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Original Article

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A phylogenomic approach to a taxonomic revision: a combination, new synonymies, and a description of two new species within the camel spider genus *Chanbria* Muma, 1951 (Solifugae: Eremobatidae)

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ABSTRACT

This study summarizes the taxonomic treatment of the camel spider genus *Chanbria* Muma, 1951. Taking an integrative taxonomic approach incorporating phylogenomic, morphological, and geographical information, the genus is herein revised. Of the four species currently placed in the genus, two are retained: *Chanbria regalis* Muma, 1951 and *Chanbria serpentinus* Muma, 1951. *Eremochelis plicatus* (Muma, 1962) is transferred to this genus because it is consistently recovered in a clade with *Chanbria* based on several phylogenetic analyses using hundreds of loci recovered from ultraconserved element data. In this study, we re-analyse previously acquired genomic data to assess former species hypotheses and identify new morphological synapomorphies that support the monophyly of *Chanbria*. The genetic data support the synonymization of *Chanbria rectus* Muma, 1962 syn. nov. with *C. regalis*. Furthermore, we synonymize *Chanbria tehachapianus* Muma, 1962 syn. nov. with *C. regalis* because *C. tehachapianus* was erected based on limited morphological information and lack of geographical separation between other populations of *C. regalis*. Two new species, *Chanbria brookharti* sp. nov. and *Chanbria mapemes* sp. nov., are described. This brings the total number of species of *Chanbria* described to five recognized species: *C. regalis, C. serpentinus, C. plicatus* com. nov., *C. brookharti* sp. nov., and *C. mapemes* sp. nov.

Keywords: phylogenomics; ultraconserved elements; mitonuclear discordance; taxonomic revision; solifuges

INTRODUCTION

Chanbria Muma, 1951 is a genus in the North American solifuge family Eremobatidae Kraepelin, 1901 distributed across the southwestern USA and northwestern Mexico (Muma 1951, 1962). Currently, this small genus includes four species: *Chanbria regalis* Muma, 1951, *Chanbria serpentinus* Muma, 1951, *Chanbria tehachapianus* Muma, 1962, and *Chanbria rectus* Muma, 1962. Polis and McCormick (1986) mention the species '*Chanbria coachellae*' but do not provide or reference a description for this taxon. Harvey (2003) listed this taxon as *nomen nudum*, and we suspect that this was likely to be a reference to *C. regalis* based on geographical location. *Chanbria* are notable for their unusual, highly modified male chelicerae (Muma 1951, 1962) and are found in the Sonoran, Mojave, and Chihuahuan Deserts, with some populations being associated with sparsely vegetated dune habitats.

In the first published molecular phylogeny of Eremobatidae (Cushing *et al.* 2015), *Chanbria* was recovered as paraphyletic in two of three phylogenetic analyses. In the Bayesian and maximum likelihood (ML) analyses, *Chanbria* was recovered as the earliest diverging lineage of the family, with low support. In their estimated BEAST topology (Bouckaert *et al.* 2014), *Chanbria* is recovered as an early-diverging, monophyletic lineage, sister to a clade with *Eremochelis nudus* Muma, 1963, *Eremochelis larreae* Muma, 1962, and *Eremochelis undulus* Muma, 1989 (Cushing *et al.* 2015). In a recent ultraconserved element (UCE) phylogeny produced by Garcia *et al.* (2024), *Chanbria* was consistently recovered as a well-supported clade. Moreover, this clade remained

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stable when analysed using multiple analytical approaches (Garcia EL, Cushing PE, unpublished data) and in another independent study with an increased taxon sampling of *Eremobates* (Jones RR, Garcia EL, Shikak G, Brookhart JO, Graham MR, Cushing PE, unpublished data), thus providing a foundation to pursue a much needed taxonomic revision of this genus.

The motivation for this study is part of a major taxonomic effort to revise the North American family Eremobatidae. Leveraging both freshly collected samples and museum representatives, we analyse genetic samples of *Chanbria* to determine the validity of previously described species. We use this information to identify new synapomorphies that can be used for a revised taxonomic key to the genus. We also estimate a dated phylogeny to understand the evolutionary history of *Chanbria* by investigating the major biogeographical events that might have been influential in maintaining species limits. Piecing together the results of our analyses with our accumulated morphological and geographical information allowed us to revise the genus and helped to provide a better understanding of the basic biology of an understudied taxon, Solifugae Sundevall, 1833.

Taxonomic history

Chanbria was originally placed within the subfamily Therobatinae Muma, 1951, in the North American family Eremobatidae, based on a single morphological character, i.e. the presence of two claws on the tarsus of leg I (Muma 1951). In an unpublished revision of Eremobatidae, Muma created a new subfamily, in addition to Eremobatinae Kraepelin, 1901 and Therobatinae Muma, 1951, named Hemerotrechinae (Muma MH, unpublished manuscript). Muma included *Chanbria* and many *Hemerotrecha* species in this subfamily based on the combination of possessing two tarsal claws on leg I and the male chelicerae with no mesal groove (flagellar groove) on the fixed finger (FF). Females within this classification were described as having a triangular, ovate, sometimes elongate, or incised opercular morphology. In 2015, Cushing *et al.* recovered Therobatinae as paraphyletic in their molecular analyses (Cushing *et al.* 2015). Furthermore, the phylogenetic result from Cushing *et al.* (2015) did not support Muma's subfamily hypothesis of Hemerotrechinae.

The genus *Chanbria* was erected by Muma (1951), with the type species *C. regalis* described from a mature male holotype and a mature male paratype collected from Twentynine Palms, CA, USA. Males of the genus were described as having a 'fixed finger distinctly sinuate and lacking mesal groove' and lacking abdominal ctenidia. The male flagellum complex was described as 'consisting almost entirely of plumose setae that tend to be flattened or clavate near the tip of the finger'. The female operculum was described only from a single specimen as 'lobate posteriorly, with the spermathecal opening occurring behind them'. The fondal teeth of the female chelicerae were described as 'graded III, IV, II, I in size' for the ectal row and 'mesal row I, III, II, IV'. Using the terminology established by Bird *et al.* (2015), this indicates that in the ectal row of fondal teeth the profondal proximal (PFP) tooth is the largest, followed by the profondal subproximal (PFSP) tooth, profondal submedial tooth (PFSM), then finally the profondal medial (PFM) tooth, which is the smallest. In the mesal row of teeth, the PFM tooth is the largest, followed by the PFP tooth, PFSM tooth, then finally the PFSP tooth, which is the smallest. Muma (1951) also described *C. serpentinus* from a single male holotype collected in Tucson, AZ, USA, remarking that the species can be differentiated from *C. regalis* by 'small size and different cheliceral dentition'.

Muma (1962) described two additional new species in the genus. *Chanbria tehachapianus* was described from a mature male holotype from the Tehachapi Mountains, Kern County, CA, USA (additional locality data for the holotype were not provided). *Chanbria rectus* was described from a mature male holotype and immature female allotype from Barstow, San Bernardino County, CA, USA. Additionally, a female allotype of *C. regalis* was described from Palm Springs, Riverside County, CA, USA. The description of additional female *Chanbria* allotypes caused Muma (1962) to revise the diagnosis of the genus for females based on fondal teeth, noting that the *C. tehachapianus* allotype possesses only two ectal fondal teeth, seemingly corresponding to teeth III and IV (corresponding to the PFP and PFSP teeth according to Bird *et al.* 2015) and that females frequently lack teeth I and II (corresponding to the PFM and PFSM teeth according to Bird *et al.* 2015) or possess them in a highly reduced state. However, Muma mentioned in the description for *C. tehachapianus* that a putative female record for this species occurred in Sonora, Mexico, suggesting that this species had a wide distribution that overlapped with *C. regalis* and *C. rectus*.

Muma (1962) also described the species *Therobates plicatus* Muma, 1962. He later synonymized *Therobates* with *Eremochelis* (Muma 1970). Although Muma placed *Eremochelis plicatus* in the *Eremochelis bilobatus* Muma 1951 species group, he speculated that this species was not a good representative of the group on the basis that 'the females of this species have the ectal fondal tooth formula different from that of the males….' Based on molecular phylogenetic evidence and shared morphological synapomorphies identified in this study (Supporting Information, Fig. S1), we unite this species with *Chanbria*.

Distribution and natural history

Chanbria is known to be distributed across the southwestern USA and northern Mexico, and species in this generally psammophilic genus are restricted primarily to the Sonoran and Mojave warm deserts (Fig. 1). The life histories and ecologies of *Chanbria* spp., like many/most solifuges, are poorly understood. The sparse presence of some *Chanbria* species (the newly described *Chanbria brookharti*) in collections might indicate a high level of geographical, habitat, or seasonal specificity (Fig. 2). Museum records suggest that *Chanbria* occurs throughout most of the year, except November–February, which might indicate that this is their overwintering period. *Chanbria regalis* appears to have bimodal phenological activity, with peak records occurring in May and August for adults (Fig. 2). Other *Chanbria* species, such as *C. plicatus* and *C. serpentinus*, also reflect a similar pattern, in which peak records occur during the third month after the first appearance in the year. This general 3-month activity trend has been reported in at least one other eremobatid species, *Eremobates marathoni* Muma 1951 (Punzo, 1998). Records indicate that *Chanbria* specimens are usually observed active and collected at night, demonstrating nocturnal habits.

In terms of overall coloration and morphology, most *Chanbria* species are light tan or reddish-yellow in coloration; however,

