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A multilocus molecular phylogeny of the endemic North American camel spider family Eremobatidae (Arachnida: Solifugae) ☆

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ABSTRACT

Camel spiders (Solifugae) are a diverse but poorly studied order of arachnids. No robust phylogenetic analysis has ever been carried out for the order or for any family within the Solifugae. We present a molecular phylogenetic analysis of the endemic North American family Eremobatidae Kraepelin, 1899, the first such analysis of a family of Solifugae. We use a multi-locus exemplar approach using DNA sequences from partial nuclear (28S rDNA and Histone H3) and mitochondrial (16S rRNA and Cytochrome c Oxidase I) gene loci for 81 ingroup exemplars representing all genera of Eremobatidae and most species groups within the genera *Eremobates* Banks, 1900, *Eremochelis* Roewer, 1934, and *Hemerotrecha* Banks, 1903. Maximum Likelihood and two Bayesian analyses consistently recovered the monophyly of Eremobatidae, *Eremorhax* Roewer, 1934 and *Eremothera* Muma, 1951 along with a group comprising all subfamily Eremobatinae Kraepelin, 1901 exemplars except *Horribates bantai* Muma, 1989 and a group comprising all *Eremocosta* Roewer, 1934 exemplars except *Eremocosta acuitalpanensis* (Vasquez and Gavin, 2000). The subfamily Therobatinae Muma, 1951 and the genera *Chanbria* Muma, 1951, *Hemerotrecha*, *Eremochelis*, and *Eremobates* were polyphyletic or paraphyletic. Only the *banksi* group of *Hemerotrecha* was monophyletic; the other species groups recognized within *Eremobates*, *Eremochelis*, and *Hemerotrecha* were paraphyletic or polyphyletic. We found no support for the monophyly of the subfamily Therobatinae. A time-calibrated phylogeny dated the most recent common ancestor of extant eremobatids to the late Eocene to early Miocene, with a mean estimate in the late Oligocene (32.2 Ma).

1. Introduction

Solifugae, known by various common names including camel spiders, sun spiders, and wind scorpions, is a poorly studied order of mostly nocturnal, cursorial, hunting arachnids noted for their powerful two-segmented chelicerae, a voracious appetite, and tremendous speed (Punzo, 1998; Beccaloni, 2009). Solifuges are dominant predatory arthropods in arid ecosystems (Banta and Marer, 1972; Cloudsley-Thompson, 1977; Wharton, 1987; Punzo, 1994; Polis and McCormick, 1986) and also serve as important prey for many other desert taxa (El-Hennawy, 1990; Henschel, 1994; Arlettaz et al., 1995; Anderson et al., 1999; Catenazzi et al., 2009).

Solifugae is the sixth most diverse order of arachnids with 12 families, 141 genera, and approximately 1100 described species (Harvey, 2002, 2003; Prendini, 2011). In addition, five monotypic fossil genera have been described (Poinar and Santiago-Blay, 1989; Selden and Dunlop, 1998; Dunlop and Rössler, 2003; Dunlop et al., 2004, 2008, 2015; Dunlop and Klann, 2009). The oldest known solifuge, *Protosolpuga carbonaria* Petrunkevitch, 1913, is from the Upper Carboniferous (Pennsylvanian) of Mazon Creek, Illinois, USA and dates back to 313–304 Ma (Selden and Shear, 1996).

Based on morphological and molecular analyses, the order Solifugae is indisputably monophyletic (Wheeler et al., 1993; Wheeler and Hayashi, 1998; Giribet and Ribera, 2000; Giribet et al., 2002) although its position within the Arachnida remains uncertain (Weygoldt and Paulus, 1979a, 1979b; Shultz, 1990; Weygoldt, 1998; Wheeler and Hayashi, 1998; Dunlop, 2000; Giribet et al., 2002; Alberti and Peretti, 2002; Dabert et al., 2010; Pepato et al., 2010; Klann and Alberti, 2010; Regier et al., 2010; Dunlop et al., 2012).

Koch (1842), Simon (1879), Kraepelin (1899, 1901) conducted cursory taxonomic assessments of solifuges. Roewer (1932, 1933, 1934) presented the first comprehensive classification of the order,

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which was criticized by several subsequent researchers for relying too heavily on spinal and setal patterns; characters that vary widely within genera and sometimes within species (Fichter, 1940; Panouse, 1950; Turk, 1960; Della Cave, 1971; Delle Cave and Simonetta, 1971; Muma, 1951, 1989). Fichter (1940) dismissed most of Roewer's characters and Muma (1951, 1962, 1963, 1970) was unable to utilize Roewer's spine-like setal patterns of legs to identify genera. Muma instead established genera based on the form of the male cheliceral fixed finger, type of modified setae in the male flagellar complex, and presence or absence and form of the male cheliceral fixed finger mesal groove. He recognized species groups within genera by minor differences in the above male characters, gross differences in the genital operculum of the female, and proportionate sizes of the cheliceral fondal teeth of both sexes. Della Cave (1971) criticized Roewer's characters and pointed out that characters used by Roewer to establish new genera are often variable within species. He suggested the need to re-assess the taxonomy proposed by Roewer but did not offer standardized characters to use instead. Brookhart and Muma (1981) established the A/CP ratio (appendage lengths/combined cheliceral + propeltidial lengths) as an approximation of leg length in relation to body size. Despite such attempts to find homologous characters for family, genus, or species group classification, Harvey (2003) decried a taxonomy devoid of any phylogenetic interpretations. Recently, however, an attempt has been made to provide homology assessment for cheliceral characters throughout the order (Bird et al., 2015).

The solifuge family Eremobatidae Kraepelin, 1899 is endemic to North America and has been recorded in southern Canada (British Columbia, Alberta, Saskatchewan), western U.S.A. (west of the Mississippi River), and in arid habitats throughout Mexico. The family presently comprises 179 described species placed in two subfamilies, eight genera, and 18 species groups (Table 1). Roewer (1933, 1934) laid the foundation for the systematics of Eremobatidae, raising Kraepelin's (1901) subfamily Eremobatinae to family status as the Eremobatidae and further dividing the family into two subfamilies, the Eremorhaxinae and the Eremobatinae, on the basis of fourth leg tarsal segmentation and the number of tarsal claws on leg I. The Eremorhaxinae was a monotypic subfamily, including only *Eremorhax magnus* (Hancock, 1888), and defined as having an unsegmented fourth tarsus and no claws on the first leg. Muma (1951) synonymized the Eremorhaxinae with Eremobatinae after re-examining *Eremorhax magnus* and added the subfamily Therobatinae. Included in the Eremobatinae were genera with one claw on the tarsus of leg I, chelicerae about twice as long as wide, a style-like fixed cheliceral finger on the males, and with a ventral or mesoventral groove on the male fixed cheliceral finger. The Therobatinae included genera with two claws on the tarsus of the first leg, chelicerae from two and one-half to three times as long as wide, and males with a style-like fixed cheliceral finger with or without a ventral or mesoventral groove and with or without modified teeth on the fixed finger. In an unpublished manuscript completed shortly before his death (in JOB's possession, available upon request), Muma created an additional subfamily, the Hemerotrechinae that included genera with two tarsal claws on leg I, and males with an indistinct, very indistinct, or no mesal groove on the fixed cheliceral finger. He placed *Chanbria* spp. and most species of *Hemerotrecha* in this new subfamily. He also moved the genus *Horribates* from the Eremobatinae to the Therobatinae.

Muma (1951) revised the North American family Eremobatidae, separating genera based upon gross morphological differences including the shape of the male fixed finger, cheliceral dentition patterns, structure of the flagellar complex, and structure of the female genital operculum. The species groups were subsequently created based upon additional morphological characters (Brookhart, 1965, 1972; Muma, 1970, 1976, 1989; Brookhart and Muma, 1981, 1987; Muma and Brookhart, 1988; Brookhart and Cushing, 2002, 2004, 2005).

Except for a morphological phylogenetic analysis of the *scaber* group of *Eremobates* (Brookhart and Cushing, 2004), the monophyly of the subfamilies, genera, and species groups of Eremobatidae has never been tested phylogenetically. We present a molecular phylogenetic analysis of Eremobatidae, the first such analysis of a family of Solifugae, to test whether the family, subfamilies, genera, and species groups are monophyletic. We conducted Maximum Likelihood and Bayesian analyses on a multilocus dataset representing all genera of Eremobatidae and most species groups of *Eremobates*, *Eremochelis*, and *Hemerotrecha* (Table 1). In addition, we used the mulitilocus data to produce a time-calibrated phylogeny using a Bayesian approach, providing the first insight into camel spider diversification and establishing a framework for future biogeographical investigations within the family.

Table 1
Taxonomy of the Solifugae family Eremobatidae (after Harvey, 2003; Brookhart and Brookhart, 2006). Numbers in parentheses indicate the number of species out of the total number represented by that group that we used as exemplars in the phylogenetic analysis.

