns of habitat preference within the North American solifuge family, Eremobatidae. A previous study demonstrated that a major taxonomic revision of Eremobatidae is warranted, however recent studies demonstrate high levels of morphological convergence within the group, thus a re-classification of generic boundaries using additional information must be prioritized before we can formally begin solid revisionary efforts. In this study, we aimed to reconstruct a well-resolved phylogenetic hypothesis of Eremobatidae by filtering UCE loci based on informativeness, by mitigating the effect of cogenic UCE on phylogenetic estimation, and by supplementing our curated UCE loci with mitochondrial information. Using our preferred topology, in conjunction with published estimated divergence dates for Eremobatidae, we inferred a time-calibrated phylogenetic hypothesis to inform the historical biogeography and patterns of habitat preference. The two major habitat types that were observed for Eremobatidae were warm deserts for early diverging taxa and a subsequent evolution to cold deserts and Mediterranean California ecoregions for later diverging taxa. Eremobatid niche space, determined by temperature and precipitation, has been conserved for at least 25 million years in North America, supporting a warm desert origin, and thus supporting high species richness in the Sonoran and Mexican Plateau. Overall, our study provides support for new generic level designations within Eremobatidae.

1. Introduction

Historical climatic oscillations have undoubtedly influenced current species distributions and genetic diversity. Modern extant populations that have persisted for millennia likely have endured periods of diversification and extinction due to an expansion or contraction of habitat availability caused by climate change. During Pleistocene glacial periods in the Northern Hemisphere, for example, contemporary species may have survived in fragmented, localized habitats, where climate was relatively stable compared to the surrounding areas (Harrison & Noss 2017). These historical climatically stable areas, known as Pleistocene refugia, house many genetically diverse, highly endemic taxa (Zink 2002; Ayoub & Riechert 2004; Riddle & Hafner 2006; Rebernig et al. 2010; Jezkova et al. 2011; Wilson & Pitts 2010b, 2012). Populations that survived in these refugial pockets were an important factor in shaping species diversification following the Pleistocene glacial periods. On the other hand, during the Holocene epoch, many desert-affiliated taxa exhibited range expansions as suitable habitat became available, subsequently leading to species diversification (Hewitt 1996, 2000; Ayoub & Riechert 2004; Bryson et al. 2013; Cushing et al. 2015; Fiorini de Magalhaes et al. 2019; Garcia et al. 2020). Thus, climate variables can influence species distributions, often restricting species to a preferred climatic niche or conversely, related species may remain in the same ecological space over long geological time. Niche divergence or niche conservatism (Harvey & Pagel 1991; Peterson et al., 1999) can have important implications when studying evolutionary questions and

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biogeographic patterns of diversification. Moreover, climate niche models, integrated with dated phylogenetic information, may illuminate patterns of speciation and niche evolution. Therefore, in the absence of diagnostic morphological characters, additional ecological information, may be adequate for informing taxonomic boundaries.

Solifuges, colloquially known as camel spiders or wind scorpions in North America, are the sixth largest order of arachnids with ~ 1,100 species described (Harvey 2003). Many arachnid groups are typically opportunistic, ambush predators with low metabolism (Anderson 1970; Lighton et al. 2001). Solifuges, on the other hand, are distinct from other arachnid groups due to their active predation strategies, consistent movement during short windows of activity, and semi- or impermanent burrowing behaviors (Muma 1966a). Solifuges are distributed on all continents, except for Australia and Antarctica and are often associated with arid environments, thus are considered indicators of desert habitats (Cloudsley Thompson, 1977). Solifuges, moreover, are among the most ancient arachnid lineages (~300 MYA; Selden & Shear, 1996; Kulkarni et al. 2023), and thus are an ideal system for studying adaptation, evolution, and diversification of taxa in ancient biomes. Until recently, several researchers have made devoted efforts to formally begin to understand the evolutionary history of this enigmatic group by adopting modern techniques necessary for taxonomic delimitation (Cushing et al. 2015; Maddahi et al. 2017; Santibáñez-López et al. 2021; Kulkarni et al. 2023). With robust phylogenetic hypotheses and genomic data, we can begin to conduct taxonomic revisions for all solifuge families on the basis that such revisions aim to reflect patterns of common ancestry inferred by phylogenies. The application of modern techniques for taxonomic delimitation using fresh and existing material, such as those housed in natural history museums, grants researchers sufficient sampling coverage for evolutionary studies.

The North American solifuge family, Eremobatidae Kraepelin 1899 is one of the most diverse family of solifuge with nearly 200 species and eight genera described (World Solifugae Catalog, 2022) and are primarily distributed in arid habitats throughout the southwestern Canada,

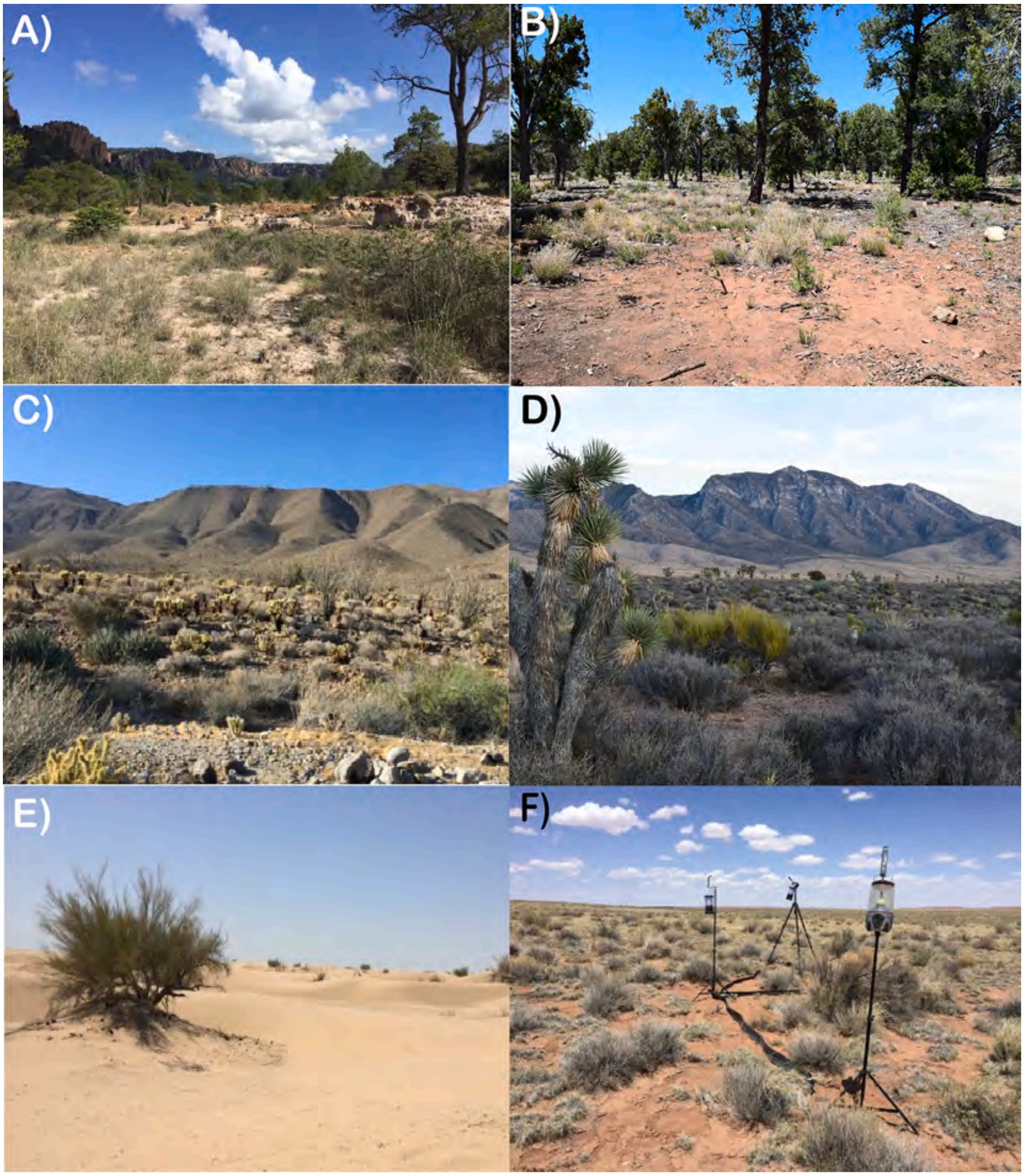

Fig. 1. Example variation of solifuge habitats A) Pine-oak Forest, Parque Nacional Sierra de Órganos, Zacatecas, México B) Pinyon-juniper Forest, Grand Canyon National Park, Arizona, USA C) Sonoran Desert, Anza-Borrego National Park, California, USA D) Mojave Desert, Lovell Canyon, Nevada, USA E) Sand dunes, Imperial Sand Dunes, California, USA F) Grasslands, Petrified Forest National Park, Arizona, USA.

western United States, and Mexico (Fig. 1). In a recent study by Garcia et al. (2024), results unveil the presence of high levels of convergence within the group, with multiple independent origins and losses of many morphological characteristics. In the case of eremobatid taxonomy, morphology alone is unable to resolve important underlying patterns that have helped promote the diversification of genera and species. Distinguishing historical and current distributional boundaries of eremobatid taxa can: 1) help to identify potential hybrid zones, 2) provide an idea of dispersal capabilities among eremobatids, or 3) illuminate areas of historical vicariance events or geodispersal (the erosion of historical vicariant barriers; Lieberman, 2005) that have shaped the species diversity in this group. Therefore, as an ongoing effort to revise eremobatid taxonomy, the goal of this study was to broadly investigate historical biogeographical patterns of eremobatid taxa.

Only thirteen species of eremobatids from deserts of the southwest United States have published ecological associated data, eight species of which belong to *Eremobates* (Muma 1966a, 1966b, 1967, 1974; Punzo, 1994, 1995, 1997, 1998). Although, information on solifuge life cycles, phenology, and other ecological features associated with seasonal adaptation are limited, of the available studies, several researchers independently allude to seasonal and habitat partitioning within Eremobatidae. For example, researchers have published on the relative abundance of solifuges, and such observations converge on the idea that solifuges are abundant in certain areas at certain times of the year (Roewer 1934; Mello-Leitão, 1938; Cloudsley-Thompson 1961; Martins et al. 2004). Similarly, in a two-year study of eremobatid solifuge population sizes in southwestern New Mexico, Muma (1974) noted seasonal differences among eremobatid species and suggested possible habitat preference tendencies among the species found in the two focal life zones. In terms of habitat tendencies, *Eremobates* were found predominately in arid grasslands; however, some of the same species were found in pinyon-juniper forests, yet in reduced numbers. *Hemerotrecha fruitana* Muma 1951, a comparatively smaller species than *Eremobates* species, was found strictly in the pinyon-juniper life zone and is suspected to be a montane species by Brookhart (1972). Empirical evidence of two eremobatid species in this same study, *H. fruitana* and *Eremobates norrisi* Muma & Brookhart 1988 (species undescribed in Muma 1974), alludes to possible ecological partitioning despite overlapping temporal occurrences. Peak abundance times for *H. fruitana* and *E. norrisi* were reported to be during March-May and April-May, respectively. Muma (1974) suggested that the presumed optimal habitat for *E. norrisi* was the arid grassland, in contrast to *H. fruitana*, perhaps due to slightly more individuals collected in the grassland habitat compared with the pinyon-juniper life zone. Thus, of the available knowledge of solifuge ecology and present knowledge gaps, solifuges are an interesting study system to investigate how abiotic patterns may have impacted taxonomic diversity.