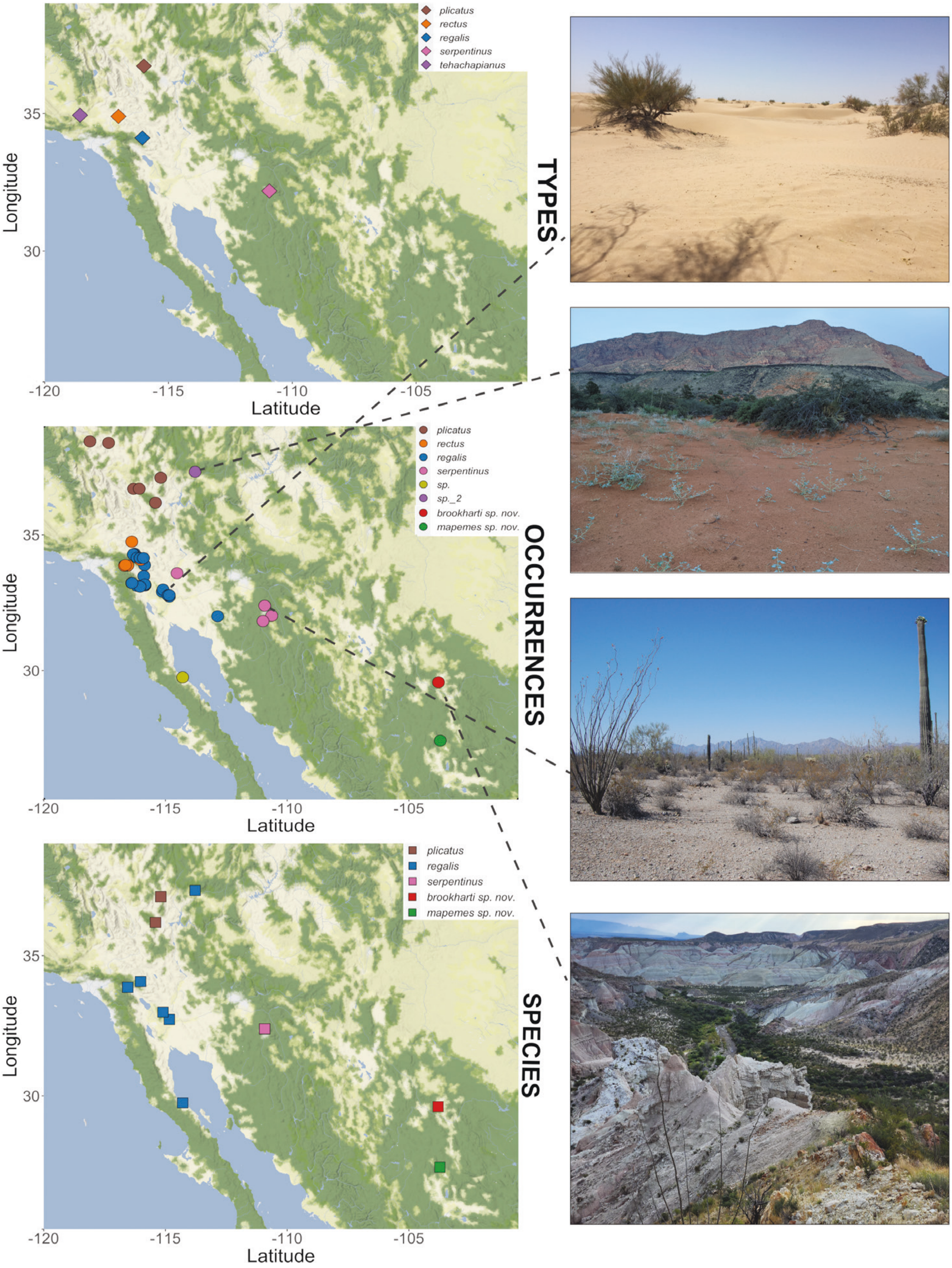

Figure 1. Maps of georeferenced type localities, museum occurrence records, and localities of DNA clades. The key in the top map refers to species type locations according to Muma (1951) and Muma (1962). The key in the middle map refers to species hypotheses according to the taxonomic descriptions. Sample 'sp' refers to specimen DMNS ZA.42397 and 'sp_2' refers to sample DMNS ZA.44237, because we were not able to identify these two with confidence based on morphology only. The key in the bottom map refers to species designations as defined in this study. The right column refers to example *Chanbria* habitats and corresponds to localities indicated by the dashed lines. The top picture is from Imperial County Sand Dunes, CA, USA. The second picture below is from Washington City, UT, USA (photograph credit: Zach Valois). The third picture below is Catalina State Park, AZ, USA (photograph credit: Paula Cushing). The bottom picture is from Dalquest Desert Research Site, near Alamo Springs, TX, USA (photograph credit: Paula Cushing).

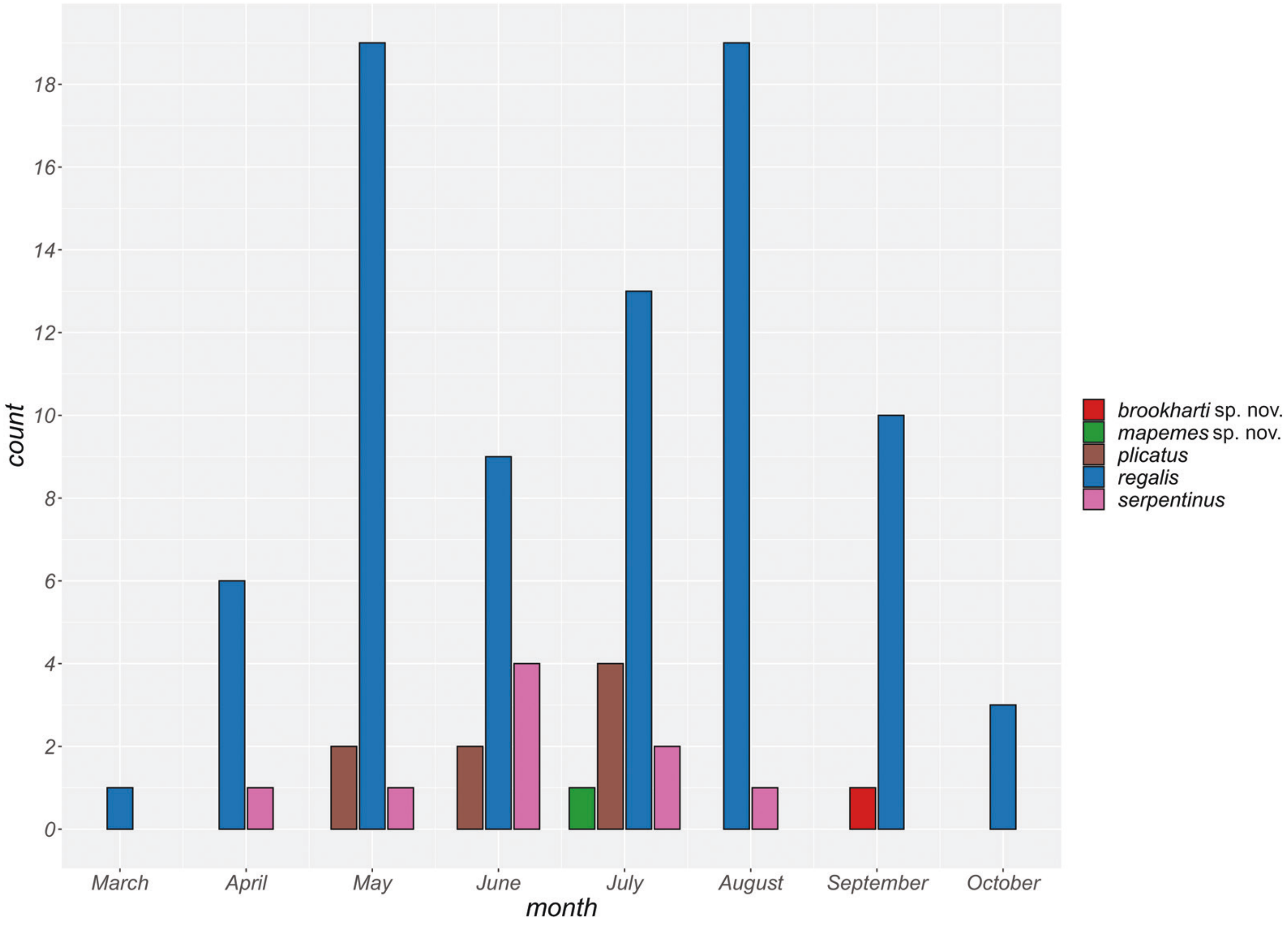

Figure 2. Summary of observed *Chanbria* adult occurrence records for species as defined in this study.

C. serpentinus, *C. plicatus*, and the newly described *Chanbria mapemes* possess dark markings on their propeltidium, legs, and pedipalps. Many of the adult specimens we examined have proportionately long legs and pedipalps, which might be an adaptation for cursoriality in open, sandy habitats. Some eremobatid males possess ctenidia, which are enlarged abdominal setae located ventrally on the fifth sternite, proximal to the unpaired spiracle. Since the creation of the genus by Muma (1951), one of the character combinations used to identify *Chanbria* was that species lacked ctenidia altogether. However, the presence of ctenidia on male *C. mapemes* challenges the assumption that ctenidia can be used as a qualitative character for delimiting generic boundaries, and therefore might not be a reliable character for taxonomic identification, as noted independently by Jones and Cushing (2021). The lack of ctenidia in most of the known male *Chanbria* (and other eremobatid taxa) might have unique ecological and behavioural implications compared with other taxa possessing ctenidia, because these structures have been hypothesized to have a sensory function (Jones and Cushing 2021). However, the exact function of ctenidia in the Eremobatidae has proved elusive, and the purpose of these structures remains unknown (Jones and Cushing 2021).

An observation of hunting behaviour in juvenile *Chanbria* by Conrad and Cushing (2011) was described as an erratic search pattern, in which juveniles occasionally reversed course to excavate a patch of sand. One individual was observed excavating a prey item from the superficial layer of sand, suggesting that *Chanbria* juveniles can sense prey, presumably using tactile and chemical cues, to locate prey items beneath the sand (Conrad and Cushing 2011). Pedipalps and malleoli were the structures hypothesized to be responsible for receiving the tactile and chemical cues, respectively. However, it is suggested that modified pedipalpal setae might also have chemosensory potential (Garcia EL, Cushing PE, Laudier D, unpublished data), which could complement their chemosensory malleoli (Brownell and Farnell, 1974). Although papillae, which are highly specialized setae located on the pedipalps of adult males, are known to have a mechanoreceptive function (Cushing *et al.* 2014), we suspect that the use of pedipalps in this hunting behaviour might be supportive of a chemosensory function, because juveniles often do not have papillae.

While measuring specimens, we encountered four gravid females, three of *C. regalis* and one of *C. serpentinus*. Eggs were visible dorsolaterally through the abdominal wall; we counted 53, 42, and 20 eggs, respectively, in each of the three *C. regalis* females and 35 eggs in the *C. serpentinus* female. We suspect that it is possible that many additional eggs are present within the abdomen of each specimen and not visible externally. Dissections of these females to count eggs to verify the presence of additional eggs within were not performed, in order to minimize damage to the specimens. These observed gravid females were collected in late May to early June, except for one *C. regalis* female, which was collected in early September.

MATERIALS AND METHODS

Institutional abbreviations

AMNH, American Museum of Natural History; ASU, Arizona State University Arthropod Collection; CAS, California Academy of Sciences; DMNS, Denver Museum of Nature and Science.

Quantitative morphological abbreviations

CH, chelicera height; CL, chelicera length; FD, fixed finger, distal tooth; FF, fixed finger; FFH, fixed finger height; FP, fixed finger, proximal tooth; FST, fixed finger, subterminal teeth; GOD, genital operculum diagonal; GOL, genital operculum length; GOW, genital operculum width; LI, leg I length; LIV, leg IV length; MD, moveable finger, distal tooth; MF, moveable finger; MM, moveable finger, medial tooth; MSM, moveable finger, submedial teeth; MST, moveable finger, subterminal teeth; PFM, profondal medial tooth; PL, pedipalp length; PPL, propeltidium length; PPW, propeltidium width; RFP, retrofondal proximal tooth.

Specimen sampling and morphometrics

We examined specimens from the following institutions based on the availability of *Chanbria* records: Denver Museum of Nature and Science (DMNS), California Academy of Sciences (CAS), American Museum of Natural History (AMNH), and Arizona State University Natural History Collections (ASU). We examined the holotypes of all known *Chanbria* species, in addition to the holotype of *E. plicatus*, all deposited at AMNH.

We recorded measurements based on previous eremobatid literature (Muma 1951, 1963, 1970, Brookhart and Muma 1981, Brookhart and Cushing 2002, 2004, 2008, Ballesteros and Francke 2008, Cushing *et al.* 2018). In these studies, 'width' is commonly used to describe the vertical length of cheliceral morphology; however, in this contribution, we refer to the vertical axis as 'height', as suggested by Bird *et al.* (2015: fig. 5), and adopt the nomenclature introduced by Bird *et al.* (2015: e.g. plates 21 and 22) to refer to cheliceral teeth. For measurements of the chelicerae of both sexes, cheliceral length (CL) was measured from the tip of the fixed finger (FF) to the midpoint of the manus, height (CH), fixed finger height (FFH), and aspect ratios (CL/CH and CH/FFH). We considered additional measurements to quantify overall shape, including tip of FF to FF distal tooth (FD) for female chelicera, tip of moveable finger (MF) to MF distal tooth (MD), and tip of MF to MF medial tooth (MM). For female opercula, we measured the genital operculum length (GOL), genital operculum width (GOW), and genital operculum diagonal (GOD), determined from measuring ~45° from the length starting point to the base outline of a single plate. In addition to quantitative measures of diagnostic structures, we also recorded measurements for total body length (TL), length of pedipalp (PL), leg I length (LI), length IV length (LIV), propeltidium length (PPL), and propeltidium width (PPW). All measurements are given in millimetres.

Images were taken using a Leica M125C stereo microscope and an Olympus SZX12 microscope. Individual images were rendered using Leica Application Suite X (LAS X) software or Helicon Focus to produce one composite image for each morphological view. Measurements were either made directly in the LAS X software, or if images were taken using the Olympus SZX12, structures were subsequently measured in Fiji (Schindelin *et al.* 2012).