- Subfamily Eremobatinae Kraepelin, 1901
  - *Eremobates* Banks, 1900
    - *angustus* species group (0/3 species)
    - *aztecus* species group (1/1 species)
    - *lapazi* species group (0/1 species)
    - *pallipes* species group (7/17 species)
    - *palpisetulosus* species group (25/41 species)
    - *scaber* species group (6/13 species)
    - *vallis* species group (0/1 species)
  - *Eremocosta* Roewer, 1934 (6/13 species)
  - *Eremorhax* Roewer, 1934 (4/10 species)
  - *Eremothera* Muma, 1951 (2/2 species)
  - *Horribates* Muma, 1962 (1/3 species)
- Subfamily Therobatinae Muma, 1951
  - *Chanbria* Muma, 1951 (3/4 species)
  - *Eremochelis* Roewer, 1934
    - *andreasana* species group (1/2 species)
    - *bilobatus* species group (4/16 species)
    - *branchi* species group (2/14 species)
    - *imperialis* species group (4/5 species)
    - *striodorsalis* species group (1/1 species)
  - *Hemerotrecha* Banks, 1903
    - *banksi* species group (3/9 species)
    - *branchi* species group (6/9 species)
    - *denticulata* species group (2/6 species)
    - *serrata* species group (1/1 species)
    - *simplex* species group (2/7 species)
    - *texana* species group (0/1 species)

2. Materials and methods

2.1. Taxon sampling

We used an exemplar approach (Prendini, 2001) to represent the diversity within Eremobatidae. The ingroup comprised 81 exemplar species encompassing 45% of the species diversity in the family (Table 2). The exemplars represented all eremobatid genera and all but the following species groups: *Eremobates angustus* (which includes *E. angustus* Muma, 1951, *E. becki* Muma, 1986, and *E. cruzi* Muma, 1951), *E. lapazi* Muma, 1986 (monotypic species group), and *E. vallis* Muma, 1989 (monotypic group); and the *Hemerotrecha texana* Muma, 1951 species group (also monotypic). Since higher level relationships within Solifugae are presently unresolved, we used representatives of three solifuge

Table 2
List of 81 exemplar taxa of the Solifugae family Eremobatidae included in this study with specimen voucher and GenBank numbers. Column 1 includes exemplar numbers used in the Fig. 1 distribution map. All voucher specimens except those with the UID prefixes LB, UNAM, or CAS are housed in the arachnology collection of the DMNS. (DMNS = Denver Museum of Nature and Science; AMNH = American Museum of Natural History; UNAM = Universidad Nacional Autónoma de México; CAS = California Academy of Sciences. Complete data for all ingroup taxa can be found at http://symbiota4.acis.ufl.edu/scan/portal/index.php.

Map #	Species	Family	Subfamily species group	Collecting locale	Specimen unique ID	GenBank#s			
						16S	CO1	H3	28S
	Ammotrechula wasbaueri Muma, 1962	Ammotrechidae		USA: California, San Bernardino Co., Joshua Tree NP, 34.072167°, −116.291517°	DMNS ZA.24695	KT276566	KT276649	KT276816	KT276732
	Eusimonia nigrescens Kraepelin, 1899	Karschiidae		TURKEY: Yolbasi, 37.266889°, 40.8000°	AMNH LP.7473	KT276633	KT276715	KT276881	KT276799
	Trichotoma michaelseni (Kraepelin, 1914)	Gylippidae	Lipophaginae	NAMIBIA: Erongo Region, Swakopmund District, Namib-Naukluft Park, 23.551667°, 15.047222°	AMNH LP.5724	KT276648	KT276731	KT276894	KT276815
1	*Chanbria rectus* Muma, 1962	Eremobatidae	Therobatinae	USA: California, Riverside Co., Palm Springs, 33.897367°, −116.54835°	DMNS ZA.24696	KT276567	KT276650	KT276817	KT276733
2	*Chanbria regalis* Muma, 1951	Eremobatidae	Therobatinae	USA: California, Imperial Co., Algodones Sand Dunes, 33.02°, −115.1°	DMNS ZA.17279	KT276568	KT276651	KT276818	KT276734
3	*Chanbria serpentinus* Muma, 1951	Eremobatidae	Therobatinae	USA: Arizona, Pima Co., Catalina SP, 32.42445°, −110.92271	DMNS ZA.26433	KT276569	KT276652	KT276819	KT276735
4	*Eremochelis andreasana* (Muma, 1962)	Eremobatidae	Therobatinae *andreasana*	USA: Arizona, Pima Co., Organ Pipe Cactus NM, 31.95471°, −112.80043°	DMNS ZA.26851	KT276609	KT276692	KT276858	KT276775
5	*Eremochelis bilobatus* (Muma, 1951)	Eremobatidae	Therobatinae *bilobatus*	USA: Texas, Presidio Co., Big Bend Ranch SP, 29.346444°, −104.079278°	DMNS ZA.21949	KT276610	KT276693	Missing	KT276776
6	*Eremochelis giboi* Muma, 1989	Eremobatidae	Therobatinae *bilobatus*	USA: California, Kern Co., Dove Springs, 35.4360°, −118.0202°	DMNS ZA.16048	KT276612	KT276694	KT276860	KT276778
7	*Eremochelis morrisi* Muma, 1951	Eremobatidae	Therobatinae *bilobatus*	USA: California, San Bernardino Co., 29 Palms, 34.1657°, −115.9033°	DMNS ZA.17240	KT276617	KT276699	KT276865	KT276783
8	*Eremochelis nudus* (Muma, 1963)	Eremobatidae	Therobatinae *bilobatus*	USA: California, Kern Co., Dove Springs, 35.4353°, −118.0357°	DMNS ZA.15992	KT276618	KT276700	KT276866	KT276784
9	*Eremochelis branchi* (Muma, 1951)	Eremobatidae	Therobatinae *branchi*	USA: California, Riverside Co., Palm Springs, 33.8974°, −116.5484°	DMNS ZA.17216	KT276611	Missing	KT276859	KT276777
10	*Eremochelis insignitus* Roewer, 1934	Eremobatidae	Therobatinae *branchi*	USA: California, San Bernardino Co., Wonder Valley Amboy Rd., 34.1657°, −115.9037°	DMNS ZA.24694	KT276614	KT276696	KT276862	KT276780
11	*Eremochelis imperialis* (Muma, 1951)	Eremobatidae	Therobatinae *imperialis*	USA: Nevada, Nye Co., Nevada Test Site, 36.95439°, −116.04933°	DMNS ZA.26853	KT276613	KT276695	KT276861	KT276779
12	*Eremochelis kastoni* Rowland, 1974	Eremobatidae	Therobatinae *imperialis*	USA: California, San Diego Co., Tenaja Corridor, 33.50320°, −117.33700°	DMNS ZA.15935	KT276615	KT276697	KT276863	KT276781
13	*Eremochelis larreae* (Muma, 1962)	Eremobatidae	Therobatinae *imperialis*	USA: California, San Bernardino Co., Wonder Valley Ambox Rd., 34.16570°, −115.90370°	DMNS ZA.24693	KT276616	KT276698	KT276864	KT276782
14	*Eremochelis undulus* Muma, 1989	Eremobatidae	Therobatinae *imperialis*	USA: California, Imperial Co., Salton Sea, 33.17370°, −115.83720°	DMNS ZA.16135	KT276620	KT276702	KT276868	KT276786
15	*Eremochelis striodorsalis* (Muma, 1962)	Eremobatidae	Therobatinae *striodorsalis*	USA: California, San Diego Co., Santa Ysabel, 33.10900°, −116.67200°	DMNS ZA.16017	KT276619	KT276701	KT276867	KT276785
16	*Hemerotrecha californica* (Banks, 1899)	Eremobatidae	Therobatinae *banksi*	USA: California, San Diego Co., Rancho Jamul, 32.67350°, −116.86100°	DMNS ZA.22152	KT276636	KT276718	KT276883	KT276802
17	*Hemerotrecha hanfordana* Brookhart and Cushing, 2008	Eremobatidae	Therobatinae *banksi*	USA: Utah, Box Elder Co., Key Springs Pass Rd., 41.60100°, −113.89100°	DMNS ZA.18363	KT276640	KT276722	KT276887	KT276806
18	*Hemerotrecha kaboomi* Brookhart and Cushing, 2008	Eremobatidae	Therobatinae *banksi*	USA: Nevada, Nye Co., Nevada Test Site, 36.98869°, −116.09665°	DMNS ZA.26890	Missing	KT276723	KT276888	KT276807
19	*Hemerotrecha bixleri* Muma, 1989	Eremobatidae	Therobatinae *branchi*	USA: Arizona, Pima Co., Organ Pipe Cactus NM, 31.95471°, −112.80043°	DMNS ZA.26444	KT276634	KT276716	Missing	KT276800
20	*Hemerotrecha branchi* Muma, 1951	Eremobatidae	Therobatinae *branchi*	USA: Nevada, Nye Co., Nevada Test Site, 36.66056°, −115.99361°	DMNS ZA.26389	KT276635	KT276717	KT276882	KT276801

Table 2 (*continued*)