To critically examine the historical biogeography and patterns of habitat preference using climate variables, the goal of this study was to investigate if such abiotic signatures are useful in aiding taxonomic revision of Eremobatidae. It is worth noting, however, that *Eremochelis* and *Hemerotrecha* historically served as a taxonomic depository for non-*Eremobates* species and taxonomic efforts over the last several decades have focused primarily on the larger taxa like *Eremobates* (Brookhart & Muma 1981; Muma & Brookhart 1988; Cushing & Brookhart 2016), *Eremorhax* (Brookhart & Muma 1987), and *Eremocosta* (Cushing et al. 2018). In terms of *Eremochelis* (38 species) and *Hemerotrecha* (34 species), these two genera present a hefty taxonomic endeavor due to their neglected taxonomic history, and a lack of updated characters necessary for accurate taxonomic identification. Therefore, we reconstructed a well-resolved phylogenetic hypothesis from UCE data by applying several analytical approaches for estimating phylogenetic relationships with focus on *Hemerotrecha* and *Eremochelis* taxa to assess the robustness of recovered clades and higher-level relationships of such clades within Eremobatidae. Using a preferred phylogenetic hypothesis, in conjunction with an estimation of molecular divergence times, we explored large-scale biogeographic patterns that may have influenced eremobatid diversity using occurrence records from natural history collections to leverage our biogeographical study. The exploration of ecological adaptation by means of analyzing abiotic factors will formally advance our knowledge of a historically neglected arachnid taxon and facilitate ongoing efforts to revise eremobatid taxonomy.

2. Materials and methods

Taxon sampling for this study included fresh specimens collected from field sites across North America as well as museum collections from the following institutions: Denver Museum of Nature and Science (DMNS), California Academy of Sciences (CAS), American Museum of Natural History (AMNH), University of Arizona (UA), College of Idaho Orma Smith Natural History Collection (CIDA), Colección Arachnológia del Centro de Investigación Biologicas Del Noroeste, S.C. (CARBIO), Essig Museum of the University of California Berkeley (ESS), Colección Naciónal Arácnidos Instituto de Biología de la Universidad Naciónal Autónoma de México (CNAN), the San Diego Natural History Museum (SDNHM), and the Florida State Collection of Arthropods (FSCA). Freshly caught specimens were prioritized for extraction of ultraconserved element (UCEs; Bejerano et al., 2004; Faircloth et al. 2012) and taxon sampling was leveraged by the inclusion of museum specimens. For biogeographical analysis, we then isolated the geographical data for solifuge records for each terminal in our UCE phylogeny Figure Supplementary Fig. 1 and for every record available for each focal taxa in our study.

To assign coordinate data to museum records that did not have associated coordinate data from the original collection event, we used GEOlocate (Rios & Bart 2010). This platform is specific for georeferencing collections data and estimates geographic coordinates in decimal degrees using the World Geodetic Survey 1984 (WGS84) datum from a provided locality string. Museum records, such as type localities that were documented to cover a large area (e.g., *Eremochelis medialis*, Muma 1951 California, USA) were not considered for georeferencing as broad geographic localities can cover multiple habitat types.

For downstream biogeographical and phylogeographical, we extracted climate and ecoregion values for all terminal taxa in our working phylogeny (Supplemental Information 2). First, we attained current climate data from WorldClim version 2.1, which represents 1970–2000, for the 19 bioclimatic variables and for the available monthly climate data (Fick & Hijmans 2017). For each coordinate pair pertaining to our ingroup taxa, we extracted climate data using the extract function found in the raster package in R (Hijmans, 2023). Level II and III ecoregion values were extracted from each coordinate pair using the United States Environmental Protection Agency (U.S. EPA) Ecoregions of North America shapefile (https://www.epa.gov/eco-research/ecoregions-north-america).

2.1. Ultraconserved elements and phylogenomic analyses

We utilized the next-generation sequencing data acquired from Garcia et al. (2024; SRA; BioProject PRJNA982881), where details on genomic DNA isolation, library preparation, and processing are provided. However, in this study, we removed the following taxa due to suspected contaminated sequences caused by poor preservation or age of the specimen: DMNS ZA.16137 *Eremochelis truncus*, ALBRCIDA3712 *Eremochelis sp.*, DMNS ZA.16782 *Hemerotrecha prenticei* and CIDA107991 *Eremochelis* sp. Recovered UCE loci were aligned using default settings in MAFFT (Katoh & Standley 2013) and were trimmed internally using TrimAI (Capella-Gutiérrez et al. 2009) with a gap-threshold value of 0.2 as recommended by Portik & Wiens (2021). To further consider for possible misalignments introduced by MAFFT and gap only columns, we used CIalign (Tumescheit et al. 2022) under a 70 % minimum identity threshold due to the distant relatedness of the selected outgroups. The application of this threshold ensures that columns within the alignment matrix are removed.

We used a moderate gene occupancy matrix (75 %) approach for our concatenated phylogenetic inference using the gene occupancy approach as the relationship of occupancy matrices is inversely related: Low-occupancy data sets contain larger amounts of UCE loci and high-occupancy matrices consist of more missing data (Kulkarni et al. 2021). It is worth noting that such gene occupancy data matrices, however, may not include all taxa of interest. If some key taxa and loci are not represented in the dataset, the exclusion of informative taxa and loci may be detrimental to phylogenomic estimation, thus producing inaccurate results (Dell'Ampio et al. 2014). Therefore, to reduce bias and the potential for systematic error in phylogenomic estimation a priori, we invoked several approaches, in addition to generating occupancy matrices, for phylogenomic estimation.

One of the key assumptions of coalescent-based phylogenetic estimation, and other common phylogenetic analyses, assumes that that the input loci are conditionally independent, meaning that such loci have indistinguishable linkage (Liu & Pearl, 2007; Bryant et al. 2012). The inclusion of more independent loci in coalescent-based analyses is important for attaining improved nodal support and increased confidence in a topology (Edwards et al. 2007; Mossel & Roch, 2007; Heled & Drummond, 2010). Violating the assumption of non-independent loci can lead to inaccurate and biased topologies. Therefore, to reduce the effect of bias in our coalescent-based analyses, we characterized the Arachnid probe set 1.1 K version1 kit (Daicel Arbor Biosciences) by genomic identity using a bark scorpion genome (*Centuroides sculpturatus* (Wood 1863), Accession Number: PRJNA168116; i5K Consortium, 2013) following the methods of (Van Dam et al. 2020) and using BLATq version 1.0.2 (Kent, 2002). In this outlined method, UCE loci are positionally located in the referenced genome and are characterized by genomic feature (e.g., intronic, exonic, intergenic). Cogenic UCE loci, otherwise non-independent determined by their location on the same gene, were subsequently merged to represent a single independent locus. Cogenic loci were merged using the *phyluce_align_concantenate_alignments* function found in the PHYLUCE (Faircloth, 2016). It is worth noting that the characterization of arachnid probes depends on the selected reference genomes (Hedin et al. 2019); however, due to the limited availability of arachnid genomes and the instability of Solifugae placement across Arachnida, we believe that this genome selection was suitable for our purpose. Following the concatenation of cogenic loci, we used such data sets for downstream coalescent-based phylogenetic estimation.

Parsimony informative sites (PIS) is a useful metric as it is often correlated with evolutionary rate and phylogenetic performance (López-Giráldez et al. 2013; Mclean et al. 2019). For example, a low number of PIS for a UCE locus would suggest a slow evolutionary rate, thus high sequence conservation, and vice versa for highly informative sites. Therefore, to determine the integrity of recovered phylogenetic clades, we created two subset UCE datasets that represented the top 300 parsimony informative loci and the bottom 300 parsimony informative loci. PIS for each UCE locus were determined using the pis function in the phyloch R package (Heibl, 2008). All parsimony informative datasets generated were implemented in coalescent-based phylogenetic estimation.

Despite the intended design of target capture in UCE methodologies, mitochondrial DNA (mtDNA) are generally sequenced alongside UCE loci as by-product (Allio et al. 2020; do Amaral et al. 2015). In target capture studies, mtDNA sequences are often abundant in sequencing results, providing the opportunity to reconstruct complete, or nearly complete, mitogenomes (do Amaral et al. 2015; Zarza et al. 2018; Imfeld et al. 2020). Therefore, to supplement our UCE data matrices, we used MitoFinder (Allio et al. 2020), bioinformatic pipeline specifically designed to extract mitochondrial sequences from UCE libraries, to extract cytochrome oxidase I (COI) loci from UCE assemblies to generate a UCE+COI concatenated dataset.

2.2. *Phylogenomic inference*

We analyzed our UCE datasets using Maximum likelihood (ML), Bayesian, and coalescent-based approaches to generate several phylogenetic hypotheses. First, for an ML approach, best-fit models of evolution were identified using ModelFinder (Kalyaanamoorthy et al. 2017) and phylogenetic estimation was performed in IQ-TREE 2 (Minh et al. 2020) with ultrafast bootstrap approximation using our concatenated 75 % occupancy matrix and 75 % occupancy UCE+COI matrix. As an additional ML approach, we executed a RaxML (Stamatakis, 2014) analysis using the same 75 % gene occupancy matrix with implemented rapid bootstrapping and a GTRGAMMA model of evolution to attain the best-scoring ML tree. For Bayesian approaches to phylogenetic estimation, we used PhyloBayes 4 (Lartillot et al. 2009) using the same datasets as our IQ-TREE analyses. In Phylobayes, two chains were run in parallel, stopping after 30,000 points and sampling every 30. We discarded the first 6,000 points as burn-in and assessed convergence by ensuring that the maxdiff value was < 0.1 using the bpcomp command (Lartillot et al. 2009). For coalescent-based phylogenetic estimation, individual gene trees using the merged UCE datasets, top 300 PIS, and bottom 300 PIS were also estimated in IQ-TREE 2 with ModelFinder. Inferred gene trees were then used as input in ASTRAL-III v 5.7.8 (Zhang et al. 2018) and nodal support values were summarized by local posterior probabilities approximated by gene tree quartet frequencies (Sayyari & Mirarab 2016).