Genomic and mitochondrial data collection and bioinformatics

We used UCE data obatined by means of hybrid enrichment from Garcia *et al.* (2024), wherein details on genomic DNA isolation, library preparation, and sequence read cleaning are provided. Clean reads were assembled *de novo* using the metaSPAdes assembler (Nurk *et al.* 2017) with default parameters.

We created two datasets: an ingroup-only dataset, which consisted of only *Chanbria* species, and an additional dataset that included *Horribates*, the hypothesized sister genus of *Chanbria* (Jones RR, Garcia EL, Shikak G, Brookhart JO, Graham MR, Cushing PE, unpublished data). The UCE loci were identified from assembled contigs using the arachnid UCE sequence probes (Starrett *et al.* 2017) and the *match_contigs_to_probes* function within PHYLUCE v.1.7.8 (Faircloth 2016) using the default matching values (min_coverage: 80, min_identity: 80). Recovered UCE loci were aligned using MAFFT (Katoh and Standley 2013) and trimmed using Gblocks (Castresana 2000) with the following parameters: b1: 0.5, b2: 0.5, b3: 10, and b4: 4. We also considered misalignments introduced by MAFFT and used CIAlign (Tumescheit *et al.* 2022) to remove gap-only columns and highly divergent sequences using a threshold of .8 under the *remove_divergent_minperc* argument for each alignment. For the dataset that included outgroup taxa representing *Horribates*, we subsequently generated 50% and 90% completeness matrices. Alternatively, for the *Chanbria*-only matrix, we generated only complete matrices.

We used MitoFinder (Allio *et al.* 2020), a bioinformatic pipeline specifically designed to extract mitochondrial sequences from UCE libraries, to isolate cytochrome oxidase I (*COI*) loci from UCE assemblies using the published mitogenome of *Eremobates* cf. *palpisetulosus* (Masta *et al.*, 2008; accession: PRJNA29951). The *COI* sequences were aligned using MUSCLE (Edgar 2004) and inspected manually for misalignments using AliView (Larsson 2014).

Single nucleotide polymorphism acquisition

We extracted single nucleotide polymorphisms (SNPs) using the methodology introduced by Andermann *et al.* (2019) and incorporated into the PHYLUCE workflow (Faircloth 2016, Andermann *et al.* 2019) for the *Chanbria*-only dataset. Initially, we mapped our assembled contigs from metaSPAdes onto adapter trimmed raw reads, because this step annotates duplicates and estimates coverage of the mapped reads. Next, we executed a correction step, which is intended to remove low-coverage and low-quality base calls. From the corrected FASTA consensus files generated, we then continued with the PHYLUCE pipeline to recover UCE loci using the *match_contigs_to_probes* command, as indicated above. Retrieved UCE loci were aligned with MAFFT using default settings. Subsequently, we used the 'snps_from_uce_alignments' python script (Anderman *et al.* 2019; available at https://github.com/tandermann/snp_extraction_from_alignments) to generate complete and missing ('--include_missing') SNP datasets.

Phylogenetic analyses

We performed fast ML analyses using concatenated and partitioned matrices in IQ-TREE v.2 (Minh *et al.* 2020), with 1000 ultrafast bootstrap replicates for both phylogenomic datasets (*Chanbria*-only and *Chanbria* + *Horribates*). Best-fitting models of evolution were identified using ModelFinder (Kalyaanamoorthy *et al.* 2017). For multispecies coalescent-based analyses, we estimated individual gene trees using IQ-TREE v.2 with ModelFinder to determine the best-fitting models of evolution for each locus. Inferred gene trees were then used as input in ASTRAL-III v.5.7.8 (Zhang *et al.* 2018), and nodal support was summarized by local posterior probabilities approximated by gene tree quartet frequencies (Sayyari and Mirarab 2016).

Divergence time estimation

Divergence times were estimated using BEAST 2 v.2.7.5 (Bouckaert *et al.* 2014) using *COI* data only, because several rates have been proposed for this locus. As an exploratory investigation into inferring divergence dates for *Chanbria*, we considered the arthropod mitochondrial rate of 2.3%/Myr (0.0115 substitutions/site/Myr) (Brower 1994) in separate partitioned and unpartitioned analyses. In our unpartitioned analyses, we specified the GTR model with estimated frequencies, substitution rates, and proportion invariant values at 0.01. Additionally, we implemented a relaxed lognormal clock model with a mean clock rate of 0.0115 and a birth–death model tree prior (Yule 1925, Kendall 1949). We specified a lognormal distribution for the birth and death priors (Mu: 1, Sigma: 1.25) and the 'ucld.stev' under a gamma distribution (Alpha: 0.5396, Beta: .3819). For our partitioned analyses, we specified a TN93 with all equal frequencies and estimated invariant sites as suggested by ModelFinder (Kalyaanamoorthy *et al.* 2017; TNe+I for all three partitions). Like the unpartitioned analysis, we implemented the relaxed lognormal clock model with the same mean clock rate and birth–death tree prior model. For the clock rate prior, we used the lognormal prior and adjusted the parameters to reflect a 95% highest posterior density (HPD) of 0.0133–.00988 (M: 0.0115, S: 0.09). The 'ucld.stev' was the same as above. Each analysis was initially run for 1 million generations, then we assessed convergence by examining the effective sample size (ESS) values to ensure that they were >200 in Tracer v.1.7.1 (Rambaut *et al.* 2018). Subsequently, we ran the partitioned and unpartitioned analyses for 10 million generations, sampling every 1000, and again reviewed ESS values. Lastly, trees were summarized using TreeAnnotator v.2.7.5 (Bouckaert *et al.* 2014) as a maximum clade credibility tree, with 25% of trees discarded as burn-in.

Investigation of species limits

To test previous species hypotheses, we performed basic clustering analyses to determine the potential for gene flow across our samples, especially between species that were nearly congruent morphologically (i.e. *C. rectus* and *C. regalis*). Samples were identified prior to sequencing and confirmed post hoc based on the morphological descriptions of *Chanbria* and of *E. plicatus* (Muma 1951, 1962, 1963). Initially, we used principal components analysis (PCA) to visualize the genetic clustering of our samples based on our recovered complete binary SNP dataset using the *smart_pca* function in the smartsnp R package (Herrando-Pérez *et al.* 2021). Likewise, we conducted a PCA for our mitochondrial *COI* locus by extracting SNPs from our *COI* alignment using the *fasta2genlight* function found in the *adegenet* R package (Jombart 2008). Initially, we ran the *glPca* function to assess the number of principal component (PC) axes that should be retained, as determined by the highest eigenvalues. We retained axes that inferred eigenvalues greater than one.

To identify the degree of relatedness, both intra- and interspecifically, we calculated genetic distances for both the *COI* and SNP datasets for the ingroup dataset (*Chanbria* only). For the *COI* locus, we initially converted our fasta alignment to a DNAbin object using the *fasta2DNAbin* function in the *adegenet* R package (Jombart 2008), then calculated pairwise distances under the Kimura 80 (K80) genetic distance model with the *dist.dna* function in the *ape* package (Paradis *et al.* 2004). We followed a similar approach for calculating SNP distance, such that we converted our SNP alignment to a DNAbin object; however, we used the *dist.snp* function found in the *pofadinr* package to determine SNP distance (Joly *et al.* 2015). The latter approach implements the GENOPOFAD method, derived from the phylogeny of organisms for allelic data (POFAD) algorithm (Joly and Bruneau 2006), to estimate sequence divergence from SNP data and is known to perform well when determining genomic mixture between individuals (Joly *et al.* 2015).

We performed Bayesian clustering analyses using our unlinked SNPs in STRUCTURE v.2.3.4 (Pritchard *et al.* 2000). We executed the admixture model for values of *K* (the number of assumed species) ranging from one to six, with five replicates for each value of *K* for 1 000 000 iterations and a 10% burn-in. After the STRUCTURE runs, we used the pophelper package (Francis 2017) in R to determine the optimal number of *K* according to the Evanno method (Evanno *et al.* 2005). Once the optimal number of *K* had been calculated, we used the *alignK* function in the pophelper package to align independent STRUCTURE runs within the same value of *K*, because this function works like CLUMPP (Jakobsson and Rosenberg 2007) and aligns replicate analyses (Francis 2017). We performed the methods detailed above with our complete and missing data SNP dataset, respectively.

RESULTS

Specimen sampling and molecular data

We accumulated measurements for both male and female *Chanbria* for a collective total of 49 individuals (species breakdown is given in the 'Taxonomy' section). For female *Chanbria*, we generated a total of 14 variables (e.g. cheliceral length) and for males 11 variables to quantify size aspects. To understand species distributions, we acquired locality information available on Ecdysis (https://ecdysis.org/) for DMNS and manually tabulated information from the other natural history collection loans mentioned above, totalling 96 records for adult *Chanbria* (Supporting Information, Table S1). Immature individuals were not considered owing to the uncertainty in species identification.

We re-analysed the mitochondrial and UCE data generated by Garcia *et al.* (2024) that were submitted to the Sequence Read Archive (SRA; BioProject: PRJNA982881). We recovered a total of 13 mitochondrial *COI* sequences from the *Chanbria* assemblies, and a total of 14 representatives were available for our UCE data analysis. For our UCE data, we attained 171 unique SNPs and 162 unique UCEs in our complete matrix for the ingroup-only dataset. For the data matrices that included *Horribates* as the outgroup, we recovered 687 UCE loci in our incomplete matrix, 468 in our 50% complete matrix, and 135 in our 90% complete matrix. *COI*, SNP matrices, and tree files can be found on Figshare (https://doi.org/10.6084/m9.figshare.24894948.v1).

Phylogenetic results

The results of our concatenated ML analysis were consistent with previous phylogenomic analyses (Fig. 3A; Garcia *et al.* 2024; Garcia EL, and Cushing PE, unpublished data; Jones RR, Garcia EL, Shikak G, Brookhart JO, Graham MR, Cushing PE, unpublished data). For all our ML analyses under different matrix completeness scenarios and with *Horribates* as the sister taxon, *Chanbria* was recovered as a monophyletic group with full support (https://doi.org/10.6084/m9.figshare.24894948.v1).

Both our ML and ASTRAL UCE phylogenetic analyses using our ingroup dataset recovered *E. plicatus* as the stem member of the *Chanbria* clade (Fig. 3C). The more traditionally recognized *Chanbria* species, *C. serpentinus* and *C. regalis*, were recovered as sister taxa with full support (Fig. 3C). Notably, both *C. regalis* and *C. rectus* were not mutually exclusive lineages.

Estimation of species limits

The results of our clustering analysis of SNP and *COI* data support three distinct clusters (Fig. 4A, B). The two anomalous *Chanbria* labelled 'sp' and 'sp_2' clustered with *C. rectus* and *C. regalis*. Additionally, both *C. serpentinus* and *C. plicatus* formed distinct clusters, distant from each opposing cluster. In the SNP PCA, PC1 explained ~58.23% of the variation observed and PC2 41.77%. Conversely, in the *COI* PCA of 258 SNPs recovered, the amount of variation that PC1 and PC2 explained was comparatively much less, with only 41.30% of the variation explained in PC1 and 30.9% for PC2, with the first six PCs explaining most of the variation owing to eigenvalues exceeding two.

The genetic distances between our three well-supported clades within *Chanbria* (*E. plicatus*, *C. serpentinus*, and *C. regalis*) were 47%–66% for the SNPs dataset and 11%–12% for the mitochondrial *COI* locus (Table 1; Supporting Information, Table S2).

Our STRUCTURE results gave an optimal K value of three for both our complete and missing SNPs datasets (Supporting Information, Figs S3, S4), with minimal shared alleles between major clades, and thus each sample was assigned to a single cluster (Fig. 4C). STRUCTURE results for our incomplete dataset suggest that the single *Chanbria* individual from Baja California, Mexico (DMNS ZA.44237) shares most of its allelic ancestry with *C. regalis* and *C. rectus*. The STRUCTURE results of the complete dataset illustrate complete shared ancestry among members assigned to the same group (Fig. 4C).