Map #	Species	Family	Subfamily species group	Collecting locale	Specimen unique ID	GenBank#s			
						16S	CO1	H3	28S
21	*Hemerotrecha milsteadi* Muma, 1962	Eremobatidae	Therobatinae *branchi*	USA: Texas, Presidio Co., Big Bend Ranch SP, 29.50333°, −103.89222°	DMNS ZA.21708	KT276641	KT276724	KT276889	KT276808
22	*Hemerotrecha nevadensis* Muma, 1951	Eremobatidae	Therobatinae *branchi*	USA: Nevada, Nye Co., Nevada Test Site, 36.66042°, −115.99344°	DMNS ZA.26768	KT276643	KT276726	Missing	KT276810
23	*Hemerotrecha sevilleta* Brookhart and Cushing, 2002	Eremobatidae	Therobatinae *branchi*	USA: New Mexico, Sandoval Co., Bandolier NP, 34.79000°, −111.76000°	DMNS ZA.18234	KT276645	KT276728	Missing	KT276812
24	*Hemerotrecha xena* Muma, 1951	Eremobatidae	Therobatinae *branchi*	USA: California, San Bernardino Co., Joshua Tree NP, 34.12869°, −116.03672°	DMNS ZA.23480	KT276646	KT276729	KT276892	KT276813
25	*Hemerotrecha denticulata* Muma, 1951	Eremobatidae	Therobatinae *denticulata*	USA: Colorado, Montrose Co., Falcon Rd., 38.59800°, −107.94770°	DMNS ZA.16085	KT276637	KT276719	KT276884	KT276803
26	*Hemerotrecha neotena* Muma, 1989	Eremobatidae	Therobatinae *denticulata*	USA: Arizona, Cochise Co., NW Bisbee, 31.52167°, −110.04583°	DMNS ZA.22648	KT276642	KT276725	KT276890	KT276809
27	*Hemerotrecha serrata* Muma, 1951	Eremobatidae	Therobatinae *serrata*	USA: California, Riverside Co., Coachella Valley Amtrak Station, 33.89740°, −116.54840°	DMNS ZA.17225	KT276644	KT276727	KT276891	KT276811
28	*Hemerotrecha elpasoensis* Muma, 1962	Eremobatidae	Therobatinae *simplex*	USA: Texas, Brewster Co., Dalquest Research Site, 29.55397°, −103.78736°	DMNS ZA.23553	KT276638	KT276720	KT276885	KT276804
29	*Hemerotrecha fruitana* Muma, 1951	Eremobatidae	Therobatinae *simplex*	USA: Colorado, Weld Co., Road 84, 40.6000°, −104.3000°	DMNS ZA.16705	KT276639	KT276721	KT276886	KT276805
30	*Eremobates aztecus* Pocock, 1902	Eremobatidae	Eremobatinae *aztecus*	MEXICO: Querétaro, Ciudad de Querétaro (no coords)	UNAMazt	KT276575	KT276658	Missing	KT276741
31	*Eremobates arizonicus* (Roewer, 1934)	Eremobatidae	Eremobatinae *pallipes*	USA: Utah, San Juan Co., E Hwy 191, 37.53800°, −109.47900°	DMNS ZA.16714	KT276573	KT276656	KT276823	KT276739
32	*Eremobates barberi* (Muma, 1951)	Eremobatidae	Eremobatinae *pallipes*	USA: Texas, Culberson Co., County Rd. 2424, 31.11000°, −104.21200°	DMNS ZA.16179	KT276577	KT276660	KT276826	KT276743
33	*Eremobates docolora* Brookhart and Muma, 1981	Eremobatidae	Eremobatinae *pallipes*	USA: Wyoming, Albany Co., Ivinson Ave., 41.31187°, −105.59192°	DMNS ZA.22649	KT276580	KT276663	KT276829	KT276746
34	*Eremobates durangonus* Roewer, 1934	Eremobatidae	Eremobatinae *pallipes*	USA: Arizona, Cochise Co., BLM NW Bisbee, 31.5222°, −110.04528°	DMNS ZA.19984	KT276581	KT276664	KT276830	KT276747
35	*Eremobates pallipes* (Say, 1823)	Eremobatidae	Eremobatinae *pallipes*	USA: Colorado, Douglas Co., Parker, 39.55472°, −104.70250°	DMNS ZA.22647	KT276592	KT276675	KT276841	KT276758
36	*Eremobates simoni* Muma, 1970	Eremobatidae	Eremobatinae *pallipes*	USA: Texas, Ward Co., outside Monahans SP, 31.62772°, −102.78825°	DMNS ZA.22986	KT276599	KT276682	KT276848	KT276765
37	*Eremobates woodruffi* Brookhart and Muma, 1988	Eremobatidae	Eremobatinae *pallipes*	MEXICO: Coahuila, Viesca, Dunas de Bilbao, 28.481417°, −102.894233	UNAMwoo	KT276608	KT276691	KT276857	KT276774
38	*Eremobates affinis* (Kraepelin, 1899)	Eremobatidae	Eremobatinae *palpisetulosus*	USA: Arizona, Cochise Co., BLM NW Bisbee, 31.5222°, −110.04528°	DMNS ZA.19983	KT276571	KT276654	KT276821	KT276737
39	*Eremobates ajoanus* Muma and Brookhart, 1988	Eremobatidae	Eremobatinae *palpisetulosus*	USA: Arizona, Pima Co., BLM south Ajo, 32.34278°, −112.85972°	DMNS ZA.20053	KT276572	KT276655	KT276822	KT276738
40	*Eremobates bajadae* Muma and Brookhart, 1988	Eremobatidae	Eremobatinae *palpisetulosus*	USA: New Mexico, Bernalillo Co., Kirtland Air Force Base, 34.94750°, −106.53194°	DMNS ZA.22471	KT276576	KT276659	KT276825	KT276742
41	*Eremobates coahuilanus* Muma, 1986	Eremobatidae	Eremobatinae *palpisetulosus*	MEXICO: Coahuila, Cuatro-Cienegas, 26.9870°, −102.0692°	CAS EC no#	KT276578	KT276661	KT276827	KT276744
42	*Eremobates gracilidens* Muma, 1951	Eremobatidae	Eremobatinae *palpisetulosus*	USA: California, Riverside Co., San Jacinto Mtns, 33.88360°, −116.62340°	DMNS ZA.17237	KT276582	KT276665	KT276831	KT276748
43	*Eremobates kastoni* Muma and Brookhart, 1988	Eremobatidae	Eremobatinae *palpisetulosus*	USA: California, San Diego Co., Little Cedar Ridge, 32.62914°, −116.86559°	DMNS ZA.19042	KT276584	KT276667	KT276833	KT276750
44	*Eremobates kraepelini* Muma, 1951	Eremobatidae	Eremobatinae *palpisetulosus*	USA: California, Orange Co., Aliso-Wood Canyon, 33.53882°, −117.72554°	DMNS ZA.18992	KT276585	KT276668	KT276834	KT276751

(*continued on next page*)

Table 2 (*continued*)