2.3. *Estimation of divergence times*

To estimate divergence times and to minimize the effect that highly variable sequences have on divergence estimation (Babkin & Babkina, 2011), we further trimmed our genomic matrices using trimAI by applying the strict method, which removes remaining columns that consist of gaps only, and removes highly variable sequences based on a logarithmic similarity distribution (Capella-Gutiérrez et al. 2009). We carried out estimation of divergence times using the RelTime-ML method implemented in MEGA4 (Tamura et al. 2007, 2012) using secondary calibrations published for Eremobatidae by Cushing et al. (2015) and Kulkarni et al. (2023). In this method, divergence estimates are inferred by estimating branch-specific divergences by assuming that the relative rate of divergence between two sister lineages is equal (Tamura et al. 2012). Since fossil calibrations are unavailable for Eremobatidae and geological calibrations are controversial due to the assumption that genetic divergence is connected to geological events (Ho & Duchêne, 2014), we believe that this method is useful for establishing a divergence time framework. Therefore, we considered two secondary calibrations for Eremobatidae from previously published works: a mean of 32.2 million years ago (Ma) estimated from Cushing et al. (2015) and 135.53–230.77 Ma estimated from Kulkarni et al. (2023). For the first secondary calibration for the time to most recent common ancestor (tMRCA), we used a lognormal distribution with an offset of 32 and standard deviation (SD) of 1, which summarized the divergence time distribution with a 95 % CI of 32.14–39.10 million years. We constrained the UCE+COI dataset to a slightly older lognormal distribution by specifying the parameters of an offset 32 and SD of 1.25, which 95 % CI divergence time of 32.09–43.63 million years. Lastly, we generated a third time-calibrated phylogenetic hypothesis using the much older divergence time of Kulkarni et al. (2023) using a lognormal distribution, offset of 135 and SD of 2.32 to generate a 95 % CI of 135.01–229.36. For the latter calibration, we used the UCE only dataset.

2.4. *Ancestral geographic ranges*

Ancestral geographic ranges for our ingroup eremobatid taxa were reconstructed using our preferred RelTime time tree and Level III ecoregion using BioGeoBEARS (Matzke 2018) in R. We reconstructed the ancestral ranges using the time-calibrated phylogeny inferred by using the Cushing et al. (2015) secondary calibration and by removing outgroups, as the inclusion of distantly related outgroups may introduce bias in ancestral states. Additionally, as suggested by Matzke (2018), we removed terminal taxa so that all terminals represented independently evolving species lineages as the use of multiple individuals of the same species can favor DEC+j models. We then fitted six ancestral geographic range models: DEC, DEC+j, DIVALIKE, DIVALIKE+j, BAYAREALIKE and BAYAREALIKE+j and selected the best-fit model determined by the lowest Akaike information criterion (AIC). Each of these models assume different biogeographical processes, such as cladogenetic events promoted by sympatric or vicariant events, or anagenetic events such as extinction or expansion into new habitats. The + j variants of such models are a parameter of founder event dispersal, otherwise known as jump dispersal, to formerly isolated geographic regions (Matzke 2018). Due to the limited knowledge on solifuge dispersal, particularly if they are capable of long-distance dispersal, we considered the + j parameter, in addition to the other biogeographical models.

2.5. Environmental distribution modeling

We identified several monophyletic clades that were consistently recovered in Garcia et al. (2024); Table 1) and sought to investigate both current and past habitat signature profiles for the representative taxa within each clade. To estimate potential distributions of our assigned clades, we curated our occurrence datasets to remove duplicate records, in addition to filtering each occurrence for each respective clade assignment by a 1 km2 radius using the 'filterByProximity' function from the R package, 'rangeBuilder' (Rabosky et al. 2016) to avoid overfitting model performance and reduce the effect of sampling bias (Radosavljevic & Anderson, 2014; Boria et al. 2014).

To reconstruct current distribution models for each clade assignment, we used bioclimatic variables derived from WorldClim version 2.1 (Fick and Hijmans, 2017). To investigate relatively recent patterns of niche evolution, we reconstructed paleo-climate distribution models using the WorldClim 1.4 databases for paleo- and associated current climate conditions (Hijmans et al. 2005). For paleoclimate conditions, we downloaded the available 19 Bioclimatic variables for mid-Holocene (~6,000 years before present) at 30 s resolution and Last Glacial Maximum (LGM; ~21,000 years before present) data at 2.5 min resolution from CCSM4 sources. For resolution consistency in model projections, we downloaded the available 19 Bioclimatic variables for current (1970–2000) at 30 s for mid-Holocene and 2.5 resolution for LGM. All raster layers were subsequently cropped to the extent of the known range for all our ingroup taxa.

We conducted a Pearson's correlation analysis for the downloaded and cropped bioclimatic variables using the removeCollinearity function found in the virtualspecies R package (Leroy et al. 2016) as the inclusion of redundant variables promotes false predictions and overparameterization. We applied a correlation threshold of 0.75 and selected one variable out of the set of highly correlated variables for downstream distribution models.

We fitted a series of Maxent model settings using the ENMevaluate function found in the ENMeval R package (Muscarella et al. 2014) for current climate data at both resolutions to improve model predictive performance. Due to our interest in estimating predictive models across geological time scales, we built a series of models implementing the 'block' partitioning method as suggested by Muscarella et al. (2014). We considered a combination of five feature classes: Linear, (Linear + Quadratic), (Linear + Quadratic + Product), (Linear + Quadratic + Hinge) and evaluated regularization multiplier (RM) values ranging from 1 to 5. Best-fit model settings were selected based on the smallest ΔAICc value. Environmental niche models (ENMs) were constructed in Maxent v 3.4.0 (Phillips et al. 2017) using the recommended settings inferred by ENMevaluate.

We reconstructed paleo-climate models using resolution-compatible climate data projected onto paleoclimate conditions. We used the cross-validate replicated run type, minimum training presence threshold, 10,000 maximum iterations, ran each for 10 replicates, and used the cloglog output format option for all Maxent runs for each respective clade assignment. Final niche distribution plots were summarized as presence/absence plots using the median ascii output files and the suggested the 10 percentile cloglog threshold.

Table 1

Clade assignments based on recovered relationships from Garcia et al. (2024) and in our preliminary phylogenomic hypotheses. Clade assignments are based on monophyletic grouping and shared morphological characteristics. Genomic data for each species in this study that represent each clade and associated taxon author for each valid species are indicated after the species name.

Clade Assignments	Species representatives
A	new genus, new species
B	*Eremochelis andreasana* Muma 1951
C	*Hemerotrecha bixleri* Muma 1989, *Hemerotrecha* sp. (branchi group), *Hemerotrecha marathoni* Muma 1962, *Hemerotrecha macra* Muma 1951, *Hemerotrecha sevilleta* Brookhart & Cushing 2002, *Hemerotrecha cornuta* Brookhart & Cushing 2002, *Hemerotrecha branchi* Muma 1951, *Hemerotrecha xena* Muma 1951 *All species here belong to the *Hemerotrecha branchi* species group established by Muma in 1951
D	*Eremochelis albaventralis* Brookhart & Cushing 2005, *Eremochelis cochiseae* Muma 1989, *Eremochelis bilobatus* Muma 1951
E	*Horribates* spp. Muma 1951
F	*Eremobates sp, Hemerotrecha nr neotena, Eremobates aztecus* Pocock 1902, *Eremobates acuitlapanensis* Vazquez & Gavino-Rojas 2000, *Eremobates gracilidens* Muma 1951, *Eremorhax joshui* Brookhart & Muma 1987, *Eremobates leechi* Muma & Brookhart 1988, *Eremobates titschacki* Roewer 1934
G	*Eremochelis plicatus* Muma 1962, *Chanbria serpentinus* Muma 1951, *Chanbria rectus* Muma 1962, *Chanbria regalis* Muma 1951
H	*Eremochelis imperialis* Muma 1951, *Eremochelis texana* Muma 1951, *Hemerotrecha serrata* Muma 1951
I	*Eremochelis kerni* Muma 1989, *Eremochelis giboi* Muma 1989, *Eremochelis nr giboi, Eremochelis acrilobatus* Muma 1962, *Eremochelis flexacus* Muma 1963, *Eremochelis branchi* spp.
J	*Hemerotrecha* sp. *denticulata* group, *Hemerotrecha delicatula, Hemerotrecha parva, Hemerotrecha proxima, Hemerotrecha denticulata, Hemerotrecha nr carsonana* *All species belong to the *Hemerotrecha denticulata* species group
K	*Hemerotrecha* sp. (*simplex* species group), *Hemerotrecha elpasoensis* Muma 1962, *Hemerotrecha fruitana* Muma 1951, *Hemerotrecha* sp.
L	*Eremochelis nudus* Muma 1963, *Eremochelis bidepressus* Muma 1951, *Eremochelis oregonensis* Brookhart & Cushing 2002, *Eremochelis undulus* Muma 1989, *Eremochelis larreae* Muma 1962
M	*Eremochelis* sp., *Eremochelis insignitus* Roewer 1934
N	*Eremochelis morrisi* Muma 1951, *Eremochelis striodorsalis* Muma 1962, *Hemerotrecha banksi* Muma 1951, *Hemerotrecha californica* Banks 1899, *Hemerotrecha kaboomi* Brookhart & Cushing 2008, *Hemerotrecha pseudotruncata* Brookhart & Cushing 2008, *Hemerotrecha vetteri* Brookhart & Cushing 2008, *Hemerotrecha hanfordana* Brookhart & Cushing 2008, *Hemerotrecha prenticei* Brookhart & Cushing 2008, *Hemerotrecha* sp. (*banksi* species group)

2.6. Multivariate analysis of climate variables, predicted niche occupancy, ancestral climate tolerances

A principal components analysis (PCA) was performed using the *prcomp* function in R for the climate values pertaining to the input coordinate data to visualize general phyloclimatic patterns. Climatic variation in climate space was summarized by assigned clade and visualized using the first two PCs.

We integrated our preferred phylogenetic hypothesis and niche models estimated from Maxent to elucidate patterns of niche evolution among our assigned clades. Since climate niche profiles often deviate from normal distributions, and thus summary statistics of central tendency and variance may not accurately encapsulate niche tolerances, we generated predicted niche occupancy (PNO) profiles for each clade of interest as proposed by Evans et al. (2009). In this method, suitability probabilities generated from Maxent are combined with single climate variables to infer multimodal summary distributions of climate tolerance for a given taxon. Under this approach, we estimated habitat suitability for each clade assignment in Maxent, limiting our analyses to the non-correlated bioclimatic variables, and building distribution models using the parameters suggested by our model testing from ENMeval. Next, we extracted PNO profiles using the pno function in the phyloclim package (Heibl et al. 2013). Using our generated predicted niche occupancy (PNO) profiles for each clade assignment and our UCE+COI ultrametric phylogeny, we estimated ancestral niche tolerances under a maximum likelihood, nonparametric approach using the anc.clim function found in the phyloclim R package (Evans et al. 2009; Heibl et al. 2013). This method assumes a Brownian model of evolution. To generate the ancestral niche tolerances, we performed 100 replicates from each of the clade's PNO profile and summarized the results using the plotAncClim found in the same R package. Niche overlap for the models of interest were quantified using the niche.overlap function in the phyloclim package (Heibl et al. 2013).