Chanbria divergence estimates

Divergence time estimates from *COI* data calibrated using the standard arthropod clock rate (0.0115 substitutions/site/Myr; Brower 1994) place the estimated origin of *Chanbria* in the Tortonian stage of the late Miocene epoch for both the partitioned (~8.43 Mya) and unpartitioned (~9.23 Mya) analyses (Fig. 5). The estimated age under this model for *C. plicatus* was ~2.35–2.37 Mya for both analyses and ~2.13–2.19 Mya for *C. regalis*.

DISCUSSION

Evolution of *Chanbria*

Our results support a modified outlook of the genus *Chanbria*, which includes moving *E. plicatus* to *Chanbria* as *C. plicatus* comb. nov. Because this species possesses strikingly different male cheliceral morphology, otherwise a 'non-traditional' *Chanbria* morphology, this evidence supports our phylogenomic hypothesis that *C. plicatus* is likely to be the earliest-diverging lineage. This species is distributed primarily in the Mojave Desert Basin in Nevada (Fig. 1). *Chanbria regalis* and *C. serpentinus* were recovered as sister taxa in our UCE topologies. This relationship is supported by one individual (DMNS ZA.44237) from the *C. regalis/rectus* clade sharing alleles with its sister species, *C. serpentinus*, more than any other individual (Fig. 4C) and from their similar male cheliceral morphologies (Fig. 6).

Both our genomic data and mitochondrial data suggest that the diagnostic characters identified by Muma (1962) to delimit *C. regalis* and *C. rectus* might represent intraspecific variation rather than species-level diagnostics. Within our recovered *C. regalis/rectus* clade, we were unable to identify confidently two samples (DMNS ZA.42397 from Washington City, Utah and DMNS ZA.44237 from Punta Final, Baja California) before our molecular analyses, but they closely fit the type description for *C. rectus* based on the straight fixed finger when viewed dorsally. The result of these two species falling within the *C. regalis/rectus* clade corroborated our PCAs by supporting a single, distinct cluster among *C. rectus*, *C. regalis*, and the unidentified *Chanbria*. Moreover, the consensus among the independent STRUCTURE analyses of both the complete and incomplete SNP datasets supports the synonymy of these two species as *C. regalis* and alludes to a wide species range, spanning both the Sonoran and Mojave deserts (Fig. 1). This species is restricted primarily west of the Colorado River except for a single record, and the sister taxon, *C. serpentinus*, is distributed east of the Colorado River in the Sonoran Desert (Fig. 1).

Although we were unable to sample DNA from *C. brookharti* and *C. mapemes*, we believe that their remote geographical locations in the Chihuahuan Desert in comparison to the genetically sampled *Chanbria* and their unusual male cheliceral morphology support new species status. We encourage future sampling and studies to help elucidate the placement of these species within the genus.

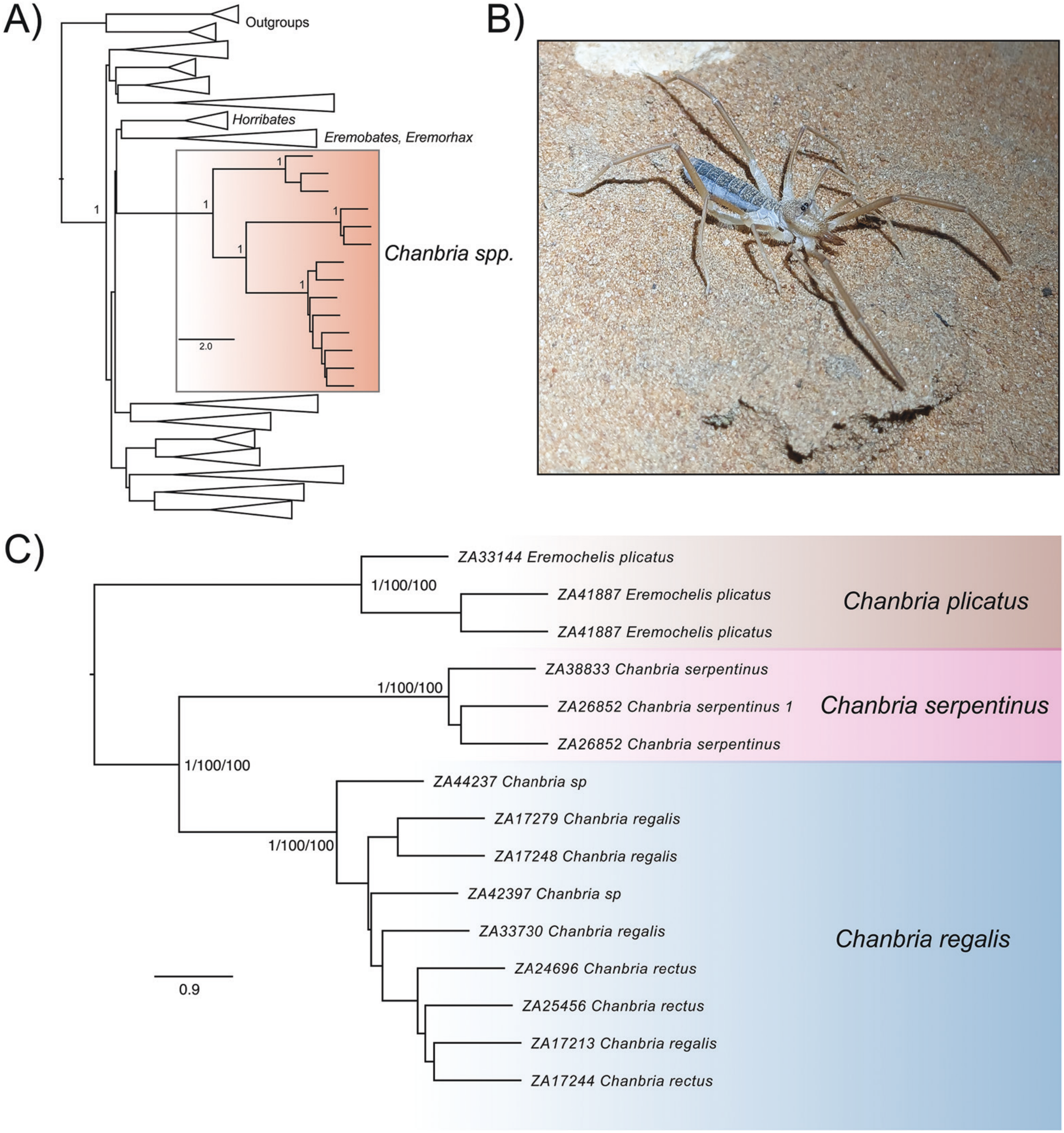

Figure 3. A, simplified Eremobatidae UCE topology estimated in ASTRAL, demonstrating the monophyly of *Chanbria* and sister taxa from Garcia EL, Cushing PE (unpublished). Nodal support values included on the topology refer to local posterior probabilities. The scale bar refers to coalescent units. B, image of male *Chanbria regalis* from Washington County, Washington City, UT, USA (photograph credit: Zachary Valois). C, UCE ASTRAL topology of *Chanbria*-only samples. New species hypotheses are highlighted by clade. Nodal support values correspond to local posterior probabilities/ultrafast bootstrap support for concatenated UCE analysis/bootstrap support for partitioned UCE analysis.

Mitochondrial signatures and mitonuclear discordance

When comparing the *COI* interspecific distances that we observed with those for other arachnid groups, there is a similar divergence trend, especially with groups that have comparatively low vagility. For example, the genetic distances between *Aphonopelma* Pocock, 1901 tarantula species from Texas were >6% divergent (Hamilton *et al.* 2011), the mean distance between *Buthacus* Birula, 1908 scorpion species was reported to be 2%–11.2% (Cain *et al.* 2021), and *Hexurella* Gertsch & Platnick, 1979 spiders ranged from 10.5% to 12.7% between species in a

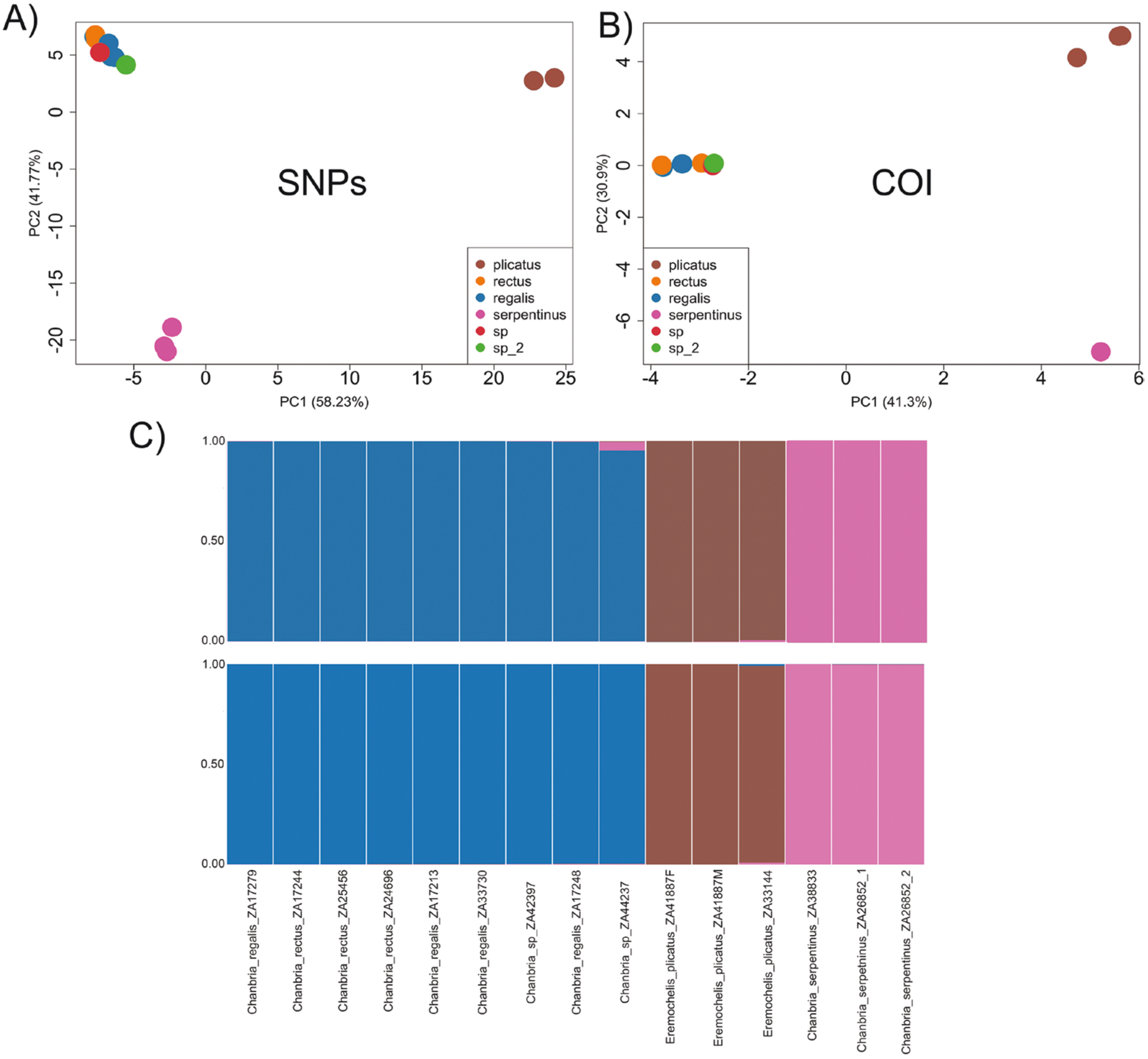

Figure 4. Summary of clustering analyses. A, PCA of the complete SNP dataset. B, PCA of mitochondrial *COI* SNPs. Keys in A and B correspond to species names based on previous taxonomic descriptions. Sample 'sp' refers to specimen DMNS ZA.42397 and 'sp_2' to sample DMNS ZA.44237. C, results of STRUCTURE analysis of SNPs, with missing data in the top panel and the complete dataset below. Sample names correspond to each bar assignment.