Map #	Species	Family	Subfamily species group	Collecting locale	Specimen unique ID	GenBank#s			
						16S	CO1	H3	28S
45	*Eremobates leechi* Muma and Brookhart, 1988	Eremobatidae	Eremobatinae *palpisetulosus*	USA: California, Monterey Co., Garrapata SP, 36.45764°, −121.92043°	DMNS ZA.23764	KT276586	KT276669	KT276835	KT276752
46	*Eremobates marathoni* Muma, 1951	Eremobatidae	Eremobatinae *palpisetulosus*	USA: Texas, Brewster Co., Dalquest Research Site, 29.55667°, −103.79333°	DMNS ZA.21651	KT276587	KT276670	KT276836	KT276753
47	*Eremobates nanus* Muma, 1962	Eremobatidae	Eremobatinae *palpisetulosus*	USA: California, San Benito Co., Pinnacles NM, 36.49726°, −121.21128°	DMNS ZA.23692	KT276588	KT276671	KT276837	KT276754
48	*Eremobates nivis* Muma and Brookhart, 1988	Eremobatidae	Eremobatinae *palpisetulosus*	USA: California, Alameda Co., Carnegie OHV, 37.63678°, −121.56589°	DMNS ZA.23457	KT276589	KT276672	KT276838	KT276755
49	*Eremobates nodularis* Muma, 1951	Eremobatidae	Eremobatinae *palpisetulosus*	USA: New Mexico, Socorro Co., Sevilleta NWR, 34.20520°, −106.37532°	DMNS ZA.16772	KT276590	KT276673	KT276839	KT276756
50	*Eremobates norrisi* Muma and Brookhart, 1988	Eremobatidae	Eremobatinae *palpisetulosus*	Mexico: Chihuahua, Janos Solere, 30.89000°, −108.19000°	DMNS ZA.18357	KT276591	KT276674	KT276840	KT276757
51	*Eremobates palpisetulosus* Fichter, 1941	Eremobatidae	Eremobatinae *palpisetulosus*	USA: Colorado, Fremont Co., Cañon City, 38.44400°, −105.35000°	DMNS ZA.16202	KT276593	KT276676	KT276842	KT276759
52	*Eremobates papillatus* Muma, 1970	Eremobatidae	Eremobatinae *palpisetulosus*	USA: California, San Diego Co., Little Cedar Canyon, 32.64300°, −116.87000°	DMNS ZA.16236	KT276594	KT276677	KT276843	KT276760
53	*Eremobates pimanus* Muma and Brookhart, 1988	Eremobatidae	Eremobatinae *palpisetulosus*	USA: Arizona, Pima Co., BLM W Corona de Tucson, 31.97417°, −110.84222°	DMNS ZA.20088	KT276595	KT276678	KT276844	KT276761
54	*Eremobates polhemusi* Muma and Brookhart, 1988	Eremobatidae	Eremobatinae *palpisetulosus*	USA: Utah, San Juan Co., on Road 230, 37.38100°, −109.51900°	DMNS ZA.16718	KT276596	KT276679	KT276845	KT276762
55	*Eremobates scopulatellus* Muma and Brookhart, 1988	Eremobatidae	Eremobatinae palpisetulosus	USA: California, San Diego Co., Camp Pendleton, 33.31851°, −117.46909°	DMNS ZA.19206	KT276597	KT276680	KT276846	KT276763
56	*Eremobates scopulatus* Muma, 1951	Eremobatidae	Eremobatinae *palpisetulosus*	USA: California, San Diego Co., Elliot Reserve, 32.89266°, −117.10002°	DMNS ZA.19146	KT276598	KT276681	KT276847	KT276764
57	*Eremobates titschacki* (Roewer, 1934)	Eremobatidae	Eremobatinae *palpisetulosus*	USA: California, Monterey Co., Seaside, 36.63090°, −121.81160°	DMNS ZA.22981	KT276603	KT276686	KT276852	KT276769
58	*Eremobates tuberculatus* (Kraepelin, 1899)	Eremobatidae	Eremobatinae *palpisetulosus*	USA: California, San Diego Co., Borrego Valley, 33.11720°, −116.19820°	DMNS ZA.23890	KT276604	KT276687	KT276853	KT276770
59	*Eremobates vicinus* Muma, 1963	Eremobatidae	Eremobatinae *palpisetulosus*	USA: California, San Diego Co., Santa Ysabel, 33.10900°, −116.67200°	DMNS ZA.16015	KT276605	KT276688	KT276854	KT276771
60	*Eremobates villosus* Muma, 1951	Eremobatidae	Eremobatinae *palpisetulosus*	USA: California, Alameda Co., Carnegie OHV, 37.63678°, −121.56589°	DMNS ZA.23767	KT276606	KT276689	KT276855	KT276772
61	*Eremobates williamsi* Muma and Brookhart, 1951	Eremobatidae	Eremobatinae *palpisetulosus*	USA: California, Riverside Co., San Jacinto Mtns, 33.7000°, −116.72000°	DMNS ZA.17238	KT276607	KT276690	KT276856	KT276773
62	*Eremobates* sp.	Eremobatidae	Eremobatinae *palpisetulosus*	USA: California, San Bernardino Co., Joshua Tree NP, 34.07711°, −116.03575°	DMNS ZA.23835	KT276601	KT276684	KT276850	KT276767
63	*Eremobates actenidia* Muma, 1989	Eremobatidae	Eremobatinae *scaber*	USA: Utah, San Juan Co., Road 248, 37.32200°, −109.50900°	DMNS ZA.18359	KT276570	KT276653	KT276820	KT276736
64	*Eremobates ascopulatus* Muma, 1951	Eremobatidae	Eremobatinae *scaber*	USA: Utah, Box Elder Co., off Winter Cabin Rd., 41.48800°, −113.89800°	DMNS ZA.18360	KT276574	KT276657	KT276824	KT276740
65	*Eremobates corpink* Brookhart and Cushing, 2004	Eremobatidae	Eremobatinae *scaber*	USA: Utah, Kane Co., Grand Staircase-Escalante NM, 37.50957°, −111.72543°	DMNS ZA.28560	KT276579	KT276662	KT276828	KT276745
66	*Eremobates icenoglei* Brookhart and Cushing, 2004	Eremobatidae	Eremobatinae *scaber*	USA: California, Riverside Co., Double Butte, 33.71380°, −117.09167°	DMNS ZA.24685	KT276583	KT276666	KT276832	KT276749
67	*Eremobates socal* Brookhart and Cushing, 2004	Eremobatidae	Eremobatinae *scaber*	USA: California, San Bernardino Co., Joshua Tree NP, 34.09327°, −116.26460°	DMNS ZA.24689	KT276600	KT276683	KT276849	KT276766

Table 2 (*continued*)

Map #	Species	Family	Subfamily species group	Collecting locale	Specimen unique ID	GenBank#s			
						16S	CO1	H3	28S
68	*Eremobates* sp.	Eremobatidae	Eremobatinae *scaber*	USA: Riverside Co., Coachella Valley Amtrak Station, 33.89737°, −116.54835°	DMNS ZA.23552	KT276602	KT276685	KT276851	KT276768
69	*Eremocosta acuitlapanensis* (Vasquez and Gavin, 2000)	Eremobatidae	Eremobatinae	MEXICO: Estado de México, Se Tonatico, 18.8168°, −99.646683°	UNAMacu	KT276621	KT276703	KT276869	KT276787
70	*Eremocosta calexicensis* (Muma, 1951)	Eremobatidae	Eremobatinae	USA: California, San Bernardino Co., Twenty Nine Palms, 34.16500°, −115.90340°	DMNS ZA.17223	KT276622	KT276704	KT276870	KT276788
71	*Eremocosta gigasella* (Muma, 1970)	Eremobatidae	Eremobatinae	USA: Texas, Brewster Co., Big Bend NP, 29.19288°, −102.94700°	DMNS ZA.22143	KT276623	KT276705	KT276871	KT276789
72	*Eremocosta spinipalpis* (Kraepelin, 1899)	Eremobatidae	Eremobatinae	MEXICO: Baja Norte (no additional locale data)	UNAMspi	KT276624	KT276706	KT276872	KT276790
73	*Eremocosta striata* (Putnam, 1883)	Eremobatidae	Eremobatinae	USA: Arizona, Santa Cruz Co., east of Amado, 31.71400°, −111.00900°	DMNS ZA.21079	KT276625	KT276707	KT276873	KT276791
74	*Eremocosta titania* (Muma, 1951)	Eremobatidae	Eremobatinae	USA: California, San Bernardino Co., Joshua Tree NP, 34.07711°, −116.03575°	DMNS ZA.23781	KT276626	KT276708	KT276874	KT276792
75	*Eremorhax joshui* (Brookhart and Muma, 1987)	Eremobatidae	Eremobatinae	USA: California, Riverside Co., Coachella Valley Amtrak Station, 33.89740°, −116.54830°	DMNS ZA.17212	KT276627	KT276709	KT276875	KT276793
76	*Eremorhax magnus* (Hancock, 1888)	Eremobatidae	Eremobatinae	USA: Arizona, Pima Co., Organ Pipe Cactus NM, 32.04167°, −112.87472°	DMNS ZA.28196	KT276628	KT276710	KT276876	KT276794
77	*Eremorhax puebloensis* Brookhart, 1965	Eremobatidae	Eremobatinae	USA: Colorado, Pueblo Co., Pueblo, 38.25400°, −104.60900°	DMNS ZA.16424	KT276629	KT276711	KT276877	KT276795
78	*Eremorhax pulcher* Muma, 1963	Eremobatidae	Eremobatinae	USA: Nevada, Nye Co., Nevada Test Site, 36.80243°, −115.98495°	DMNS ZA.26432	KT276630	KT276712	KT276878	KT276796
79	*Eremothera drachmani* Muma	Eremobatidae	Eremobatinae	USA: Arizona, Pima Co., Catalina SP, 32.42445°, −110.92271°	DMNS ZA.28191	KT276631	KT276713	KT276879	KT276797
80	*Eremothera* sp (nr *sculpturata*)	Eremobatidae	Eremobatinae	USA: California, Imperial Co., near Salton Sea, 33.12593°, −115.52132°	DMNS ZA.22651	KT276632	KT276714	KT276880	KT276798
81	*Horribates bantai* Muma, 1989	Eremobatidae	Eremobatinae	USA: California, San Bernardino Co., Granite Cove, 34.78000°, −115.65000°	DMNS ZA.17691	KT276647	KT276730	KT276893	KT276814

families as outgroups in our phylogenetic analyses: *Eusimonia nigrescens* Kraepelin, 1899 (Karschiidae Kraepelin, 1899), *Ammotrechula wasbaueri* Muma, 1962 (Ammotrechidae Roewer, 1934), and *Trichotoma michaelseni* (Kraepelin, 1914) (Gylippidae Roewer, 1933). Additional outgroups were used for the divergence dating analysis (see Section 2.4 Divergence time estimation). In preliminary higher level phylogenetic analyses of the order Solifugae carried out in LP's lab (L.P. unpubl. data), Eremobatidae was monophyletic and was most closely related to Karschiidae or to Gylippidae (depending on the analysis). Thus, we chose a gylippid and a karschiid to represent outgroups. We also chose an ammotrechid for outgroup comparison because this is the other family commonly found in North America. Complete collecting data for the DMNS specimens can be found at http://symbiota4.acis.ufl.edu/scan/portal/index.php. The collecting localities of the ingroup exemplars are presented in Fig. 1 and summarized in Table 2.