3. Results

3.1. Genomic characterization of arachnid probes and phylogenomic matrices

We characterized the Arachnida probe set introduced by Starrett et al. (2017) using the genome of *Centruoides sculpturatus*, which resulted in 602 UCE loci pertaining to exons, 185 to introns, 22 spanning both exon and introns, and 20 to intergenic segments. After screening the

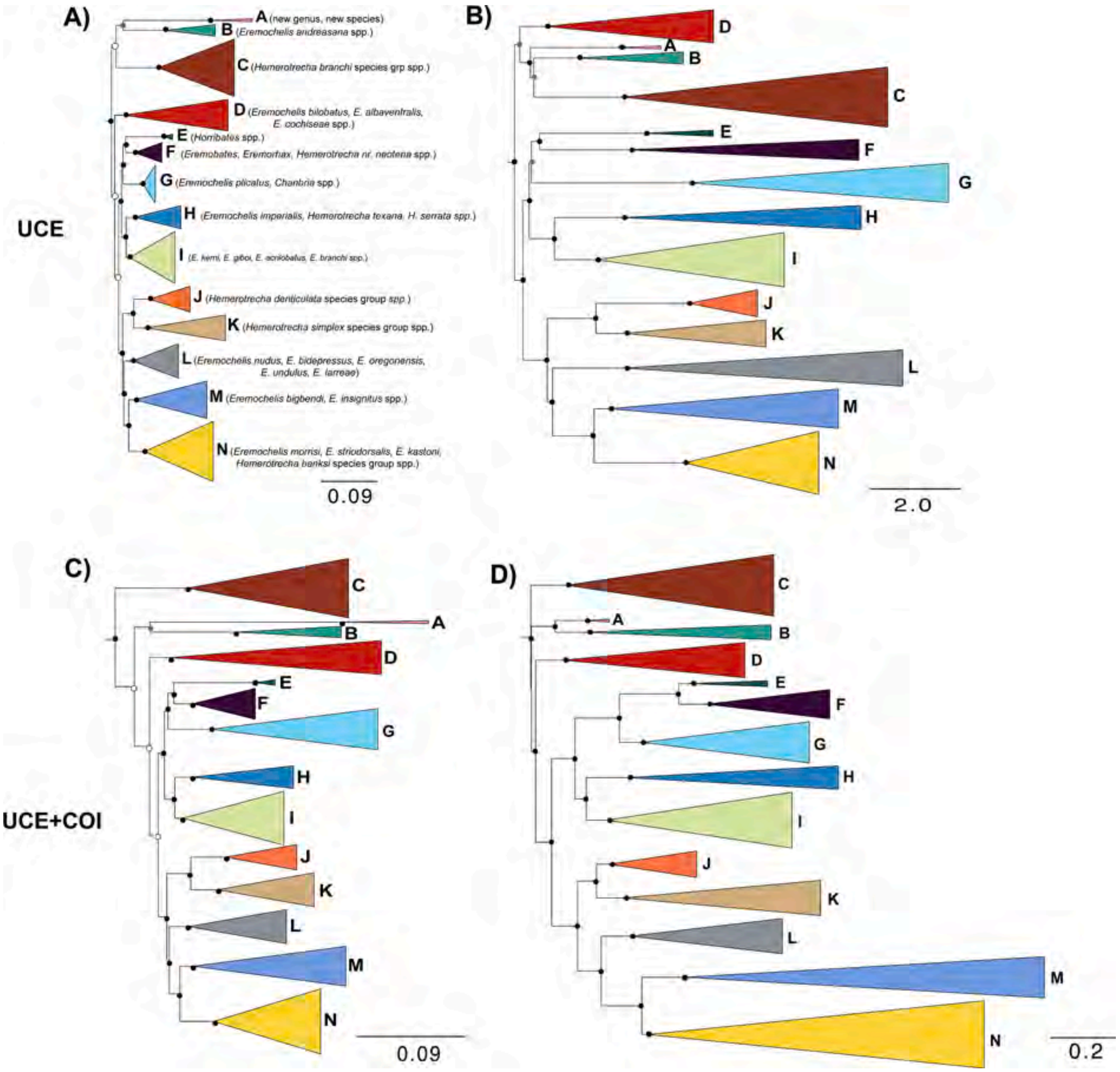

Fig. 2. Altering phylogenomic hypotheses across different input sequence matrices and phylogenomic estimation approaches. **A)** Phylogenomic hypothesis using a 75 % completeness matrix estimated under a maximum likelihood approach in IQ-TREE2. Scale bar refers to the average number of substitutions per site. Circles on nodes are indicative of bootstrap support values. We have included some of the exemplar species of each clade for reference. **B)** Coalescent-based phylogenomic hypothesis estimated from the independent and merged cogenic UCE loci in ASTRAL. Scale bar refers to the branch length scale in coalescent units. Circles on nodes indicate local posterior probabilities estimated based on gene tree quartet frequencies in ASTRAL. **C)** Topology estimated using the 75 % completeness matrix with complementary UCE loci estimated in IQ-TREE2. Circles on nodes refer to bootstrap support. **D)** Bayesian topological hypothesis estimated in Phylobayes using 75 % completeness matrix with complementary UCE loci. Circles on nodes indicate posterior probabilities. In all panels, black nodal circles refer to posterior probabilities or bootstrap support values of $> 95/.95$, grey circles $> 71/.71$, white circles $\leq 70/.70$. Recovered clade assignments are illustrated by unique color.

genomic affinities for the Arachnid probe set, 109 sets of loci, comprising 297 individual UCE loci were determined to be cogenic loci. However, from our total recovered UCEs, we merged 225 loci as they spanned the same exon. We subsequently attained 769 unique loci for downstream coalescent-based analyses from the recovered loci rendered from our ingroup taxa.

The number of terminals for the UCE phylogeny in the 75 % coverage matrix recovered 166 terminal taxa after removing old museum samples that were suspected to be represented by damaged DNA. For the UCE+COI dataset, we utilized the taxa recovered from the 75 % matrix and the COI sequences isolated from our next-generation sequencing efforts to generate a representative matrix of 180 terminal taxa for input in our phylogenomic analyses.

3.2. Phylogenomic relationships of eremobatid taxa

The results of the phylogenetic analyses under the several analytical approaches in this study consistently support many of the clade assignments from Garcia et al. (2024; Fig. 2; Supplemental Figure S2; Table 1). However, despite this result, across the different input matrices and phylogenetic reconstruction analysis approaches, the deeper level relationships beyond our clade designations were inconsistent. First, one major phylogenetic incongruence that was observed was for the bottom 300 parsimony informative loci data set. This result is expected due to the lack of information provided by conserved sequences; thus, the data set is unable to resolve some cladogenetic events. Nonetheless, despite several odd placements of individual taxa and discordance between the interrelationships of the clades, most of original clade designations were recovered, save four (Fig. 2B). Some of those clades that were not recovered or lacked support entirely included Clade A, Clade D, Clade E, Clade K. For each of those mentioned clades, the two putative new genus representatives forming Clade A were in disparate parts of the tree, *Eremochelis cochiseae* Muma 1989 + *Eremochelis albaventralis* Brookhart & Cushing 2005 were not included in Clade D, the relationships between the *Horribates* Muma 1962 resulted in a polytomy, and *Hemerotrecha fruitana* Muma 1951*, Hemerotrecha elpasoensis*, *Hemerotrecha* sp. (simplex species group), members forming clade K were also located in discordant parts of the tree (Fig. 2B). However, when considering the top 300 parsimony informative loci, the phylogenetic relationships and clade assignments mirrored those estimated in Garcia et al. (2024; Supplemental Figure S2 A). Similarly, the top 300 phylogeny recovered the relationship between Clade A and B and the monophyletic relationship between clades D-F with low support (Supplemental Figure S2B).

The phylogenomic results from the differing input data sequence matrices and subsequent phylogenomic approaches all produced distinct topological hypotheses (Fig. 2). First, the 75 % completeness matrix analyzed in IQ-TREE2 resulted in the same phylogenetic relationships as the Garcia et al. (2024) topology despite correcting for misalignments and removing taxa with presumably old DNA sequences (Fig. 2A). In this topology, all assigned clades were recovered with bootstrap support values > 95, however, several of the backbone nodes were recovered with weak support (≤70). Next, the topology estimated from our merged UCE dataset and a coalescent-based approach resulted in a distinct phylogeny compared to the others in Fig. 2B. Although the descending evolutionary relationships were conserved between clades E-N, this topology was the hypothesis to have Clade D as the earliest diverging lineage (Fig. 2B). This clade, containing species representatives for *Eremochelis cochiseae*, *E. albaventralis*, and multiple independent lineages of *E. bilobatus* also formed a moderately supported (>70) clade with clades A, B, and C – a relationship only recovered in this tree. Moreover, many of the nodes were supported by high local posterior probability values. When examining the topologies estimated using our UCE+COI dataset, Clade C was the earliest derived independent lineage in contrast to the phylogenies presented in Fig. 2A and Fig. 2B (Fig. 2C & D). Additionally, these two presented topologies included Clade D and an independently derived lineage, with Clades A and B as sister lineages. Despite some of the major differences in each of the inferred topologies in Fig. 2, some of the consistencies include clades E-I and J-N forming well-supported clades, respectively, with clades E-I descending earlier than clades J-N. Other than the bottom 300 PIS topology, our outcomes suggests that Clade N, a clade that is formed by *Eremochelis morrisi, E. striodorsalis, E. kastoni*, and members of the *Hemerotrecha banski* species group is likely the most recently derived eremobatid lineage.

3.3. Divergence dating and ancestral geographic ranges

We estimated the age of eremobatid taxa using our UCE+COI dataset under two different divergence hypotheses. The 95 % confidence interval (CI) divergence estimate of Eremobatidae using the Cushing et al. (2015) estimated age for the family was between 32.4906–41.2398 million years during the Eocene. Alternatively, the 95 % CI for the root node of Eremobatidae using the Kulkarni et al. (2023) suggested that Eremobatidae was comparatively older with an interval of 139.8428–217.6761 dating back to the Triassic.

In our time-calibrated phylogeny using the Cushing et. al (2015) calibration, most of the eremobatid ancestors began to diversify in the Oligocene, apart from the ancestor of Clade A and B and the ancestor of A, B, D-N, of which began to diversify at the end of the Eocene (Fig. 3). The MRCA of clades A, B, C, and D were among the oldest clade lineages, with divergence dates estimated to have emerged during the Oligocene. As time progressed, the common ancestors of our clade assignments began to appear by the early to mid-Miocene, yet none appear to have emerged near the Plio-Pleistocene boundary. Under our alternative time-calibrated phylogeny, the origin of the family and most of the ancestral nodes emerged prior to 100 Ma (Supplemental Figure S3). The MRCA of each of the designated clades was suggested to have originated between 100–150 Ma, apart from Clades E and J, which has estimated origins in the Cenozoic.