Table 1. Genetic distances between and within *Chanbria* clade designations for our SNP and *COI* dataset. Values in parenthesis are the range of distance values from minimum to maximum.

Species Clade	SNP distance between clades (%)	*COI* distance between clades (%)	Within-clade SNP distance (%)	Within-clade *COI* distance (%)
C. plicatus	*C. regalis* (62.6–70.4)	*C. regalis* (3.4–12.1)	~3	4
C. regalis	*C. serpentinus* (45.2–50.4)	*C. serpentinus* (12.3–12.9)	1–7	0.08–4
C. serpentinus	*C. plicatus* (66.1–69.6)	*C. plicatus* (12.8–13.5)	0.8–2	0

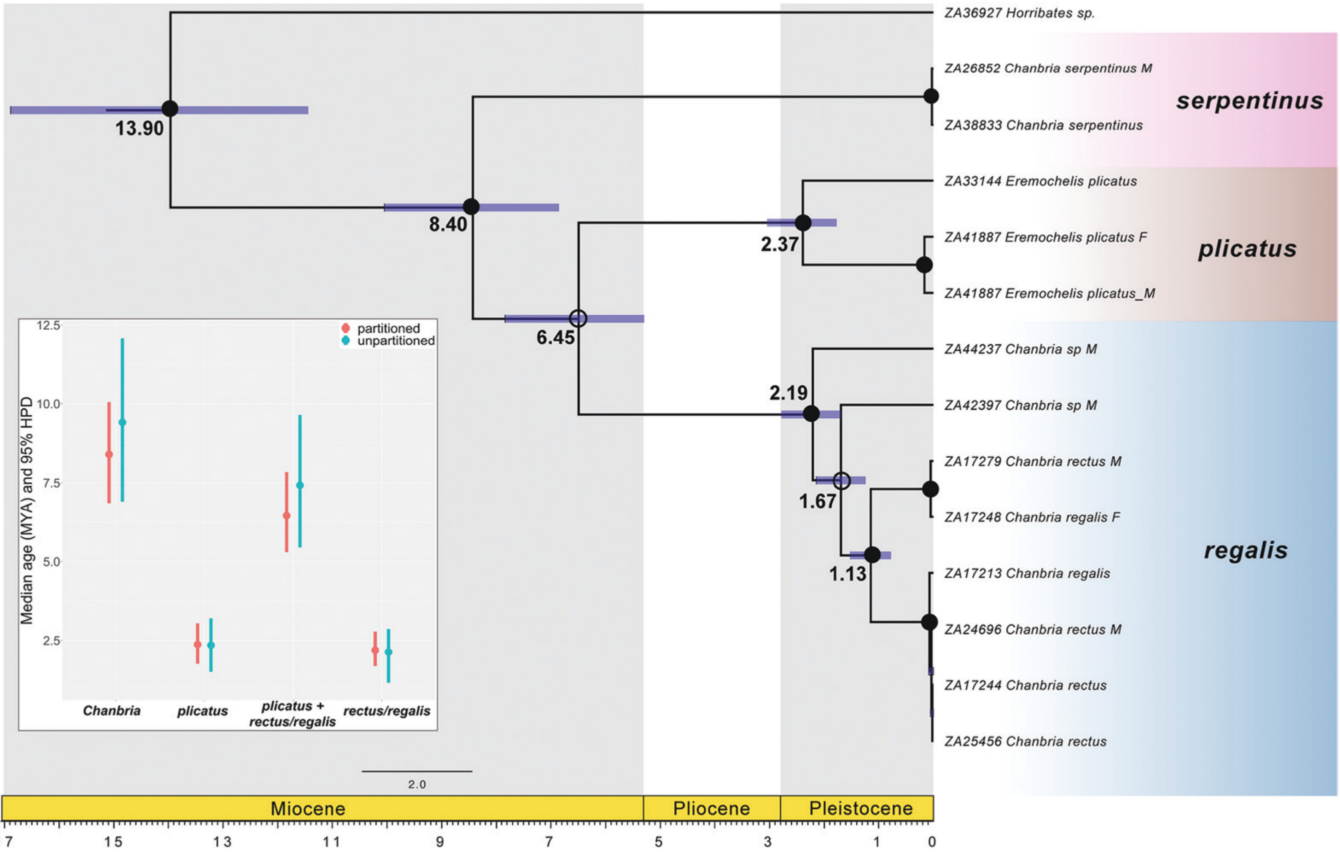

Figure 5. Dated mitochondrial *COI* phylogeny, with 95% HPD node bars and new species hypotheses highlighted. Dark circles on nodes refer to posterior probabilities of one and those with unfilled circles to probabilities of .99. Numbers near nodes correspond to estimated median height ages. Bottom left inset summarizes the node height estimates for each major clade along with their respective 95% HPD for the partitioned and unpartitioned *COI* analysis, respectively. The *rectus/regalis* value refers to the *regalis* clade on the topology.

clade (Monjaraz-Ruedas *et al.* 2023). Likewise, the intraspecific genetic distances for the *COI* locus in our data are congruent with other arthropod data, such as those for pseudoscorpions (Pfeiler *et al.* 2009), beetles (Ma *et al.* 2022), and cryptic spider mites (Matsuda *et al.* 2013). When considering shared geographical distributions, the intraspecific mitochondrial genetic distance for co-occurring *Homalonychus* Marx, 1891 was 0%–4% for *Homalonychus theologus* Chamberlin 1924 distributed in Baja California, California, and Nevada, and 0%–6% for *Homalonychus selenopoides* Marx, 1891 distributed primarily on the eastern side of the Colorado River (Crews and Hedin 2006), which is a pattern consistent with our data.

Mitochondrial markers are popular loci for assigning samples to species owing to the general pattern in which recovered mitochondrial clades often match phenotypic or nuclear structuring (Kerr *et al.* 2007, Derkarabetian and Hedin 2014, Sánchez-Vialas *et al.* 2020, Vázquez-Miranda *et al.* 2022). Additionally, mitochondrial markers are expected to coalesce approximately four times faster than nuclear markers (Ballard and Whitlock 2004) owing to smaller population sizes and mode of inheritance (Edwards and Beerli 2000). Therefore, such markers have also proved useful in investigating phylogeographical patterns of population structure that were often undetected with nuclear genes (Zink and Barrowclough 2008, Lee *et al.* 2021). However, reports of mitonuclear discordance have increased steadily over the last several decades, probably owing to the easier accessibility of incorporating both nuclear and mitochondrial loci in phylogenetic studies and because near-complete mitogenomes are recoverable from next-generation sequencing data (Toews and Brelsford 2012, Allio *et al.* 2020). Several biological mechanisms have been proposed to explain the origin of mitonuclear disagreement in several groups. This can include sex-biased dispersal (Roca *et al.* 2005, Petit and Excoffier 2009, Rheindt and Edwards 2011), adaptive introgression (Bonnet *et al.* 2017), demographic disparities between two taxa (Currat *et al.* 2008), ancient *Wolbachia* infections that lead to selective sweeps (Hale and Hoffmann 1990, Charlat *et al.* 2009), or mito-introgression between sister species (Jäckel *et al.* 2013). Phylogenetic analyses of both nuclear and mitochondrial data in our study recover well-supported clades that represent separately evolving lineages, hence we suggest the following new species designations for *Chanbria*: *C. plicatus*, *C. serpentinus*, and *C. regalis* (Figs 1, 3–5). However, we recovered notable mitonuclear discordance among the interspecific relationships rendered in our phylogenetic analyses. *Chanbria plicatus* is the earliest diverging *Chanbria* species in all our UCE analyses, with *C. serpentinus* and *C. regalis* being sister taxa (Fig. 3C). This result is consistent with the phylogenomic analyses of Garcia *et al.* (2024), Garcia EL Cushing PE (unpublished data), and Jones RR, Garcia EL, Shikak G, Brookhart JO, Graham MR, Cushing PE (unpublished data). However, there is major discordance in our mitochondrial analyses using both ML and

Bayesian approaches, with and without an outgroup taxon. In our mitochondrial topologies, *C. serpentinus* is the stem lineage to *C. plicatus* + *C. regalis* (Fig. 5), yet the morphological similarity between *C. regalis* and *C. serpentinus* supports the sister relationship recovered in our phylogenomic analyses. In addition to *Chanbria*, we have observed this mitonuclear discordance in preliminary eremobatid phylogenomic analyses, hence we suggest that this recurring trend might be a result of real biological processes within Eremobatidae. However, with our available data in this study and with limited knowledge regarding solifuge biology, the exact mechanism of what might be causing this observed mitonuclear discordance is unknown. Future studies that investigate the precise causes for the observed mitonuclear discordance will illuminate important implications regarding solifuge general biology and evolutionary history.

Biogeography of *Chanbria*

During the late Miocene, increasing temperature stratification between polar and equatorial regions resulted in increased aridification of subtropical regions (Herbert *et al.* 2016), potentially providing ample arid habitat to facilitate the speciation of the *Chanbria* clade. Several notable palaeobiogeographical events have been suspected to influence relatively recent biogeographical patterns in the desert southwest, particularly among taxa with an east–west phylogenetic break across the Colorado River region. Some examples include a marine incursion of the Gulf of California as far north as the San Gorgonio Pass in Riverside County during the late Miocene (~6.5–6.0 Mya; Winker and Kidwell 1996, Dorsey *et al.* 2007, McDougall 2008), the imposition of the Colorado River onto the southern Colorado Plateau and subsequent integration with the Gulf of California during the late Miocene into the early Pliocene (~4.80 Mya; Spencer *et al.* 2013), and flooding along the trajectory of the present-day Colorado River attributable to either a marine incursion of the Gulf of California or development of the Bouse Formation hypothesized to have formed as late as 4.80 Mya (Spencer *et al.* 2013) to as early as 5.3 Mya (McDougall and Miranda Martínez 2014). In our dated topology, we recovered an east–west phylogenetic break between *C. serpentinus*, occurring primarily on the east of the Colorado River, and *C. plicatus* + *C. regalis* distributed principally on the western side of the river. The median age estimate for the east–west split was 8.40 Mya (95% HPD: 6.81–10.05)