2.2. Tissue samples

Specimens for DNA analysis were collected throughout the deserts of the southwestern U.S.A. between 2007 and 2012. Gylippid and karschiid outgroup specimens were collected during trips to Kazakhstan and Namibia. Collecting was carried out as close as possible to type localities of target species. Specimens were collected at lights in the desert and placed directly in 100% ethanol, kept cool in the field, and stored between −20° and −80 °C in the lab. Some specimens were collected in pitfall traps with 95% propylene glycol (lab grade) placed for 4–5 weeks at various field sites and were then transferred to 100% ethanol. Vink et al. (2005) demonstrated the efficacy of lab grade propylene glycol for molecular tissue preservation. Additional material was sent in by collaborators and colleagues.

2.3. Molecular techniques

We isolated genomic DNA from leg tissues using a standard phenol–chloroform extraction and DNeasy Extraction Kits (Qiagen Inc., Valencia, CA, USA). A multilocus dataset was produced from four gene loci found to be phylogenetically informative in studies of other arachnid taxa (Edgecombe et al., 2000; Prendini et al., 2003, 2005; Arnedo et al., 2004; Boyer et al., 2005): two mitochondrial gene fragments, the cytochrome oxidase subunit I gene (CO1) and the 3′ end of the 16S rRNA gene (16S); and two nuclear gene fragments, the D3 large subunit ribosomal RNA 28S gene (28S) and a variable fragment of the histone H3 protein-coding gene (H3) (Table 3). Gene fragments were amplified using the polymerase chain reaction (PCR). Two to five μL of genomic template was used per 25 μL reaction. For most of the 25 μL reactions, we used the AccuPrime™*Taq* DNA Polymerase System (Invitrogen, Carlsbad, California, USA) protocol: 2.5 μL 10X Buffer II; 0.125 additional $MgCl_2$ (50 mM); 1 μL forward primer; 1 μL

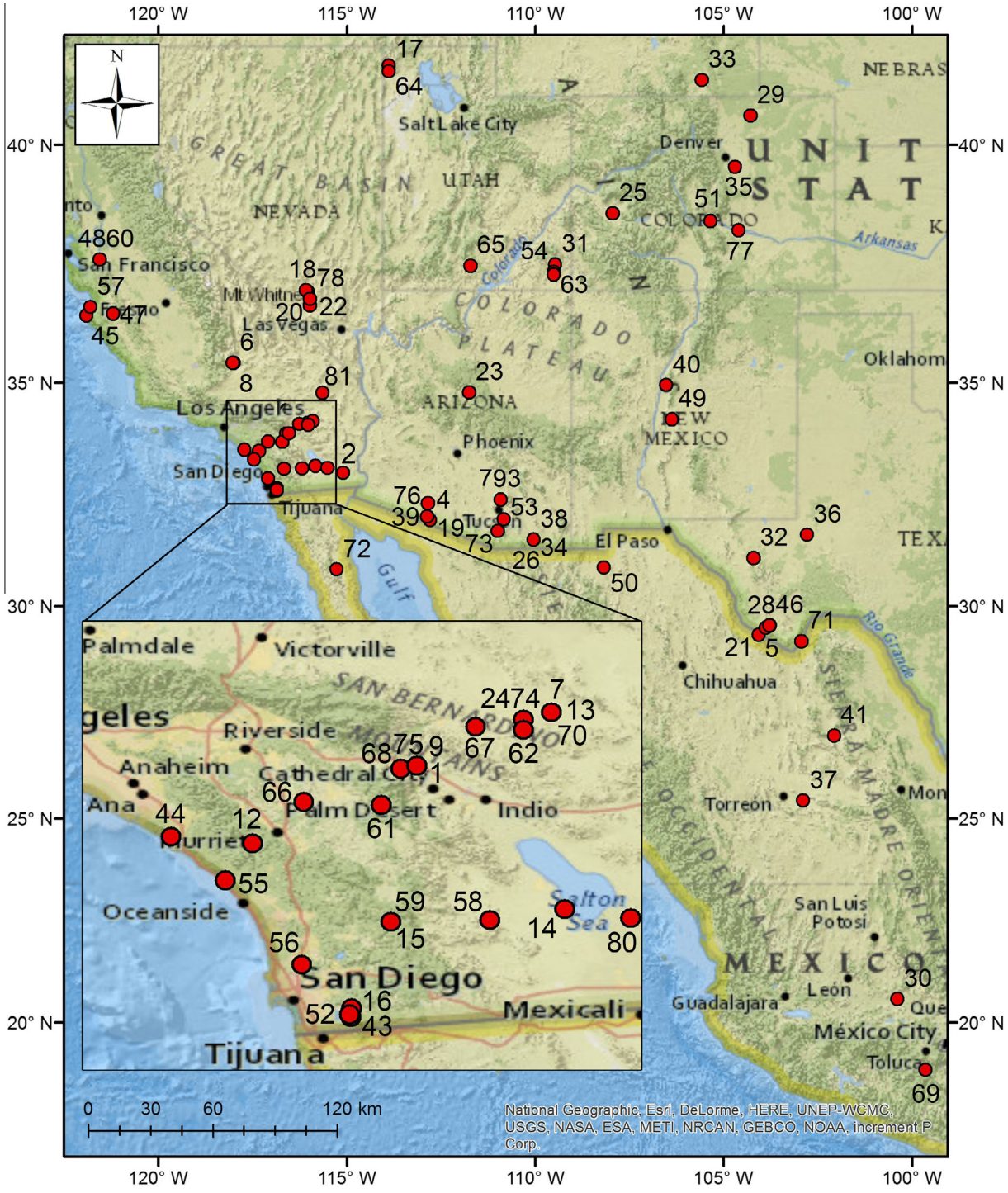

Fig. 1. Map of southwestern North America showing collection localities for ingroup exemplar species used in the phylogenetic analysis of the solifuge family Eremobatidae. Numbers correspond to map numbers in Table 2.

reverse primer 0.5 μL AccuTaq polymerase; 0.175 μL Bovine Serum Albumin (BSA); 2–5 μL template DNA; and 17.7–14.7 μL ddH2O. The optimum annealing temperature was determined for each primer pair (Table 3). PCR products were cleaned to remove excess dNTPs and unincorporated primers using ExoSap-IT (Afymetrix, Inc., Santa Clara, California, USA). Purified products were sent to the University of Washington High Throughput Sequencing Center (http://www.htseq.org) for sequencing. Purified PCR products were cycle sequenced using Big Dye Terminator v.3.1 (Life Technologies, Grand Island, New York, USA), for cycle sequencing in a 5 μL reaction at 1/20th Big Dye. The sequencing reactions were then cleaned with Life Technologies Big Dye Xterminator solution and sequenced on an ABI 3730xl DNA automated sequencer.

2.4. Phylogenetic analysis

The chromatograms were checked visually and assembled into contigs using Geneious 6.1.6 (Biomatters, http://www.geneious.com). The consensus sequences for individual loci were aligned in Geneious using MUSCLE (Edgar, 2004). Alignments were then

Table 3
Primers used to amplify and sequence DNA for the phylogenetic analysis of the Solifugae family Eremobatidae. Forward and reverse primer sequences are presented (5′–3′) as well as the optimal melting temperature (*Tm*) for the primer pairs (the lower *Tm* of the oligonucleotide pair was used as the annealing temperature) (Rychlik et al., 1990).

Gene	Primer	Sequence (5′–3′)	*Tm* (°C)	References
16S rRNA	16Sar	CGCCTGTTTATCAAAAACAT	49°	Simon et al. (1994)
	16Sbr	CTCCGGTTTGAACTCAGATCA		Simon et al. (1994)
CO1	HCOoutout	GTAAATATATGRTGDGCTC	45°	Prendini et al. (2005)
	LCO	GGTCAACAACAAATCATAAAGATATTGG		Folmer et al. (1994)
28s rRNA	28Sa	GACCCGTCTTGAAACACGGA	58°	Nunn et al. (1996)
	28Sbout	CCCACAGCGCCAGTTCTGCTTACC		Prendini et al. (2005)
H3 histone	H3af	ATGGCTCGTACCAAGCAGACVGC	54°	Colgan et al. (1998)
	H3ar	ATATCCTTRGGCATRATRGTGAC		Colgan et al. (1998)

checked by eye for accuracy and trimmed to minimize missing characters. The final data matrix comprised 497 bp for 16S, 714 bp for CO1, 323 bp for H3, and 438 bp for 28S for a total of 1972 bp when concatenated. Seven exemplars, missing data for one or more loci (Table 2), were nevertheless included in the analysis upon the grounds that partially resolved exemplars can improve phylogenetic accuracy (Wiens and Tiu, 2012). All sequences generated for this study were deposited in GenBank (Table 2).