Ancestral geographic areas were reconstructed using the Cushing et al. (2015) calibrated chronogram as our preferred dated hypothesis (see Discussion). The optimal model, determined by smallest AIC score, was the Dispersal-Extirpation-Cladogenesis with jump dispersal (DEC+j; Matzke, 2014). Warm deserts, which includes Sonoran, Chihuahuan, and Mojave Basin and Range ecoregions was the most probable state for our ingroup taxa (Fig. 3). In the Oligocene, around 25 Ma, our BioGeoBEARS model suggested that the MRCA for Clade J+K dispersed to Cold Deserts from warm desert habitats. Clade N, on the other hand, dispersed from Warm Deserts to Mediterranean California during the Miocene (~17 Ma).

3.4. Clade assignments and climate space

We assigned clade designations in alphabetical order based on the descending evolutionary relationships from the phylogenetic hypothesis presented in Garcia et al. (2024; Table 1; Fig. 2A, Fig. 4A). In addition to assigning groups based on common descent, we considered shared morphological characteristics as inspiration for establishing clades for biogeographical comparative analysis and to explore potential generic limits. Some of these clade assignments can be explained by geography, such that some clades are strictly located east of the Colorado River or West of the Colorado River as determined by the state line boundary between Arizona and California (Fig. 4B). For instance, the terminal taxa comprising Clade D are restricted to central Mexico, the central United States plains, and eastern Arizona. Similarly, Clades L-M are restricted to habitats west of the present-day Colorado river.

We analyzed the distribution of climate affinities for each species sampled for genomic data in this study and accumulated a total of ca. 1,700 natural history collection records, most of which pertain to museum records maintained by the DMNS. Results of our principal components analysis (PCA) using the extracted values from our 10 uncorrelated bioclimatic variables (Bio2, Bio5, Bio7, Bio8, Bio9, Bio12,

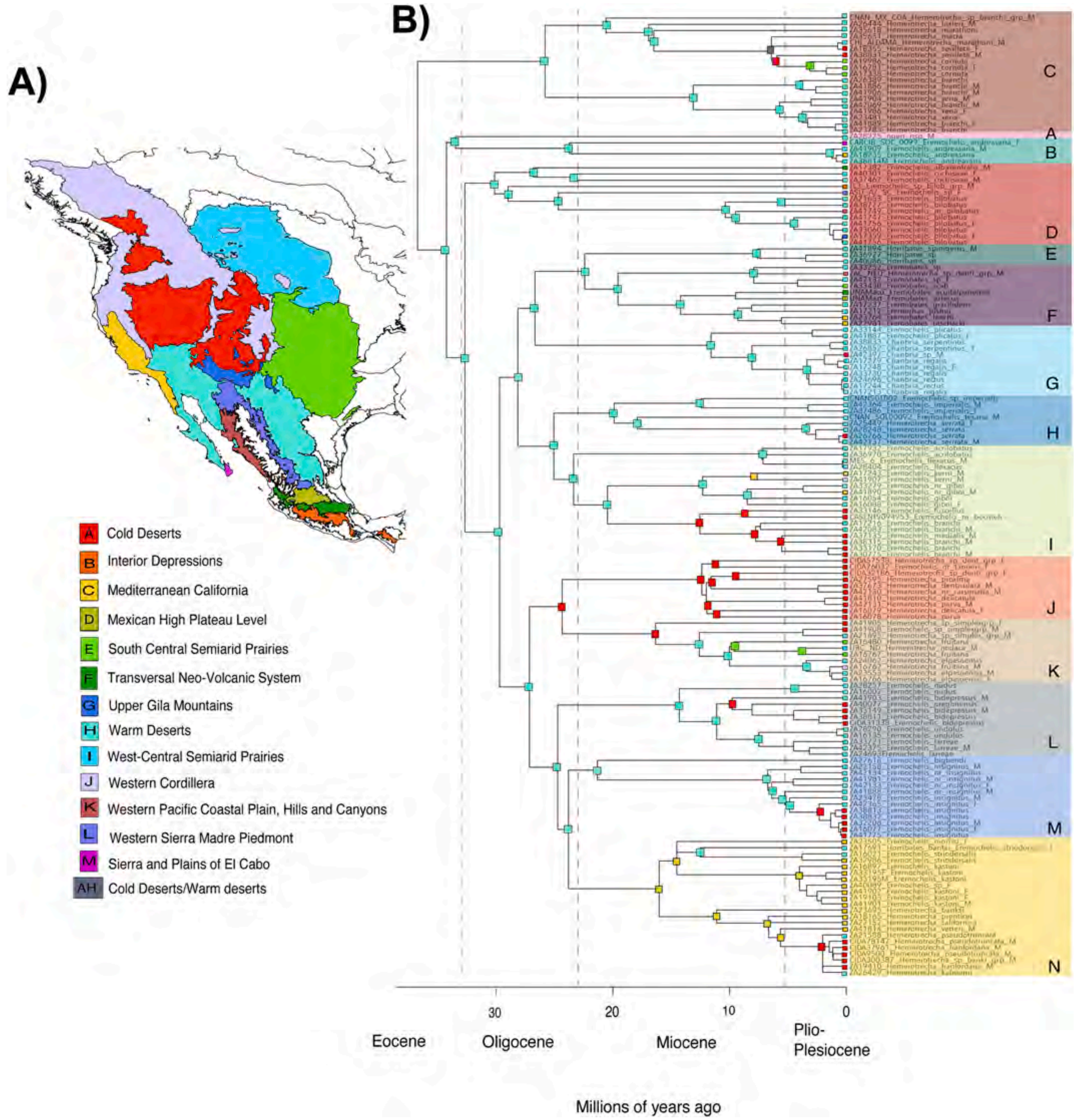

Fig. 3. Historical biogeography of our ingroup eremobatid taxa. Ancestral geographic ranges estimation was conducted in BioGeoBEARS using DEC+j model as the suggested best-fit model and optimized estimated ranges were mapped onto the MRCA nodes in our time-calibrated phylogeny using the Cushing et al. (2015) secondary calibration. Outgroups were removed for clarity and colors of our clade assignments match those in Figs. 3, 4, and 5. A) Ecoregion map and associated colored key for each of the ecoregions used to estimate ancestral geographic ranges. Ecoregion map was generated using the shapefile for ecoregion level II available from the United States Environmental Protection Agency (EPA; http://epa.gov/eco-research/ecoregions-north-america). B) Time-calibrated phylogeny with optimized ancestral ranges estimated in BioGeoBEARS mapped onto the phylogeny. Ancestral range states were determined by maximum likelihood estimation and is the most probable ancestral state for that node. Numbers on scale bar below the phylogeny indicate age in million years and dotted lines refer to geological epoch boundary.

Bio14, Bio15, Bio18, Bio19) from World Clim 2 reported that PC1 explained 68.41 % of the bioclimatic variation and PC2 explained 27.9 % of the variation in climate space (Fig. 4C). Regarding the distribution of climate affinities in climate space, the orientation of each sample pertained mostly to one of two major clusters (Fig. 4C). With respect to the PC2 axis, the first cluster was oriented on the positive end of the Y-axis, extending throughout the limits of the PC1 axis. Members that pertained to this major cluster primarily were collected from localities west of Colorado and New Mexico. The other major cluster, on the other hand, was oriented on the negative end of the PC2 axis but did not

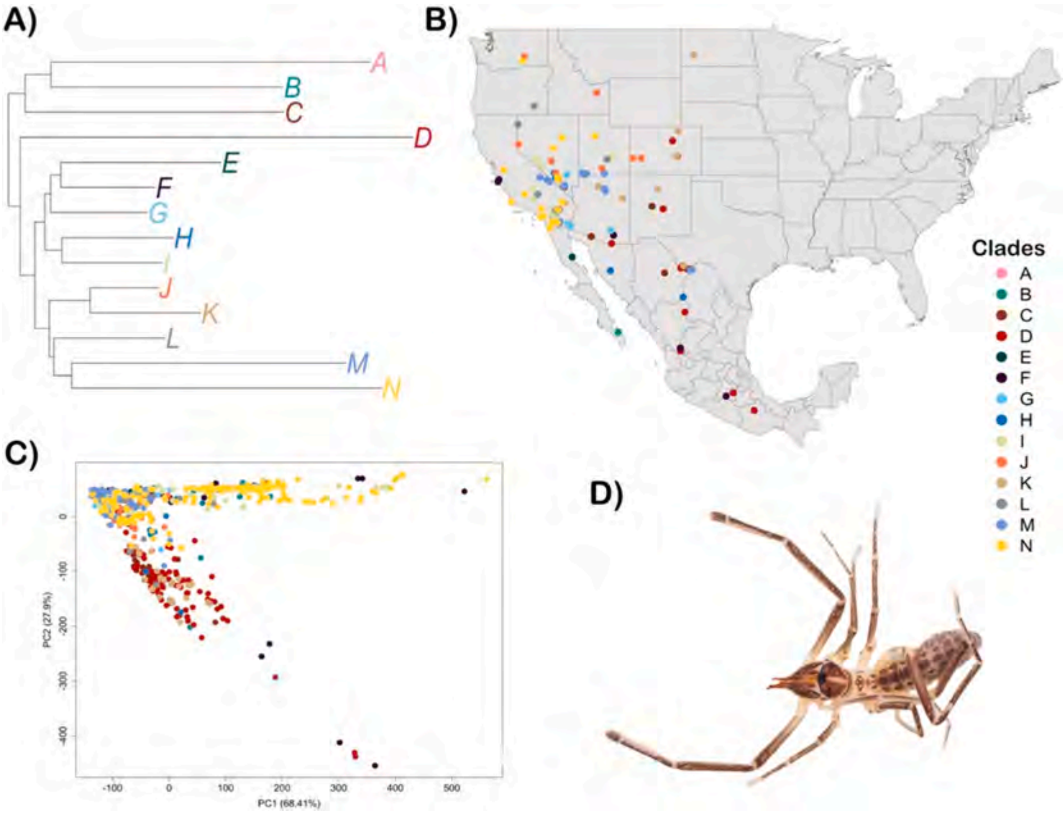

Fig. 4. Clade assignments and climate affinities of the ingroup taxa pertaining to each clade in climate space. **A)** The clade assignments using the phylogenomic hypothesis estimated in Garcia et al. (2024). **B)** Distribution map of each terminal representative from the Garcia et al. (2024) topology colored by clade assignment. **C)** Principal components analysis (PCA) of the uncorrelated Bioclim variables determine by a Pearson's correlation test and 0.75 correlation cut off. **D)** Habitus view of *Eremochelis albaventralis* ♂ (DMNS ZA. 17382). Photo credit: Christopher Grinter. Color coded clade key represents the assigned clades is illustrated to the right of panel B and D.

extend throughout the PC1 axis (Fig. 4C). Such records are mainly distributed in central Mexico, Colorado Plateau, and the Central US Plains. However, in some rare cases, samples were nondiscriminatory and appeared to have wide climate tolerances (e.g., Clade B and F). Here, clades L-N had the least amount of overlap in climate space between clades C, D, and K.