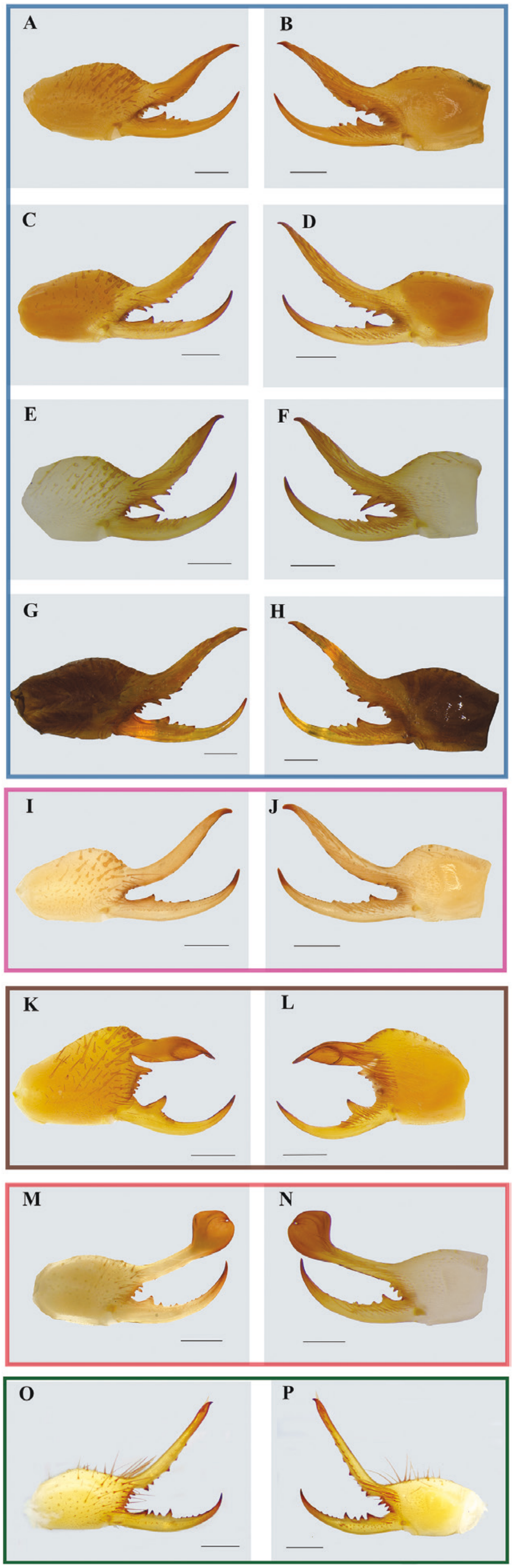

Figure 6. Ectal and mesal views of male *Chanbria* species chelicerae coloured by the revised species designations. A–H illustrate the morphological variation found in *Chanbria regalis*. A, B, ectal view (A) and mesal view (B) of male DMNS ZA.16460 from Salton Sea, Imperial County, CA, USA. C, D, ectal view (C) and mesal view (D) of male DMNS ZA.17285 from Coachella Valley, San Bernardino County, CA, USA. E, F, ectal view (E) and mesal view (F) of male DMNS ZA.44237 from Punta Final, Baja California, Mexico. G, H, ectal view (G) and mesal view (H) of male AMNH holotype of *Chanbria tehachapianus* syn. nov. from Tehachapi Mountains, Kern County, CA, USA. I, J, ectal view (I) and mesal view (J) of *Chanbria serpentinus* (DMNS ZA.38728) from Catalina State Park, Pima County, AZ, USA. K, L, ectal view (K) and mesal view (L) of *Chanbria plicatus* (DMNS ZA.33144) from near Calico Basin Road, Clark County, NV, USA. M, N, ectal view (M) and mesal view (N) of ***Chanbria brookharti*** (*DMNS ZA.36968*) from Dalquest Desert Research Site, TX, USA. O, P, ectal view (O) and mesal view (P) of ***Chanbria mapemes*** (IBUNAM CNAN SO106) from Sierra Mojada, Coahuila, México. Scale bars: 1 mm.

and 9.24 Mya (95% HPD: 6.90–12.08) for our partitioned and unpartitioned divergence time analyses, respectively (Fig. 5; https://doi.org/10.6084/m9.figshare.24894948.v1). The lower bound ages of this east–west break pre-date any of the geological events mentioned above, suggesting that this break might be correlated with increased tectonic activity responsible for the formation of the Gulf of California beginning ~12 Mya (Spencer and Normark 1979, Stock and Hodges 1989, Henry and Aranda-Gomez 2000, Dolby *et al.* 2015). The proto-gulf extension in the surrounding area of the modern Gulf of California (Gulf Extensional Province) during the mid-Miocene can be attributed to the separation of the Pacific and North American plate (Spencer and Normark 1979, Hausback 1984, Stock and Hodges 1989, Lee *et al.* 1996) and pre-dates the opening of the seafloor of the present-day Gulf of California (Karig and Jensky 1972, Gastil 1975, Hausback 1984, Lee *et al.* 1996). Given the estimated divergence time of the east–west phylogenetic break and observed interspecific differences within *Chanbria*, we suspect that these initial stages of tectonic rifting during the mid-Miocene and early marine incursions resulting from this tectonic movement might have initiated the cladogenesis of this group (Stock and Hodges 1989, Holt *et al.* 2000, Dorsey *et al.* 2007). This hypothesis has been supported in rosy boas (Wood *et al.* 2008), arid-adapted rodents(Hafner and Riddle 2011), and other taxa with deep divergences (Wood *et al.* 2013).

When comparing co-occurring taxa from the same desert regions as *C. regalis*, there is a consistent pattern regarding recently diverged, population-level structuring influenced by Pleistocene climate cycles. In an investigation regarding the validity of two subspecies of *Smeringurus vachoni* (Stahnke, 1961) scorpions distributed in the Sonoran and Mojave deserts, Graham *et al.* (2017) determined that this wide-ranging species consisted of distinct mitochondrial clusters, rather than distinct subspecies. In that study, the authors emphasized that the primary denticle count, a character often used for taxonomic delimitation in scorpions, was highly variable and therefore provided insufficient evidence to for retaining subspecies designations (Graham *et al.* 2017). Likewise, the Arizona hairy scorpion, *Hadrurus arizonensis* Ewing, 1928, mostly found in sandy dune habitats like *C. regalis*, reflected population-level structuring, rather than species-level divergence (Graham *et al.* 2013). Moreover, the morphological characteristics used to divide this species into subspecies were not supported by the recovered, geographically supported mitochondrial clades. Geometric morphometric analyses of co-distributed *Homalonychus theologus* resulted in non-significant morphological differences between mitochondrial clades across the geographical range (Crews 2009).

Based on the evidence presented here, we hypothesize that the evolution of *C. regalis* follows the 'Mojave Assembly Model' (Bell *et al.* 2010, Graham *et al.* 2013) as observed in other vertebrates, invertebrates, and plant taxa that putatively emerged during the Pleistocene (Crews and Hedin 2006, Bell *et al.* 2010, Graham *et al.* 2013). We observe a similar pattern for our representatives of *C. regalis*, a taxon that is comparatively more recently evolved and more vagile than the specific arachnid examples presented above. We hypothesize that the populations of *C. regalis* were subdivided by Pleistocene refugia, then these populations subsequently expanded northwards post-glaciation, creating large panmictic populations of individuals. This hypothesis is supported by both our divergence dating and our genetic analyses, and this pattern has been documented in other arachnid taxa, such as *Homalonychus* (Crews, 2009). *Chanbria regalis* is a recently derived species that originated in the Pleistocene, with an estimated median age of ~2.15 Mya (Fig. 5). Within this clade, specimen DMNS ZA.44237 from Baja California was recovered as the stem member of the clade in both our UCE and divergence dating analyses, with subsequent clades following a gradual northward expansion (Figs 3C, 5). The northward expansion can be supported by the two derived clades within *C. regalis*: a clade that is distributed southeast of the Salton Sea in California, and a more derived clade that is distributed north of the Salton Sea (Figs 1, 3C, 5). We propose that the widespread distribution of *C. regalis*, from northern Baja California to the southwest corner of Utah, is a relic from the repeated retreat of rivers and lakes in this region during Pleistocene climate fluctuations, and ancestral populations of *C. regalis* are likely to have followed sandy corridors (palaeo-valleys) along the retreated palaeo-lakes and rivers (Muhs and Bettis 2003, Van Dam and Matzke 2016, Graham *et al.* 2017) to achieve their current distribution.

CONCLUSION

In this study, we use phylogenomics to inform a taxonomic revision of the North American camel spider genus *Chanbria* with geographical and morphological data. We propose *Chanbria*, as defined here, to support five recognized species: *C. regalis*, *C. serpentinus*, *C. plicatus*, *C. brookharti*, and *C. mapemes*. Our molecular divergence analysis estimated *Chanbria* to have origins in the Miocene; however, our mitochondrial analysis unveils a pattern of mitonuclear discordance. *Chanbria plicatus*, a species formerly placed in the eremobatid genus, *Eremochelis*, was recovered consistently as a member of the *Chanbria* clade. Our genetic analyses revealed nearly indistinguishable genetic affinities between the formerly recognized species *C. regalis* and *C. rectus*, which inspired us to make a conservative decision to synonymize these two geographically and morphologically proximate species. After careful consideration of the morphological variation and geographical distributions of *C. regalis* and *C. rectus*, this provided us with a foundation to synonymize *C. techachanianus* based on the subtly variable traits observed between the three species, thus resulting in one widespread species, *C. regalis*. *Chanbria* species were formerly known from the Mojave and Sonoran deserts only; however, we describe two new species from the Chihuahuan Desert, adding to the known diversity and the known range of *Chanbria*.

TAXONOMY

Family Eremobatidae Kraepelin, 1899

Genus *Chanbria* Muma, 1951

Revised diagnosis

Chanbria are medium-sized eremobatids, with mature individuals ranging from 14 to 27 mm in length when measured from the distal tip of the abdomen to the distal-most portion of the chelicerae.

They are generally a uniform light tan to yellowish in colour, with some individuals taking on a darker, sandy reddish brown that might be dependent on substrate association. Coloration is interspecifically variable among some species, notably among the pedipalps and legs of *C. serpentinus*, *C. plicatus*, and *C. mapemes*, hence these taxa are noticeably darker in overall coloration than *C. regalis*. Papillae are present on the palpal tarsi in all species; however, this character is absent in specimens of *C. plicatus* and *C. regalis*, possibly owing to habitat association. Leg I possess a single terminal claw (Supporting Information, Fig. S1A, B). The female genital opercula vary both inter- and intraspecifically (Fig. 7A–D), with simple lobate, thin, angular, triangular, or broad anterior pillars, with laterally curving lobes. Dentition on the FF of the male chelicerae is heavily reduced or absent distally, but present proximally in *C. regalis* and *C. mapemes* (Fig. 7). The MF of the male chelicerae displays a prominent, recurved proximal tooth, with MSM, an MM, and MST, except in *C. plicatus*. Female chelicerae are noticeably anteroposteriorly elongate and dorsoventrally slim in comparison to other eremobatids. Females also display between seven and nine teeth on the FF (Supporting Information, Fig. S2). Except for *C. mapemes, Chanbria* lack ctenidia. Synapomorphies for *Chanbria* include a distinctively shaped MF of the male chelicerae that forms the shape of an exponential curve (Supporting Information, Fig. S1C, D) and extreme morphologies of the FF not observed in any other eremobatid genus, such as sigmoidal shapes, modified folded tips, or FF in a positive slope position with respect to the manus. Pedipalpal tarsi possess a high density of setae. Legs are also slim and long (e.g. Fig. 3B).

Note on spine-like setae

Chanbria brookharti (Fig. 8) and *C. mapemes* (Fig 9) are the first observed *Chanbria* species known to have enlarged, moveable palpal spines. Similar palpal spines have been found in other eremobatids and is a current synapomorphy for the genus *Horribates* Muma, 1962 (Muma, 1989). In eremobatids, such spines are motile, having a ~45° range of movement between their extended state perpendicular to the pedipalp and their relaxed state. Histological cross-sections of such spines indicate that haemolymph pressure might be responsible for extending and retracting these spines in a hydraulic fashion. Likewise, the presence of pores at the tip of these specialized spines that open into the subcutaneous tissue suggests a sensory function (Garcia EL, Laudier D, Cushing PE, unpublished data). In some eremobatid specimens that possess these spines, a notched base is present which allows the spines to be 'locked' in an extended position. Similar moveable spines are also present on the appendages of other solifuge families (WGarcia EL, pers. obs.) and arachnid groups, such as in the lycosid spider *Zoropsis spinimana* (Dufour, 1820), which uses these spines to aid in subduing prey during capture (Eggs *et al.* 2015). Eremobatid solifuges have been observed capturing and manipulating prey with their pedipalps (Willemart *et al.* 2011), hence the palpal spines of *C. brookharti*, *C. mapemes*, and other eremobatids that possess these structures might play a similar role in subduing prey.

Chanbria regalis Muma, 1951

(Figs 6A–F, 7A–D)

Chanbria rectus Muma, 1962, male holotype and immature female from Barstow, San Bernardino County County, CA, USA (AMNH). Image of type examined; new synonymy.