Sequences were concatenated by hand. We used PartitionFinder (Lanfear et al., 2012, 2014) to select the best-fitting partitioning schemes and models of molecular evolution for the alignments from the pool of models available in MrBayes v3.2.2 (Ronquist and Huelsenbeck, 2003). We did not use models of invariant plus gamma (I + G models) since other studies have suggested a strong correlation between the proportion of invariable sites and the gamma shape parameter (Ren et al., 2005; Jia et al., 2014). We used the Bayesian Information Criterion (BIC) for model selection. PartitionFinder indicated that the concatenated data set should be partitioned by loci for the non-coding gene regions (16S and 28S) and by codon for the coding genes (CO1 and H3). GTR + G was the best model for the 16S locus; SYM + G was the best model for CO1 codon 1; F81 + I for CO1 codon 2; HKY + G for CO1 codon 3; K80 + I for H3 codon 1; K80 + G for H3 codon 2; SYM + G for H3 codon 3; and K80 + I for the 28S locus.

Phylogenetic relationships were reconstructed from the concatenated data set with Maximum Likelihood (ML) and Bayesian Inference (BI) on the Cyberinfrastructure for Phylogenetic Research cluster (CIPRES Gateway v 3.1; Miller et al., 2010) at the San Diego Supercomputer Center. ML was conducted using RAxML (Stamatakis, 2006) with 1000 rapid bootstrap replicates, and the likelihood of the final tree was evaluated and optimized under the GTRGAMMA model (Stamatakis, 2006). The BI analysis was conducted using MrBayes and run for 100 million generations, with 4 chains (one cold, three heated), sampling every 5000 generations. To facilitate convergence, we used the ML phylogeny as a starting tree in the MrBayes analysis, as recommended by Hall (2011). The first 25% of trees were discarded as burn-in. A stopval of 0.01 was set to ensure the analysis would run to convergence, which was verified using Tracer (Rambaut et al., 2014). Nodes with posterior probabilities (PP) of $\geqslant$0.95 or bootstrap support (BS) of $\geqslant$0.70 were considered strongly supported (Hillis and Bull, 1993; Felsenstein, 2004). We used FigTree v 1.4.0 (Rambaut, 2009) to visualize results from both analyses.

2.5. Divergence time estimation

We estimated the timing of diversification among eremobatids in BEAST v. 1.8.0 (Drummond and Rambaut, 2007). For this analysis, we included data representing four additional outgroups available from GenBank: a Daesiidae sp. (JN018379.1), a Rhagodidae sp. (JN018167.1 & JN018381.1), a Galeodidae sp. (JN018166.1 & JN018380.1), and a *Nothopuga* sp. (Ammotrechidae, EU024482.1). Based on the results from our BI and ML analyses, as well as morphological observations (by J.O.B.), we removed the following taxa from the original data set as they are likely to represent synonymous species: *Eremobates* n. sp. (*palpisetulosus* group) (= *Eremobates gracilidens* Muma, 1951); *Eremobates vicinus* Muma, 1963 (= *Eremobates scopulatus* Muma, 1951); *Eremobates corpink* Brookhart and Cushing, 2004 (= *Eremobates actenidia* Muma, 1989); *Eremobates docolora* Brookhart and Muma, 1981 (= *Eremobates pallipes* (Say, 1823)); *Eremobates ajoanus* Muma and Brookhart, 1988 (= *Eremobates pimanus* Muma and Brookhart, 1988); *Eremobates bajadae* Muma and Brookhart, 1988 (= *Eremobates polhemusi* Muma and Brookhart, 1988); *Eremobates socal* Brookhart and Cushing, 2004 (= *Eremobates icenogelei* Brookhart and Cushing, 2004); *Eremochelis morrisi* (Muma, 1951) (= *Eremochelis insignitus* Roewer, 1934); and *Eremocosta titania* (Muma, 1951) (= *Eremocosta calexicensis* (Muma, 1951)).

Solifugae fossils are sparse (Dunlop, 2010; Dunlop et al., 2015), but by using the additional samples from GenBank we were able to calibrate a lineage based on age estimates of an amber inclusion *Palaeoblossia groehni* Dunlop, Wunderlich, and Poinar, 2004, a daesiid from Baltic amber, was used to calibrate a lineage representing the common ancestor of Daesiidae. Setting maximum age bounds for calibration priors is difficult due to gaps and uncertainty of the fossil record, so we assigned long tails to the probability distribution of gamma distributed calibration priors (Ho and Phillips, 2009). Minimum date estimates for *P. groehni* range from 49 to 44 Ma (J. Dunlop, pers. comm.), so parameters were adjusted (shape = 1.0 scale = 101.0 offset = 38.5) such that the 95% highest posterior density (HPD) of the lower bound was 43.68. Higher-level relationships among solifuge families are not yet understood, but pseudoscorpions (i.e. Shultz, 2007) and acariform mites (i.e. Pepato et al., 2010) have been proposed as the sister group to camel spiders. The pseudoscorpion fossil record extends to ca. 390 Ma and the fossil record for acariform mites dates to ca. 411 Ma, so we chose parameters such that the 97% HPD upper bound (411.1 Ma) included the oldest likely origin for solifuges.

Given the broad distributions of our fossil calibrations, we added a biogeographic calibration to the ingroup by calibrating a node shared by two species that span the Trans-Mexican Volcanic Belt; *Eremobates aztecus* Pocock, 1902 in the north and *Eremocosta acuitlapanensis* (Vasquez and Gavin, 2000) to the south (Fig. 1). Volcanic uplift of the Trans-Mexican Volcanic Belt from 7 to 3.5 Ma is thought to have been a strong driver of diversification in a variety of taxa now distributed on both sides of the mountain range (reviewed in Bryson et al., 2012). Although they currently represent different genera, our ML and BI analyses suggested that *E. aztecus* and *E. acuitlapanensis* are sister taxa, and we hypothesize that their divergence can be attributed to uplift of the Trans-Mexican Volcanic Belt. Therefore, we applied a normal distribution with parameters adjusted (mean = 5.25 stdev = 1.1) such that the 95% HPD bounds included the timeframe of volcanic uplift.

Preliminary BEAST runs failed to converge with high ESS values (>200), so we conducted the analysis using the less complex HKY substitution model. In addition, initial runs using an uncorrelated lognormal clock for all genes revealed low ucld.stdev (<1.0) for CO1 and 16S partitions, suggesting clock-like evolution. Therefore, we conducted subsequent analyses using a strict clock for CO1 and 16S (as suggested in the BEAST manual) and a Yule tree prior. We assigned broad uniform priors to the clock-rate and ucld.mean; 0.2 and 0.002 for the mtDNA genes and 0.01 and 0.0001 for the nuclear genes. We conducted three MCMC runs with 40^6 generations sampled every 1000 generations. Log files were imported into Tracer v. 1.6 (Drummond and Rambaut, 2007) to assess convergence and to ensure adequate ESS values (>200 for each parameter). We summarized output trees using TreeAnnotator v. 1.8.0 (Drummond and Rambaut, 2007), discarding the first 20% as burn-in, and visualized the maximum clade credibility tree in FigTree. However, given the uncertainty associated with fossil estimates, we treat the BEAST chronogram as a working hypothesis.

3. Results

3.1. Phylogenetic analysis

Maximum Likelihood (ML) and Bayesian analysis (BI) of the concatenated mulilocus dataset support similar tree topologies with high support values present for most nodes (Fig. 2). Eremobatidae, *Eremorhax*, and *Eremothera* were monophyletic along with a group comprising all subfamily Eremobatinae exemplars except *Horribates bantai* Muma, 1989 and a group comprising all *Eremocosta* exemplars except *Eremocosta acuitalpanensis*. The