3.5. Environmental distribution modeling

We fitted several models using a combination of feature classes and regularization multipliers. Per the smallest ΔAICc value, the best-fit model recommended for both the World Clim 2 and World Clim 1 climate variables was feature classes L, Q, and H with a regularization multiplier of one. Among the 11 non-correlated variables used for reconstructing niche models, precipitation was the variable that contributed most to the models inferred for each clade designation. Annual Precipitation (Bio 12), Precipitation of the Driest Month (Bio 14), and Precipitation of the Warmest Quarter (Bio 18) was the highest contributing variables for clades (D, G, H, M), (B, E, F), and (I, J, L, N), respectively. Due to the limited museum records for representatives of Clade A, we were unable to reconstruct habitat models for this clade.

During the Last Glacial Maximum (LGM), our models suggest that nearly all clades were restricted to the southwest United States, Mexican Plateau, and south of the Mexican trans volcanic belt (Fig. 5). Some clades, like Clades I, J, and L, nonetheless were suited for northern latitudes, extending as far north as approximately 45° latitude during this epoch (Fig. 5C, 5D). Clades B+C (Fig. 5A) and E-H (Fig. 5B), persisted in heavily restricted ranges compared to Clades C, I-N. Clades I-K had the widest suitable area compared to the other clades (Fig. 5C). Predictive models for Clades F and N suggest that these two clades had disjunct ranges, with relictual habitat suitability in pockets of the Mexican Plateau.

Comparing the habitat models of LGM with the Mid-Holocene, all clades exhibited a range expansion both latitudinally and longitudinally (Fig. 5; Supplemental Figure S4). Clade C was estimated to have undergone a dramatic range expansion during this time, by extending from a restricted area in present-day California to the central US and Mexico (Supplemental Figure S4A). The habitat model for Clade D, the clade with only *Eremochelis bilobatus* morpho-species, exhibited an ample distribution growth with the suitable habitat extending from modern-day northern Chiapas to northern Colorado. Next, the models built for Clades E-G support habitat suitability restricted to the southwestern North America, yet the model for Clade H inferred a disjunct distribution with viable habitat in the Sonoran and Chihuahuan Deserts. Clades I+J extended into regions of central Washington and southern Canada, respectively. However, Clade K presumably circumvented the high elevations of the Rocky Mountains and continued range expansion northward into southern Wyoming (Supplemental Figure S4C). The habitat viability for Clade L, conversely, increased both northward into southern Washington and southward into the Baja California peninsula (Supplemental Figure S4D).

The niche models constructed for the near present (1970–2000) indicates that the suitable habitats for each clade assignment are virtually unchanged since the Mid-Holocene (Fig. 6). Some notable range expansions include Clade D, extending into the southern extent of the present-day Colorado Plateau and Clade K, with a range reaching into the southern latitudes of the Mexican Plateau, and as far north as Canada.

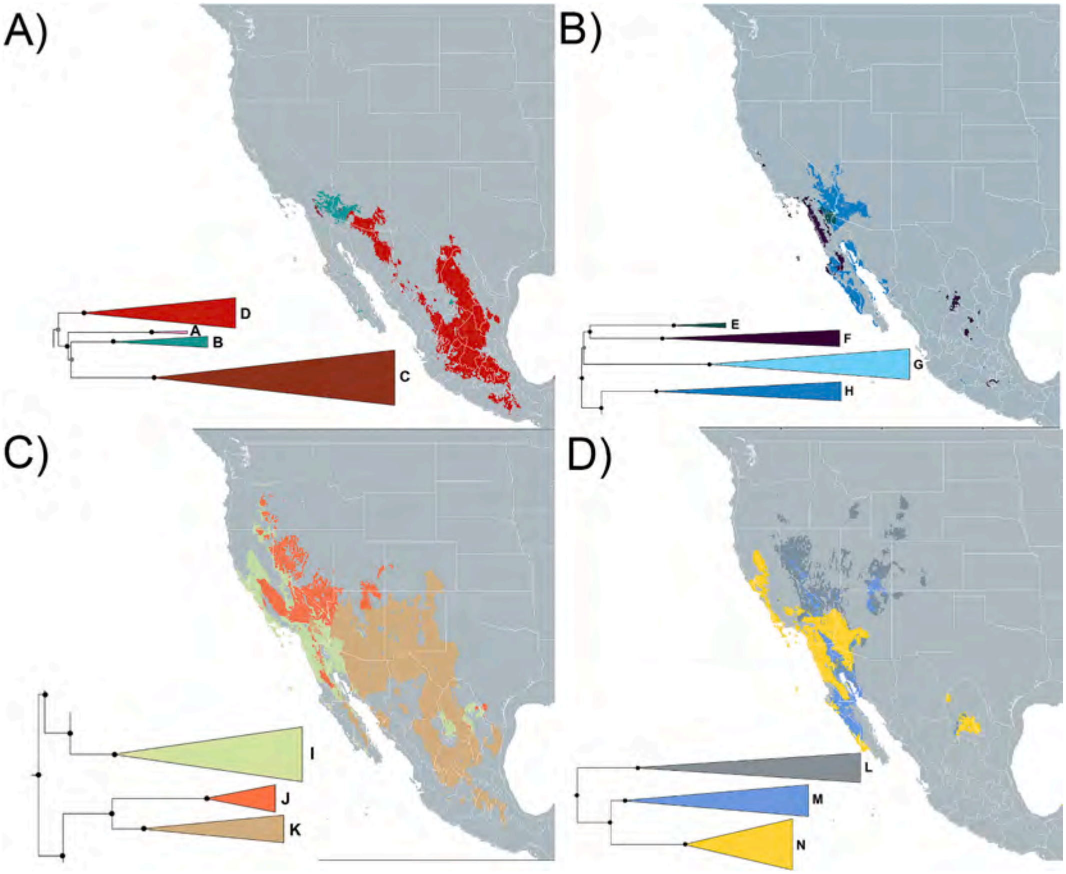

Fig. 5. Paleo-niche modeling for our clade assignments during the Last Glacial Maximum (LGM;~21,000 years before present) at a 2.5 m resolution. Phylogenetic depictions pertain to our estimated Phylobayes topology using our UCE+COI dataset. **A)** LGM models of clades B-D only. Museum specimens of Clade A were too few to estimate niche models, thus are omitted from the panel. LGM models for **B)** clades E-H **C)** clades I-K and **D)** clades L-N.

3.6. Ancestral climate tolerances and niche overlap

We examined four climate variables that we suspected would be biologically meaningful in determining habitat boundaries for each of our respective clades. As characteristically desert-associated arachnids, we sought to explore if there was a detectable difference between the climate distributions of two variables of temperature, and if certain clades are adapted to precipitation conditions other than those that are fundamentally desert conditions. The climate distributions for Maximum Temperature of the Warmest Month inferred that the ancestral temperature for our ingroup eremobatids was approximately 34 °C (Supplemental Figure S5A). The inferred distribution for maximum temperature for Clade G was among the highest distributions. This clade comprises species representatives of the sand dune associated genus, *Chanbria* (Brownell & Farley, 1974; Conrad & Cushing, 2011), and *Eremochelis plicatus*. Clade H, on the other hand, consisting of species *Eremochelis imperialis*, *Hemerotrecha texana*, and *H. serrata*, was the second highest distribution. All clades, however, were summarized by wide temperature distributions and no clades were particularly distinct in comparison, thus suggesting a conservation of temperature tolerance for this variable at the clade level. A similar pattern was recovered when we analyzed Temperature Annual Range (Supplemental Figure S5B), where most clades were recovered to have wide temperature tolerances annually, and the ancestral temperature for all ingroup eremobatids was around 36 °C.

Our analysis results for Precipitation Seasonality, summarized in part by the standard deviation of monthly precipitation estimates, rendered the ancestral estimate as 60 mm of precipitation. Like the other variables mentioned previously, analysis of this climate variable recovered each clade with a wide precipitation distribution, with Clade J having the narrowest distribution (Supplemental Figure S5C). For the variable for Precipitation of the Warmest Quarter; conversely, we observed signal niche specificity for some clades. Specifically, Clades B, D, G, I, J, L, M, and N tolerate low precipitation during the warmest quarter of the year in North America and are restricted to habitats with < 100 mm of rain during this period (Supplemental Figure S5D). However, taxa within Clades C, D, F, H, K, in addition to being endemic to areas with little rainfall, also exist in habitats that experience heavy rain on average, at nearly 250 mm.

4. Discussion

4.1. Phylogenetic relationships of eremobatid taxa

Here, we present several phylogenomic hypotheses for the North American camel spider family, Eremobatidae. In this study, one of our objectives was to test the robustness of the major eremobatid clades that were recovered from Garcia et al. (2024) using a series of alternative input matrices and analytical approaches. Our study indicates that our clade designations, apart from some not recovered within our bottom 300 PIS topology, were supported unanimously with strong support values. However, despite consistently recovering most of the clades, the interrelationships between these clade designations varied among early diverging clades. While the most ancient eremobatid lineage is currently uncertain, due to the resultant inconsistencies between early diverging clades, we believe that our efforts provide a better understanding of eremobatid evolution in North America and affords a premise for taxonomic revisions on the generic level.

The interrelationship instability recovered across our phylogenomic hypotheses primarily include the relationships between Clades A-D.