Chanbria tehachapianus Muma, 1962, male holotype from Tehachapi Mountains, Kern County, CA, USA (AMNH). Image of type examined; new synonymy.

Type material: Male holotype and one male paratype from Twentynine Palms, CA, USA. Female allotype from Palm Springs, CA, USA (AMNH). Holotype examined.

Other material examined: ***México***: Baja California: Ensenada: South of Punta Final, 29.743587°N, 114.292885°W, 25 April 2019, one ♂, H. Munillo; K. Munguia; E. Lopez, DMNS (DMNS ZA.44237); ***USA***: Arizona: Pima Co.: South of Punta Final, 29.743587°N, 114.292885°W, 25 April 2019, one ♀, H. Munillo; K. Munguia; E. Lopez, DMNS (DMNS ZA.44238); Organ Pipe National Monument, 32.035706°N, 112.857283°W, 472 m, 23 May 1959, one ♂, K.E. Lucas, CAS (CASENT9033503); California: Imperial Co.: near Ogilby, 32.814682°N, 114.841597°W, 545 m, 23 May 1959, three ♂, two ♀, V. Roth, CAS (CASENT9033512); Salton Sea, 33.1872°N, 115.8376°W, July 2001, one ♀, USGS San Diego, Pitfall Trap Array, DMNS (DMNS ZA.16444); Salton Sea, 33.1802°N, 115.8379°W, August 2001, one ♂, one ♀, USGS San Diego, Pitfall Trap Array, DMNS (DMNS ZA.16445); Salton Sea, 33.1867°N, 115.8457°W, August 2001, one ♀, USGS San Diego, Pitfall Trap Array, DMNS (DMNS ZA.16447); Salton Sea, 33.1974°N, 115.8374°W, 761 m, August 2001, one ♂, USGS San Diego, Pitfall Trap Array, DMNS (DMNS ZA.16456); Salton Sea, 33.1872°N, 115.8376°W, 763 m, April 2001, one ♂, USGS San Diego, Pitfall Trap Array, DMNS (DMNS ZA.16457); Salton Sea, 33.1868°N, 115.8431°W, 780 m, July 2001, one ♂, USGS San Diego, Pitfall Trap Array, DMNS (DMNS ZA.16458); Salton Sea, 33.1734°N, 115.84°W, 80 7m, July 2001, one ♂, USGS San Diego, Pitfall Trap Array, DMNS (DMNS ZA.16459); Salton Sea, 33.1734°N, 115.84°W, July 2001, one ♂, USGS San Diego, Pitfall Trap Array, DMNS (DMNS ZA.16460); Salton Sea, 33.1872°N, 115.8376°W, June 2001, one ♂, USGS San Diego, Pitfall Trap Array, DMNS (DMNS ZA.16461); Salton Sea, 33.1802°N, 115.8379°W, April 2002, one ♀, USGS San Diego, Pitfall Trap Array, DMNS (DMNS ZA.16462); Salton Sea, 33.197°N, 115.8452°W, August 2001, one ♂, USGS San Diego, Pitfall Trap Array, DMNS (DMNS ZA.16463); Salton Sea, 33.1872°N, 115.8376°W, August 2001, one ♀, USGS San Diego, Pitfall Trap Array, DMNS (DMNS ZA.16464); Salton Sea, 33.173°N, 115.8518°W, July 2001, one ♂, USGS San Diego, Pitfall Trap Array, DMNS (DMNS ZA.16465); Salton Sea, 33.2039°N, 115.8407°W, August 2001, one ♀, USGS San Diego, Pitfall Trap Array, DMNS (DMNS ZA.16466); 3 miles down dirt road off Olgilby Road headed N road on left, 32.7965°N, 114.871°W, 9 May 2001, one ♀, M. Hedin; D. Wood, DMNS (DMNS ZA.16467); Algodones Sand Dunes Cahuilla Ranger Station Gecho Road just S of Highway 78, 32.94°N, 115.13°W, 8 October 2004, one ♀, Wendell R. Icenogle, DMNS (DMNS ZA.17219); Algodones Sand Dunes Ted Kipf Road 11/2 & S of Highway 78 (GIAMIS), 32.76°N, 114.84°W, 61 m, 8 September 2005, one ♀, Wendell R. Icenogle, sand dunes below low Palo Verde tree limb, DMNS (DMNS ZA.17248); Algodones sand dunes Ted Kipf Road 1.5 miles S Highway 78 Chamis, 33.02°N, 115.1°W, 207 m, 9 September 2005, one ♂, Wendell R. Icenogle, DMNS (DMNS ZA.17279); Salton Sea, 33.20293°N, 115.84905°W, 98 m, August 2001, one ♂, USGS San Diego,

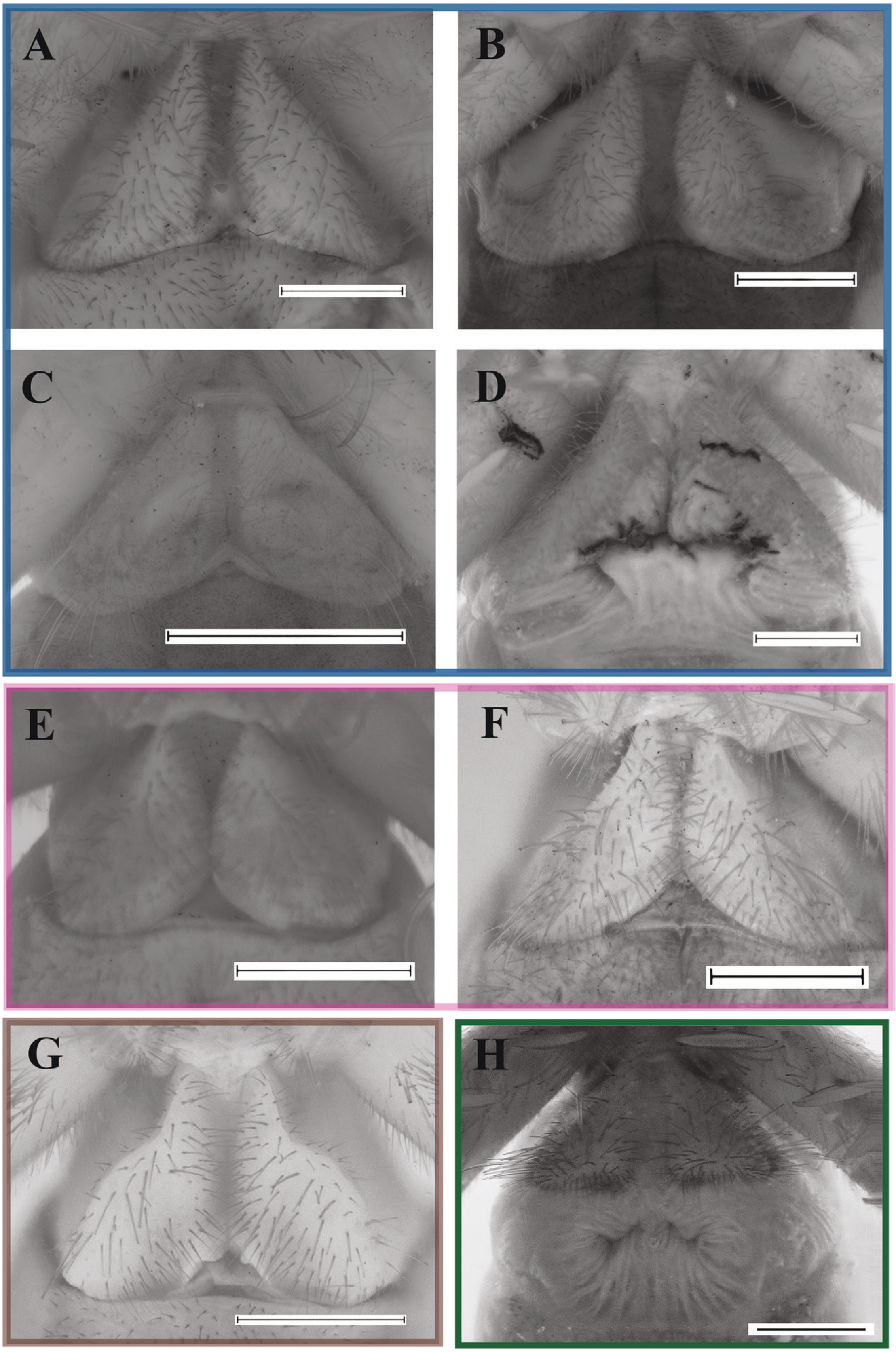

Figure 7. Ventral views of *Chanbria* female genital operculum according to the new species designations. A–D show the intraspecific variation of *Chanbria regalis.* A, DMNS ZA.28409 from Twentynine Palms in San Bernardino County County, CA, USA. B, DMNS ZA.17213 Coachella Valley, Riverside County, CA, USA. C, DMNS ZA.29497 8.5 miles east of Twentynine Palms, San Bernardino County, CA, USA. D, DMNS ZA.44238 Punta Final, Baja California, Mexico. E, F represent the intraspecific variation of *Chanbria serpentinus* from the same locality (DMNS ZA.38728) from Catalina State Park Campground, Pima County, AZ, USA. G, *Chanbria plicatus* (DMNS ZA. 41887) off Calico Basin Road, Clark County, NV, USA. H, ***Chanbria mapemes*** *IBUNAM CNANSO106* from Sierra Mojada, Coahuila, Mexico. Scale bars: 1 mm.

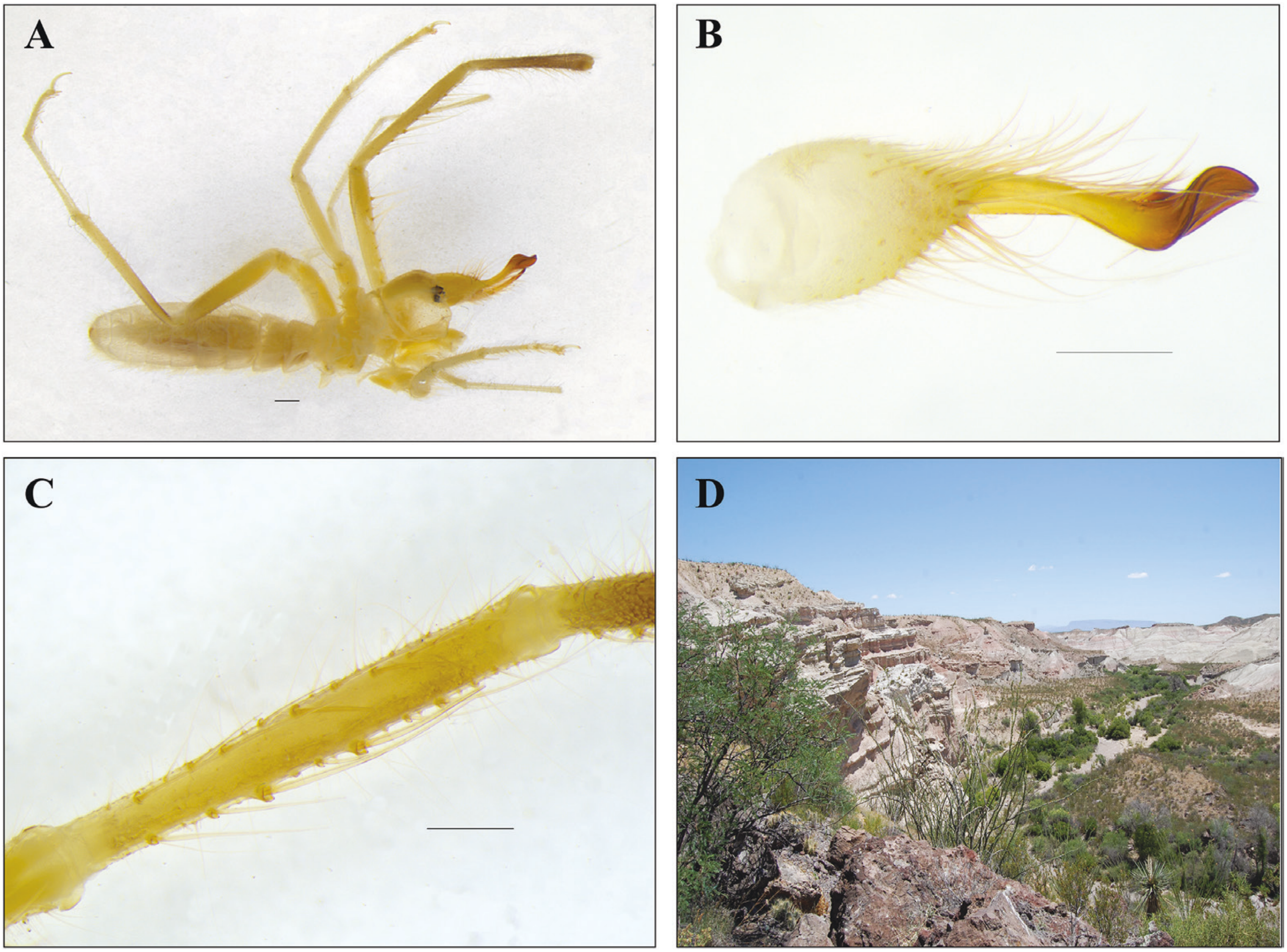

Figure 8. ***Chanbria brookharti***. A, lateral habitus view of male holotype. B, dorsal view of right male chelicera. C, ventral view of pedipalp. D, canyon habitat of male holotype in Alamo Springs at Dalquest Research Site (photograph credit: Paula E. Cushing). Scale bars: 1 mm.