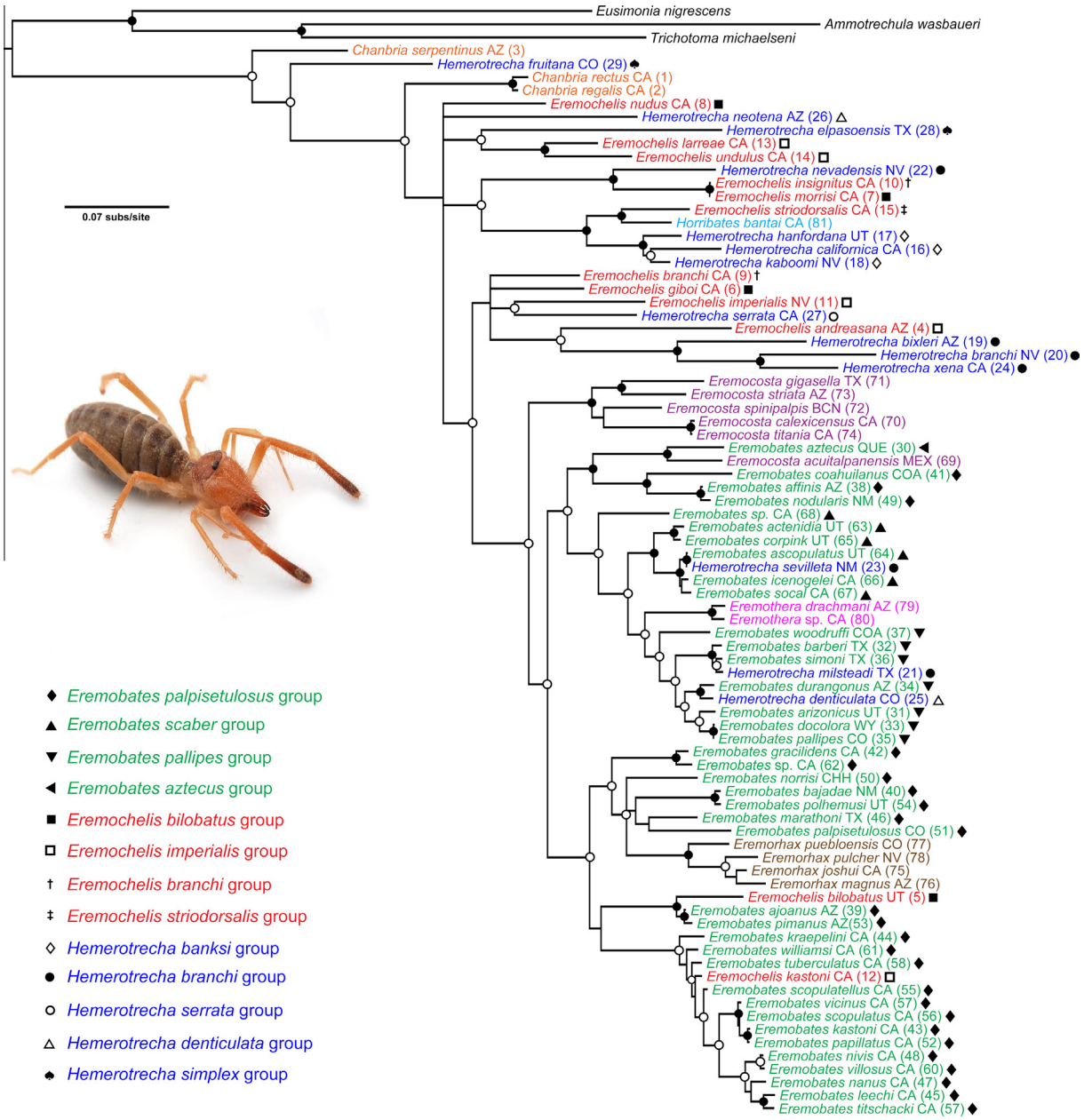

Fig. 2. Majority rule (50%) consensus tree depicting results of Bayesian phylogenetic analysis of the multilocus dataset for the North American solifuge family Eremobatidae. Terminal taxa are colored by genus, with adjacent symbols representing species groups, as depicted in the legend. Nodes with strong support in Bayesian (PP $\geqslant$ 0.95) and Maximum Likelihood (BS $\geqslant$ 0.70) analyses are represented by black circles, whereas nodes supported by only one analysis are indicated by white circles.

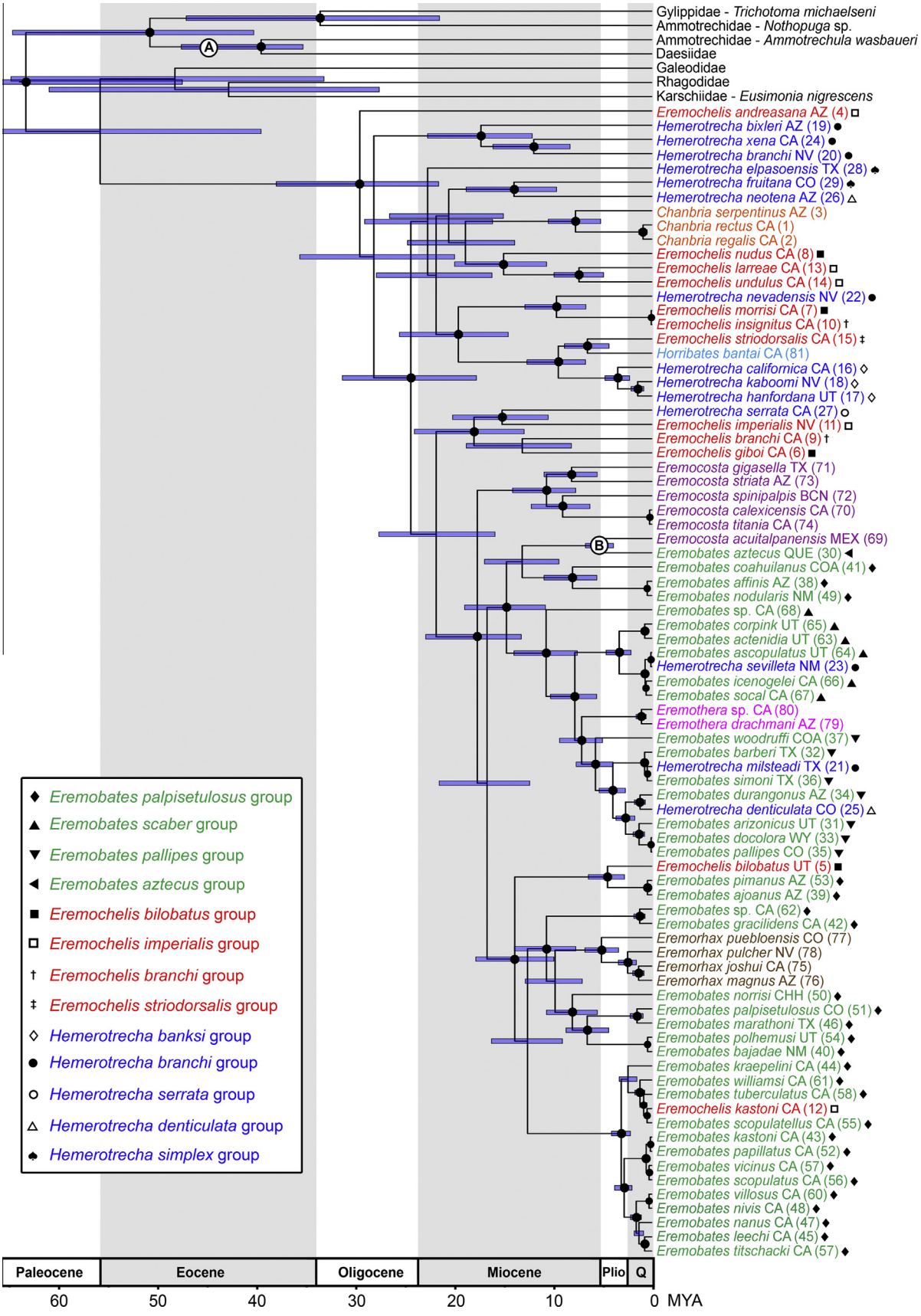

Fig. 3. Rate-calibrated chronogram obtained by BEAST analysis of the multilocus dataset for the Eremobatidae. Bars represent highest posterior densities (95%) around mean date estimates. Terminal taxa are colored by genus, with adjacent symbols representing species groups, as depicted in the legend. Black circles indicate nodes with posterior probabilities of $\geqslant$0.95; white circles represent posterior probabilities of $\geqslant$0.90. Node calibrations were based on a solifuge fossil from Baltic amber (A) and hypothesized vicariance associated with uplift of the Trans-Mexican Volcanic Belt (B).

subfamily Therobatinae and the genera *Eremobates*, *Eremochelis*, and *Hemerotrecha* were polyphyletic. Of the 14 species groups analyzed only the *H. banksi* group was monophyletic. The *Eremobates scaber* group was paraphyletic with respect to *Hemerotrecha sevilleta*. The placement of *Hemerotrecha milsteadi* and *H. denticulata* rendered the *Eremobates pallipes* group paraphyletic. Only a single sample was available for the *Eremobates aztecus* group, *Eremochelis striodorsalis* group, and *H. serrata* group so their monophyly could not be assessed. The remaining species groups recognized within *Eremobates*, *Eremochelis*, and *Hemerotrecha* were polyphyletic. However, components of the *E. palpisetulosus* species group formed well supported regional subgroups including a California/Mojave subgroup and a Texas/Chihuahuan/short grass prairie subgroup. The California/Mojave Desert subgroup included *E. leechi* Muma and Brookhart, 1988, *E. kraepelini* Muma, 1951, *E. kastoni* Muma and Brookhart, 1988, *E. nanus* Muma, 1962, *E. nivis* Muma and Brookhart, 1988, *E. papillatus* Muma, 1970, *E. scopulatus* Muma, 1951, *E. scopulatellus* Muma and Brookhart, 1988, *E. titschacki* (Roewer, 1934), *E. tuberculatus* (Kraepelin, 1899), *E. vicinus* Muma, 1963, *E. villosus* Muma, 1951, and *E. williamsi* Muma and Brookhart, 1988. The Texas/Chihuahuan/short grass prairie subgroup included *E. bajadae* Muma and Brookhart, 1988, *E. marathoni* Muma, 1951, *E. norrisi* Muma and Brookhart, 1988, *E. palpisetulosus* Fichter, 1941, and *E. polhemusi* Muma and Brookhart, 1988, which are all paraphyletic with respect to *Eremorhax* (Fig. 2).