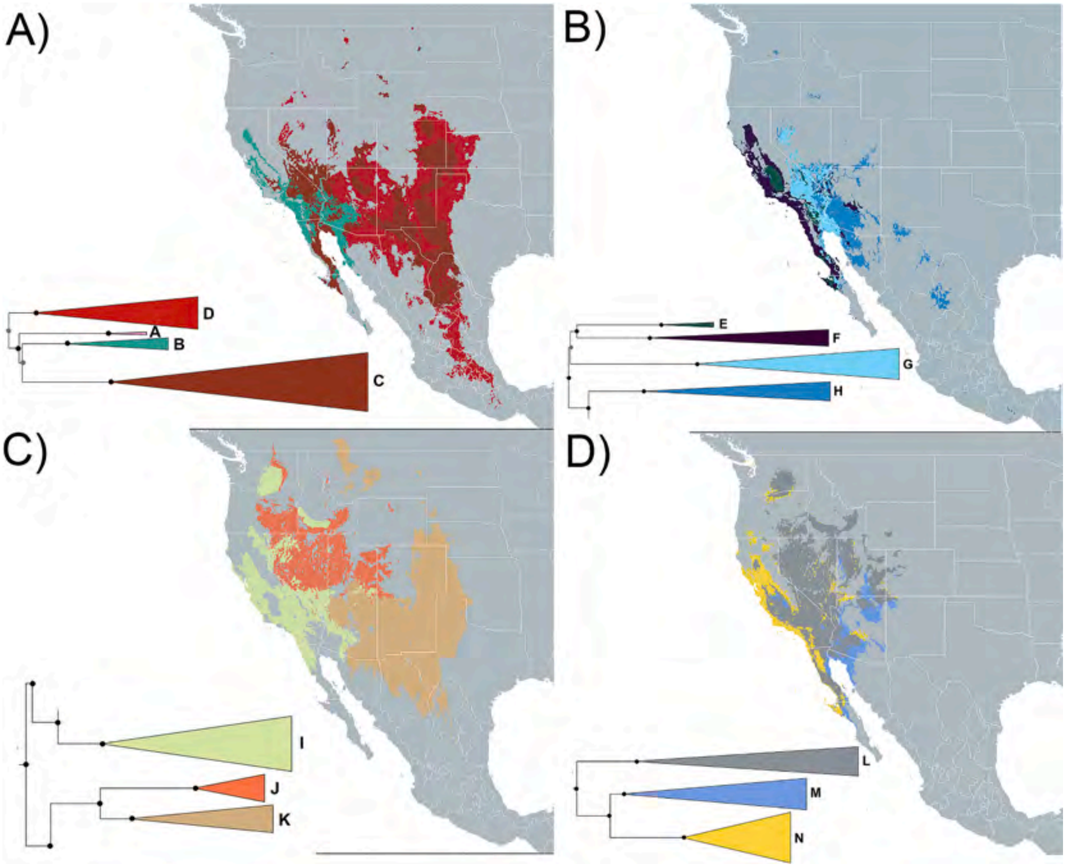

Fig. 6. Historical niche modeling for our clade assignments during the years 1970–2000 at 30 s resolution. Phylogenetic depictions pertain to our estimated Phylobayes topology using our UCE+COI dataset. **A)** Niche models of clades B-D only. Museum specimens of Clade A were too few to estimate niche models, thus are omitted from the panel. Models for **B)** clades E-H **C)** clades I-K and **D)** clades L-N.

First, in our phylogenomic hypothesis (Fig. 2A) that was identical to the Garcia et al. (2024), Clade A was recovered as the earliest diverging lineage. Exemplars of this clade are endemic to Big Bend National Park located in Texas and are arguably the smallest eremobatid species that have yet to be documented. Recovered as another hypothesis, was Clade D, formed by species representatives of *Eremochelis cochiseae, E. albaventralis*, and multiple specimens of *E. bilobatus*, as the most ancient diverging lineage in relation to the rest of the eremobatids. Species within this clade are distributed from the Mexican Plateau to the Central US plains in Colorado. And lastly, as a third hypothesis, members of the *Hemerotrecha branchi* species group were rendered as the oldest eremobatid clade. Species of this clade, on the other hand, are endemic to the Sonoran and Chihuahuan Deserts of North America. These results are distinct from those basal relationships recovered in Cushing et al. (2015), which recovered *Chanbria serpentinus* and *Eremochelis andreasana* as the earliest diverging taxa in their MrBayes (Ronquist & Huelsenbeck, 2003) and BEAST (Drummond & Rambaut, 2007) topologies, respectively. Additional slowly evolving genes sampled for Eremobatidae will do much to clarify the relationships of these four clades and will give us a better understanding of the ancestral states of early eremobatids and their center of geographic origin.

Despite the notable instability of early emerging eremobatid lineages, there were several interrelationships that were steadily recovered across our phylogenomic treatments and sequence data. Other than our bottom 300 PIS topology, Clades E-I, consistently formed a monophyletic relationship with strong support and was persistently a lineage that succeeded Clades A-D (Supplemental Figure S2B). This monophyletic group comprises species that are large-to-moderately sized (>30 mm in body size) compared to the other species of eremobatids. In independent surveys of first leg tarsal claw morphologies, a characteristic used to diagnose the suggested subfamily designations for Eremobatidae by Muma (1951), representatives found within Clades E-G possess a single claw condition (Cushing, PE; Hansen, Quincy G.; unpublished data). Since other taxa do not exhibit this character state, and instead possess two claws, we suggest that the single claw character state can be used as a synapomorphy to solidify the monophyletic relationship of these three clades.

Another consistent phylogenetic pattern that we observed across our altering analytical approaches, was the monophyletic relationship between Clades J-N. The interrelationships between each of these clades were in accord with the descending alphabetical order of our clade designations across our differing approaches. Given this consistent pattern, we can conclude that Clades J-N are derived eremobatid lineages, with Clade N consisting of *Eremochelis morrisi, E. striodorsalis,* and *Hemerotrecha banksi* species group representatives being the latest evolved eremobatids. The known distribution for these taxa is wide, extending from coastal California to the Sonoran Desert, and the cold deserts of the Colombia Basin, Central Basin and Range, and Colorado Plateau.

4.2. Age divergence and historical biogeography of eremobatid taxa

When considering the age estimates for our ingroup taxa under the secondary calibration by Kulkarni et al. (2023), Eremobatidae is five times older than the proposed aged estimate of Cushing et al. (2015). Currently, due to our limited taxon sampling for regions in southern Mexico and southern Baja California in Mexico, it is unclear which divergence time estimate is more favorable. At this time, we cannot completely rule out the possibility that eremobatids have origins prior to the Cretaceous. Future sampling in southwestern Mexico and a more developed understanding of the major biogeographic processes that likely influenced eremobatid diversification would give us a comprehensive understanding of the precise age of Eremobatidae as a whole. However, with our current sampling and results herein, there are several geological events and biogeographical patterns that lead us to be skeptical of a pre-Cretaceous diversification model. First, Eremobatidae is undoubtedly far more diverse than anticipated, with a surplus of new species and genera yet to be described. Considering this observed diversity, our estimated divergences using the Kulkarni et al. (2023) suggest that most of the extant lineages we observe today are derived from ancestors that persisted around 100 million years ago. This implies that eremobatids would have survived the Cretaceous-Paleogene mass extinction event (Hallam and Wignall, 1997), dramatic changes in terrestrial ecosystems (Mitchell et al. 2012), and considerable changes in climate (Hallam & Wignall, 1997). Moreover, under this model, eremobatids would have escaped a diversity bottleneck, an evolutionary outcome observed among other terrestrial invertebrates (Labandeira et al. 2002). Next, during the mid-Cretaceous, nearly 100 million years ago, North America was recognized by two major landmasses: Laramidia, located in the west, and Appalachia, oriented in the east (Scheinvar et al. 2020). If Eremobatidae is truly approximately 150 million years old, we would expect that the earliest diverging lineages would have originated from southwestern Mexico (Laramidia) as the habitats were readily available throughout geological time in contrast to those in present day central United States. This is due to the Western Interior Seaway (WIS), an ancient inundation of North America that divided the continent during the Cretaceous epoch. The WIS extended from the Arctic Ocean to the Gulf of Mexico, reaching an approximated width of more than 1000 km (Byrum & Lieberman, 2021). The relative duration of this continuous seaway, estimated from historical marine faunistic records, indicates that the WIS lasted between 100–60 million years (Slattery et al. 2015). Given that many of central U.S. states were completely submerged during this epoch (e.g., Colorado, Wyoming, Texas, New Mexico), we would expect that many eremobatid lineages would have gone extinct during this historical period of inundation. One notable example is the estimated node between Clade J and K, where the mean estimate for the most recent common ancestor (MRCA) was 108 million years (Fig. 3). Extant taxa within these two respective clades are endemic to the Colorado Plateau and modern-day central US states (e.g., North Dakota, Colorado, Texas), therefore it would be inconceivable that the ancestor, responsible for the subsequent diversification of these two clades, would have occupied this area during the epoch of the WIS. Moreover, we would expect that this incursion would have disturbed paleobiogeographical units, thus would have disturbed the local endemic taxa, causing a mass extinction of the solifuge diversity of this time.

Many of the later diverging species that comprise Clade N, specifically *Eremochelis morrisi, Eremochelis striodorsalis, Eremochelis kastoni, Hemerotrecha californica, Hemerotrecha prenticei,* and *Hemerotrecha vetteri*, are taxa that are currently endemic to coastal and southern California. California is known to have a complex geological history, much of which has shaped the biodiversity of the region; however, California was substantially inundated for most of the Oligocene, including western California (Schierenbeck, 2014). Exposure of the southern California margin is suggested to be attributed to the subduction of the Farallon Plate during the mid-Cretaceous (Sharman et al. 2015) and further marine evidence in the coastal Peninsular Ranges (Kodama & Ward, 2001) indicates that coastal California was likely unavailable for this clade at the inferred age of ~ 70 Ma. Additionally, fossil floras during the early Eocene indicate that a subtropical savanna was the dominant ecotone during this epoch (Raven and Axelrod, 1978), and not warm deserts as inferred by our BioGeoBEARS analysis for the ancestor of Eremobatidae.

The orogeny of the North American cordillera during the mid-Miocene and the subsequent desert formation because of rain shadows incurred by prominent mountain ranges undoubtedly was a major driving force in the diversification of xeric-adapted taxa (Wilson & Pitts, 2010a). The Laramide uplift (~55–80 Ma), one of the first major periods of geological uplift, was an active period of orogenesis and is hypothesized to responsible for the foundation of the western American Cordillera (English & Johnston, 2004). However, despite mountain uplift being strongly associated with aridity in adjacent habitats, there is lack of evidence that this dynamic period resulted in an increase in arid habitats (Wilson & Pitts, 2010a). As generally desert-adapted animals, we suspect that the relatively recent aridification of landscapes in North America, beginning during the Eocene, and expansion of deserts after the Cretaceous may be a more plausible explanation for the diversification of Eremobatidae as this pattern has been documented in several desert-adapted taxa (Riddle et al. 2000; Wilson & Pitts, 2010b; Zhang et al. 2014; Zheng et al. 2015; Cushing et al. 2015; Garcia et al. 2020). Furthermore, the age for North American Eremobatidae, suggested by the Kulkarni et al. (2023), would also dramatically predate some arid-adapted plant taxa in North America (Moore & Jansen, 2006), of which the earliest evidence of arid adaptation of floras began as early as the late Cretaceous (Axelrod 1950, 1958, 1972, 1979). Considering this and that most of the global warm deserts are no older than the late Miocene (Berggren et al. 1995), we suspect that the rapid diversification of eremobatids between 100–150 years ago may be an overestimation in age.

Since terrestrial southwestern Mexico and United States were available during the inundation of North America by the WIS, we would expect patterns of northward and westward expansion of eremobatid taxa into historically submerged areas. Using our phylogenies to understand the biogeographic patterns of eremobatid taxa, we observe such patterns in many of our clades. First, we observe basal Mexican lineages (determined by descending evolutionary order and branch length) in Clade B with a lineage from Baja California Sur (CARCIB_SOL_0099), in Clade C with a taxon from present day Coahuila, México (CNAN_MX_COA), Clade D with a specimen from Estado de México, México, and Clade H with a lineage from Sonora, México (Fig. 3 and Supplementary Fig. 3). In terms of the earliest diverging eremobatid lineage, due to the large inland sea during most of the Cretaceous, we hypothesize that either Clade C or Clade D, clades with origins in the Mexican Plateau, is the earliest diverging eremobatid lineage. Curiously, Clade A has origins from Big Bend National Park in Texas, which would have been completely submerged and these species presumably would have gone extinct during the Cretaceous. If Clade A is the unequivocal basal eremobatid lineage, then present-day eremobatid diversity would date to the retreat of the WIS.

In addition to a northward expansion from México, many of the other clades that do not have Mexican origins, putatively emerge from present day California and Arizona (Sonoran Desert). These two areas were also areas that were continuously available throughout the Cretaceous and there are several exemplar clades that are representative of this general pattern. First, we observe this pattern in the subclade of Clade C with DMNS ZA.26389 from the Mojave Desert in California and subsequent expansion into Nevada in later diverging taxa. Second, we observe this in the subclade of clade B with species of *Eremochelis andreasana* Muma 1962 originating in southern California, then expanding eastward into present day Arizona. Similarly, the taxa that comprise Clade E are restricted to southwestern California and northern Baja California. Lastly, Clade I and Clade L also represent southwestern California origins and a later expansion north and northeastward. Our ancestral geographic range reconstruction analysis and our habitat niche modeling also corroborates a northward/northwest expansion into cold deserts and northern latitudes (Figure 5, 6 and Supplementary Fig. 4). Specifically, the ancestor of Clades J and K and many extant taxa are endemic to cold desert environments such as those in the Colorado Plateau and Central Basin and Range and, considering the distributions of current taxa, we suspect that there was a northward expansion from the Sonoran/Mojave Deserts. Additionally, the ancestral state for several lineages in Clades L-N were inferred to support an ancestral cold desert geographic range from a Sonoran/Mojave range. These observations, in contrast to the ancestral state results recovered in earlier eremobatid lineages, suggest that the adaptation to cold deserts is a derived state for many of the later diverging eremobatid clades.

For many arid-adapted taxa, several researchers have corroborated a northward expansion from warm desert regions, although there are disagreements on the precise warm desert origin. For example, in a study of palaeobotanical flora, Axelrod (1979) hypothesized that much of the arid-adapted flora observed today originated from the Sonoran Desert. Conversely, Morafka (1977) proposed that modern desert taxa originated in Mexican Plateau/Chihuahuan Desert as these geographic regions were climatically stable during the Miocene. Despite this discordance, previous studies have supported the idea that these regions were important areas for Pleistocene refugia, thus house high levels of species diversity (Wells & Hunziker, 1976; Douglas et al. 2006; Rebernig et al. 2010; Loera et al. 2017). Therefore, both the Sonoran and southern Chihuahuan Desert have unquestionably played a major role in the diversification as our results indicate that many of our clade designations have origins from these warm desert regions, in addition to modern endemicity.

4.3. *Evolution of climate tolerances and habitat preference*

The two major habitat types that were observed for Eremobatidae were warm deserts for early diverging taxa and a subsequent evolution to cold deserts and Mediterranean California ecoregions for later diverging taxa. Although our analyses did not partition to a finer ecoregion scale, such that warm deserts (e.g., Mojave, Sonoran, Chihuahuan) were divided by distinct desert types, the results of our ancestral niche occupancy profiles suggest that temperature tolerance, to a large degree, is conserved across our clade lineages (Figure Supplementary Fig. 5, Table S1). This result suggests that across Eremobatidae, species tolerate similar temperature within their respective range and there is convergence toward similar temperature parameter spaces. This niche conservatism, determined by similar temperature and precipitation profiles, help to confirm the large-scale species richness we observe in desert habitats for eremobatids. Coupled with our ancestral geographic range reconstruction, and apparent niche preference for high temperature and low precipitation conditions for millions of years, our findings support the hypothesis of a warm desert origin. Since eremobatid species likely originated from warm deserts, we expect that the species richness is the highest in the Sonoran and Mexican Plateau as lineages have persisted there over long periods.

When examining the ancestral profiles for precipitation during the warmest quarter of the year, this climate variable appears to be an influencing factor in distinguishing clades and perhaps is evidence, in part, for niche partitioning into cold versus warm deserts habitat types. In cold desert habitats, like in the Great Basin, characteristic climate signatures include a lack of summer precipitation, high precipitation in the southern regions, and consistent snow cover in the winters (West 1983). Species that are distributed in these cold deserts, such as those in Clade J reflect niche conservatism as suggested by our ancestral geographic range analyses. We hypothesize that these species have likely evolved a different physiological strategy, such as cold tolerance, to allow for adaptative success to the characteristic climate regimes offered by cold desert habitats.

Our analysis of abiotic factors suggests that the extant distribution of Eremobatidae has a complex evolutionary history due to the amount of niche convergence inferred by our analyses of ancestral niche profiles for single variables and our historical biogeography. Although the historical biogeography of Eremobatidae is complex, in terms of niche space determined by temperature, eremobatids temperature tolerance has been conserved for at least 25 million years in North America. We recognize, however, that our clade designations encompass deep divergences and perhaps single climate variables do not provide sufficient fine-scale resolution for identifying specialized niches. For example, some of our clade designations, such as Clade F which consists of some species of *Eremobates* and *Eremorhax*, cover a wide distribution across multiple habitat types, thus we observe wide distributions for precipitation and temperature (Supplemental Figure S5). Despite the large climate overlap for many taxa (Supplemental Table S1), there appears a phylogeographic divide between taxa distributed east and west of the Cochise filter-barrier located along the Arizona and New Mexico border (Fig. 4C). The origin of this vicariant barrier was influenced by the uplift of the Sierra Madre Occidental cordillera, during which this area experienced dramatic landscape alterations (Hafner & Riddle, 2011). Additionally, subsequent climate oscillations during the Plio-Pleistocene in the northern section of this barrier produced climatic instability in this region (Morafka 1977). Thus, the Cochise filter-barrier, a well-known ecological transition zone, perhaps promoted niche divergence among eremobatid taxa as in other ectothermic, non-flying organisms (Provost et al. 2018).

4.4. *Future Directions*

Due to the limited knowledge of eremobatid species' abundance and phenology, the under-collection of many described eremobatid species may partially be attributed to unknown phenological differences within Eremobatidae. Eremobatids in natural history collections are biased toward large eremobatid species and collection efforts for eremobatid species were prioritized for the warmest months of the year when species were presumed to be in high abundance. However, based on recent collection attempts by the authors, it is now suspected that optimal maturation times for many species likely circumvent the warmest periods of the year. Considering the outstanding eremobatid diversity in warm desert spaces, we hypothesize that temporal niche partitioning evolved among eremobatids such that the smaller eremobatid species emerge sooner and later than their larger counterparts. In addition to temporal partitioning, species that divide available niche space by exploiting different habitats or resources is a common phenomenon of species radiations (Colombo et al. 2016; Hu et al. 2016; Ojeda Alayon et al. 2017; Kennedy et al. 2019). Our results support significant diversification and range expansions to newly available warm habitats during the Miocene and Holocene epoch. Thus, if eremobatids underwent adaptive radiation during this crucial period, ecological niche partitioning may have also played a role in the diversification of eremobatids in shared desert spaces. For example, the natural history description for the type and paratype species of *Eremochelis larreae* Muma 1962 was from beating creosote bush, *Larrea*, from the Mojave Basin and Range. Since most solifuge records are collected either serendipitously or restricted to ground-focused collection methods, it is likely that bush-dwelling species of solifuges exist and have historically been overlooked. Moreover, the empirical observations made by Muma (1974) and Brookhart (1972) further allude to the possibility of habitat preference and niche partitioning in eremobatids. Therefore, future studies that focus on aspects of niche partitioning on a community or clade level will further illuminate our understanding of eremobatid evolution.

Here, we presented two time-calibrated phylogenies with drastically contrasting divergence times. When considering the information available for time-calibration within solifuges, it is worth noting that solifuges are among the rarest arachnids represented in the fossil record (Dunlop et al. 2015). Of the few unequivocal solifuge fossils available, such fossils have been assigned to other, non-eremobatid, solifuge families. Although some outgroup families were included in this study, an order level phylogenetic hypothesis was non-existent at the initiation of this study, thus family level relationships were uncertain for Solifugae. For similar reasons, without a densely sampled phylogeny with strongly supported interrelationships, identifying a candidate vicariant barrier known to separate two lineages, was highly ambiguous at this early stage of taxonomic re-consideration for Eremobatidae. Thus, we recognize the limitations in our approach to estimating the divergence times for Eremobatidae, especially when considering that the use of secondary calibrations is considered a last-resort option (Ho & Phillips, 2009). However, considering the recent taxonomic efforts and rekindled research interest in Solifugae, we are formally advancing toward a better understanding of solifuge evolution, and this consequently gives us a framework for identifying appropriate vicariant barriers for future calibration of divergence times. In terms of Eremobatidae, future sampling efforts are required to obtain a sound picture of Eremobatidae evolution across geological time, particular in southern Baja California and southern Mexico.

5. Conclusion

The overarching goal of this study was to test the robustness of recovered eremobatid clades from Garcia et al. (2024) across altering genomic data sets and phylogenomic approaches. We assigned specific clade designations based on shared morphological traits with the premise that such designations represented hypotheses for new generic boundaries. With a taxonomic focus on two of the three most diverse genera, we sought to elucidate patterns of biogeographic diversification across spatial and temporal scales as an integrative approach to supporting new generic boundaries. The investigation of climatic variables and niche evolution using a dated phylogenetic context offered a framework for understanding biogeographic patterns that have shaped diversity of *Eremochelis* and *Hemerotrecha*, two genera that have historically lacked attention and need taxonomic revision. Our results indicate that niche conservatism is present within many of the early diverging clades, suggesting that the center of origin for eremobatid taxa are warm deserts, with subsequent evolution into cold desert spaces. However, further sampling in under-collected areas such as those in southern Mexico and Baja California is required to elucidate if eremobatids originate from the central Mexican Plateau/Chihuahuan Desert or the Sonoran Desert of North America. Based on the results of this study, we suggest that those clades that independently evolved from warm deserts into cold deserts and Mediterranean California (i.e., Clades J, K, and Clade N) should be elevated to generic status in future taxonomic works.

6. Data Accessibility

Alignment files and phylogenetic trees associated with this study are available on Figshare (https://doi.org/10.6084/m9.figshare.26575129). Raw sequence reads are available from the NCBI Sequence Read Archive, under BioProject accession PRJNA982881.

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Declaration of Competing Interest

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ympev.2024.108193.

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