3.2. Divergence time estimation

Rate estimates were 0.0379 for CO1, 0.0087 for 16S, 0.0068 for H3, and 0.0004 for 28S. These are in line with rates published for other arachnid groups, i.e., Bryson et al. (2014), Bidegaray-Batista and Arnedo (2011). The topology of the BEAST analysis (Fig. 3) was largely congruent with the BI phylogeny but differed at several nodes that were not well resolved in the BI analysis and suggested that *Chanbria* is monophyletic. In the BEAST analysis, in which we included additional outgroups, the family Eremobatidae remained monophyletic with a 100% posterior support. Additionally, some of the relationships within the California/Mojave subgroup of the *E. palpisetulosus* species group differed slightly from the BI analysis; however, most of the species from California in this group remained monophyletic.

The time to the most recent common ancestor of extant eremobatids was estimated to be within the late Eocene to early Miocene, with a mean estimate in the Oligocene (32.2 Ma). Subsequent diversification rate appears to have been rather constant in the family, with mean estimates for 2 nodes in the Oligocene, 36 in the Miocene, 10 in the Pliocene, and 31 in the Quaternary. Of all species groups, the California clade of the *E. palpisetulosus* species group underwent the greatest diversification in the Quaternary. *Chanbria* was monophyletic with strong support and with a TMRCA estimate in the late Miocene. *Eremothera* and *Eremorhax* were both monophyletic with TMRCA estimates in the Quaternary and Pliocene respectively.

4. Discussion

4.1. Eremobatid systematics

The results presented here support the monophyly of Eremobatidae and a large group comprising all species of the subfamily Eremobatinae except *Horribates*, which should be removed from the subfamily to restore its monophyly. Muma (1962) tentatively placed this genus in Eremobatinae based upon the presence of only one tiny tarsal claw on leg I, the diagnostic character for Eremobatinae. *Horribates* differs from all other eremobatid genera based on the presence of movable spines on the pedipalps. Our results support Muma's recommendation in his unpublished manuscript to remove *Horribates* from inclusion in Eremobatinae.

The analyses unequivocally demonstrated that Therobatinae is artificial and should be redefined. The diagnostic character for Eremobatinae is the presence of a single claw on the tip of the first leg although, according to the original diagnosis of the subfamily (Kraepelin, 1901), claws are absent on the first leg (probably because they are greatly reduced and were difficult to visualize at the time). The single claw is flattened with a broad base and represents a synapomorphy because most arachnids possess two to three claws on all legs (Dunlop, 2002). The genera currently placed in Therobatinae – *Chanbria*, *Eremochelis*, and *Hemerotrecha* – possess the more common arachnid condition of two tarsal claws on the first leg and no morphological synapomorphies uniting them. Although the genus *Chanbria* was rendered paraphyletic in the BI and ML analyses, it was monophyletic with strong support in the BEAST analysis. We suspect this was due to a less parameterized analysis with a simpler partitioning scheme.

In addition to dispensing with Therobatinae, its component genera, especially *Eremochelis* and *Hemerotrecha*, are in need of revision. Both genera, and most of the species groups recognized within them, were polyphyletic in the analyses presented here. Only the *H. banksi* species group was recovered as monophyletic. *Therobates* Muma, 1951, synonymized with *Eremochelis* by Muma (1970), was originally defined by the presence of a mesal or mesoventral groove on the fixed finger of the male chelicera; a flagellar complex composed of a dorsal row or group of simple tubular bristles, a mesal row or group of plumose bristles, and a ventral or basal row or group of tubular bristles; and ctenidia on the post-spiracular abdominal sternite of the male. *Hemerotrecha* was defined by the presence of a style-like fixed finger of the male chelicerae, with a faint mesal groove and a variable shaped lower edge; and a flagellar complex composed of a dorsal row of striate bristles, the striae formed by tiny setae, and a ventral row of curved plumose setae (Muma, 1951). None of the characters used to diagnose *Eremochelis* or *Hemerotrecha* could be considered synapomorphic for these genera because they occur in various combinations throughout the family Eremobatidae.

The large eremobatine genus *Eremobates* was also polyphyletic and should be re-assessed. However, some of the species groups within *Eremobates*, e.g., the *pallipes* and *scaber* groups, are phylogenetically and geographically cohesive. The *palpisetulosus* species group formed several separate clades, one distributed throughout the deserts of California and another restricted to the Chihuahuan desert and short grass prairie, and two other clades less well defined geographically: one including *E. coahuilanus*, *E. affinis*, and *E. nodularis*; the other including *E. gracilidens* and an undescribed species from California.

Other eremobatid genera, or major components thereof, were recovered as well supported groups. The eremobatine genera *Eremorhax* and *Eremothera* were consistently monophyletic. *Eremocosta* was rendered paraphyletic or not monophyletic in all or most analyses by a single species, *E. acuitalpanensis*, the generic placement of which will require reevaluation.

4.2. Eremobatid diversification

Results from our BEAST analysis (Fig. 3) suggest that Eremobatidae originated in the Cenozoic, with early diversification probably occurring in the Oligocene as steppe and semidesert habitats began to replace forests and savannas in western North America (Axelrod, 1979, 1983). Divergence date estimates indicate that diversification continued throughout the Miocene. These were periods of vibrant tectonic activity resulting in widespread lithospheric deformation in western North America, with a pulse of

block-faulting and extension that formed the Basin and Range Province (Atwater and Stock, 1998; Wernicke and Snow, 1998). The concurrent orogeny of the North American Cordilleras effectively blocked moist tropical air currents from the Pacific Ocean and Gulf of Mexico causing a gradual increase in aridity and leading to the formation of modern warm deserts by the middle Miocene (Axelrod, 1979; Hafner and Riddle, 2008). Uplift along the Coast and Cascade ranges in southern Oregon then formed a rain shadow, bringing additional aridity to more northern regions such as the Great Basin Desert and Colorado Plateau (Baldwin, 1964). Given that nearly all solifuges reside in xeric habitats, we hypothesize that early Eremobatidae diversification was associated with the complex geologic history of western North America and resultant changes in aridity that gave rise to the region's modern deserts.

Phylogenetic analyses of several other groups of arid-adapted animals from North America also indicate origins in timeframes associated with desert formation. The mean estimate for the most recent common ancestor of New World rattlesnakes (Crotalinae Oppel, 1811) was 22.7 Ma (Douglas et al., 2006), 18.5 Ma for night lizards (*Xantusia* Baird, 1859; Leavitt et al., 2007), and approximately 20 Ma for giant hairy scorpions (Hadrurinae Stahnke, 1974; MRG unpubl. data). The earliest identifiable fossil representatives of desert and grassland rodent subfamilies Heteromyinae Gray, 1868 and Perognathinae Coues, 1875, as well as representatives from several extant phyrnosomatid lizard genera occur in the early Miocene (Wood, 1935; Holman, 1970, 1995; Robinson and Van Devender, 1973; Yatkola, 1976; Alexander and Riddle, 2005). Thus, eremobatids and other arid-adapted taxa appear to have radiated into novel desert environments in North America as they became available. Interestingly, this is contrary to biogeographic patterns inferred from genetic studies of several South American desert taxa, which proposes that they required long timescales to adapt to arid environments (Guerrero et al., 2013).

The BEAST analysis suggests that diversification continued during the geologically active Pliocene. Many additional divergence estimates fall within the Quaternary, indicating that considerable species-level diversity within the Eremobatidae may be attributed to Pleistocene climate fluctuations. In particular, a clade containing *Eremobates palpisetulosus* group species (along with *Eremochelis kastoni*) distributed along the Coast, Transverse, and Peninsular ranges of California was estimated to share a common ancestor in the Pliocene and subsequently diversified mostly during the Pleistocene.

Eremobatidae are clearly arid-adapted, have limited vagility (compared to winged insects and ballooning spiders), and are distributed almost exclusively in North American deserts and semi-deserts. Phylogenetic evidence now places their history within the timeframe when these regions began to develop. Based on these results, we hypothesize that the history of diversification within Eremobatidae is tied to the origin and evolution of modern deserts as well as to Pleistocene climate change. Therefore, we propose that camel spiders could be an ideal, but underexplored system with which to study to the evolution of desert biotas. For instance, an historical biogeographic analysis of Eremobatidae has the potential for assessing the impact of major geologic events of the Neogene on lineage formation. Furthermore, phylogeographic investigations of the family present opportunities for learning about the influence of historical climate change on current patterns of arid-adapted arthropod diversity.

5. Conclusion

This study provides the first family-level phylogenetic analysis of camel spider relationships and provides a baseline phylogeny to inform future taxonomic revisions of the North American family Eremobatidae (this taxonomic revision is in prep. by JOB and PEC). Although several genera and a major group comprising most species of the subfamily Eremobatinae are monophyletic, the subfamily Therobatinae and its component genera are not and require taxonomic revision.

The family Eremobatidae appears to have originated in the Cenozoic, diversifying in the Oligocene and Miocene as the North American deserts began to form. Diversification continued during the geologically active Miocene and Pliocene, and throughout the Quaternary, suggesting that extant eremobatid diversity could predominantly be a product of historical landscape alterations and climate fluctuations related to desert formation.

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