Pitfall Trap Array, DMNS (DMNS ZA.19092); Highway 78 at junction San Felipe Creek 10.5 miles W. junction Highway 86, 33.12563°N, 116.0443°W, 195 m, 26 September 2009, one ♂, Wendell R. Icenogle, Alcohol Sprayed, DMNS (DMNS ZA.25437); Highway 78 at junction San Felipe Creek, 10.5 miles W. junction Highway 86, 33.12563°N, 116.0443°W, 195 m, 17 June 2010, one ♂, Wendell R. Icenogle, Alcohol Sprayed, At Lights, DMNS (DMNS ZA.25439); Highway 78 at junction, San Felipe Creek, 10.5 miles W. junction Highway 86, 33.1256°N, 116.0443°W, 109 m, 7 June 2008, one ♂, Wendell R. Icenogle, Alcohol Sprayed, At Lights, DMNS (DMNS ZA.25442); Highway 78 at junction, San Felipe Creek, 10.5 miles W. junction Highway 86, 33.1256°N, 116.0443°W, 7 m, 1 May 2008, one ♂, Wendell R. Icenogle, Alcohol Sprayed, At Lights, DMNS (DMNS ZA.25443); Imperial Sand Dunes, 32.80883°N, 114.89218°W, 545 m, 15 May 2021, one ♂, one ♀, Paula E. Cushing; E.L. Garcia, Pitfall trap, DMNS (DMNS ZA.42066); Imperial Sand Dunes, 32.8105°N, 114.89265°W, 545 m, 15 May 2021, one ♂, one ♀, Paula E. Cushing; E.L. Garcia, DMNS (DMNS ZA.42071); San Bernardino Co.: Pisgah Crater, 34.756044°N, 116.38388°W, 392 m, 22 August 1968, one ♂, W. Savary; R.M. Haradon, CAS (CASENT_NoNumber); Pisgah Lava Flow, 34.756044°N, 116.38388°W, 472m, 1 August 1974, one ♂, B. Banta, CAS (CASENT9033500); Pisgah Lava Flow, 34.756044°N, 116.38388°W, 472 m, 28 July 1956, one juvenile, B. Banta, CAS (CASENT9033508); Pisgah Lava Flow, 34.756044°N, 116.38388°W, 488 m, 24 May 1960, one ♂, B. Banta, CAS (CASENT9033511); Marine Corps Air Ground Combat Center, 34.2994°N, 116.32067°W, August 1999, one ♀, USGS San Diego, Pitfall Trap Array, DMNS (DMNS ZA.16442); Marine Corps Air Ground Combat Center, 34.2998°N, 116.3003°W, July 1999, one ♀, USGS San Diego, Pitfall Trap Array, DMNS (DMNS ZA.16443); Marine Corps Air Ground Combat Center, 34.3177°N, 116.26689°W, 816 m, October 1999, one ♀, USGS San Diego, Pitfall Trap Array, DMNS (DMNS ZA.16448); Marine Corps Air Ground Combat Center, 34.2834°N, 116.2998°W, 780 m, July 1999, one ♂, USGS San Diego, Pitfall Trap Array, DMNS (DMNS ZA.16449); Joshua Tree National Park, 33.90925°N, 115.85617°W, May 2000, one ♀, Jack Brookhart, DMNS (DMNS ZA.16450); Marine Corps Air Ground Combat Center, 34.2826°N, 116.2414°W, August 1999, one ♂, USGS San Diego, Pitfall Trap Array, DMNS (DMNS ZA.16451); Maine Corps Air Ground Combat Center, 34.3177°N, 116.26689°W, August 2000, one ♂, USGS San Diego, Pitfall Trap Array, DMNS (DMNS ZA.16452); Marine Corps Air Ground Combat Center, 34.2998°N, 116.3003°W, 766 m, June 2001, one juvenile, USGS San Diego, Pitfall Trap Array, DMNS (DMNS ZA.16453); Marine Corps Air Ground

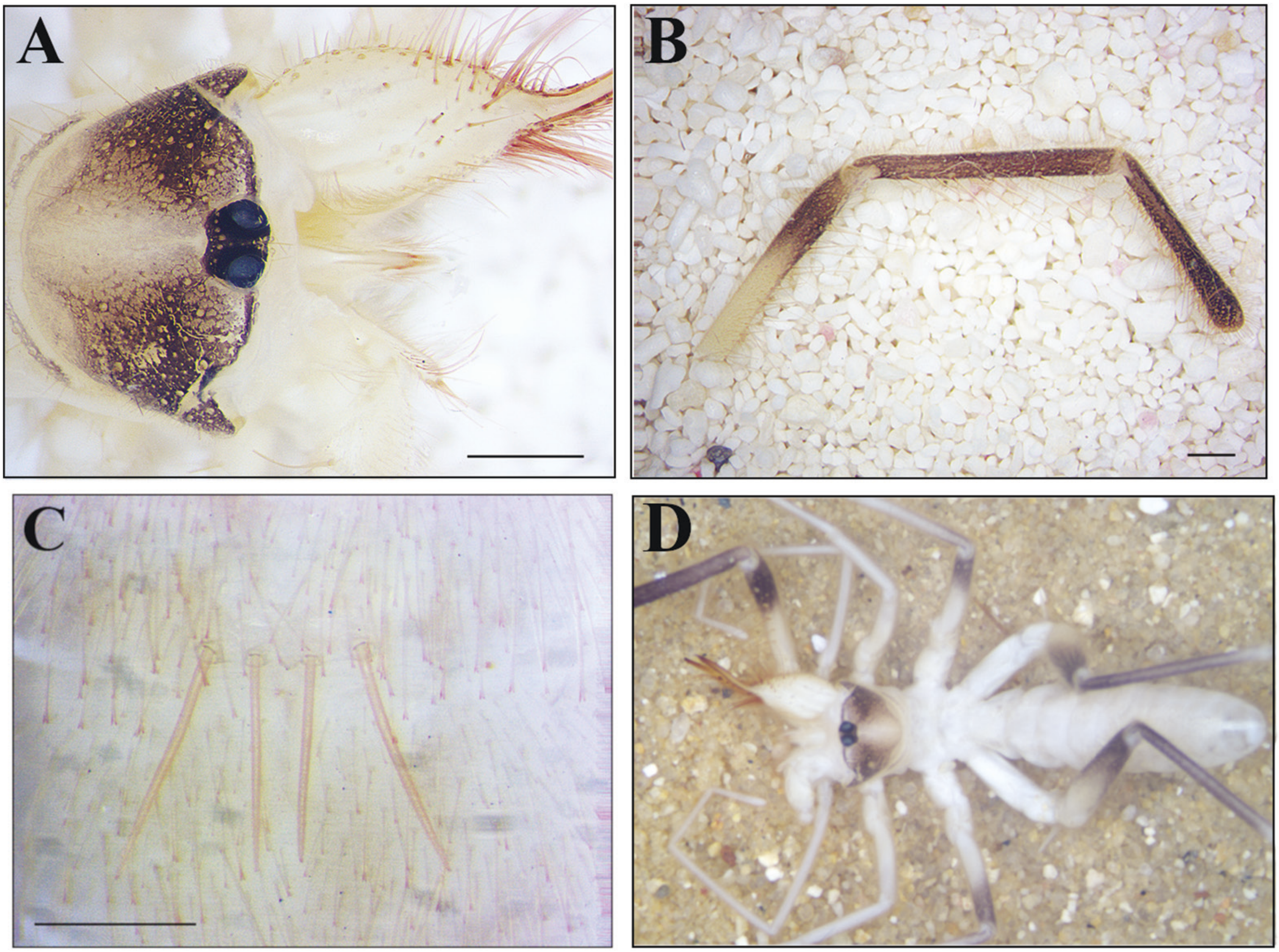

Figure 9. ***Chanbria mapemes*** male holotype (*IBUNAM CNANSO106*). A, dorsal view of propeltidium. B, retrolateral view of right pedipalp. C, ventral view of abdominal ctenidia. D, habitus dorsal view, with no scale bar available. Scale bars: 1 mm.

Combat Center, 34.2994°N, 116.32067°W, 804 m, July 1999, one ♂, USGS San Diego, Pitfall Trap Array, DMNS (DMNS ZA.16454); Joshua Tree National Park, 33.90925°N, 115.85617°W, 539 m, May 2000, one juvenile, USGS San Diego, Pitfall Trap Array, DMNS (DMNS ZA.16455); Twentynine Palms junction Utah Trail & Amboy Road, 34.1652°N, 116.0368°W, 207 m, 2 August 2006, one ♂, Wendell R. Icenogle, Sand dunes nearby, ground below yellowish street light, DMNS (DMNS ZA.17246); 29 Palms West of Surprise Springs, 34.18°N, 116.167°W, 1–30 June 2007, three ♀, three juveniles, G. Pratt, DMNS (DMNS ZA.22756); Coachella Valley at Train Station 1/2 mile S Junction Inoian Cyn Drive and Highway 10, 33.897367°N, 116.54835°W, 24 May 2007, one ♂, Wendell R. Icenogle, DMNS (DMNS ZA.24696); Wonder Valley, Amboy Road, 8.5 miles E. Twentynine Palms (at Adobe Road junction), 34.1657°N, 115.9037°W, 7 m, 2 May 2007, one ♂, Wendell R. Icenogle, Alcohol Sprayed, DMNS (DMNS ZA.25444); Coachella Valley, Amtrak Station, 5 miles S junction Indian Canyon Drive and Highway 10, 33.89736°N, 116.54835°W, 487 m, 7 September 2009, one ♂, Wendell R. Icenogle, DMNS (DMNS ZA.25456); Twentynine Palms, Amboy Road 1 mile E junction Adobe Road, 34.164917°N, 116.038167°W, 550 m, 19 September 2011, one ♀, one juvenile, Wendell R. Icenogle, Alcohol Sprayed, DMNS (DMNS ZA.28407); Twentynine Palms, Amboy Road 1 mile E junction Adobe Road, 34.164917°N, 116.038167°W, 550 m, 25 July 2011, one ♂, Wendell R. Icenogle, Alcohol Sprayed, DMNS (DMNS ZA.28408); Twentynine Palms, Amboy Road 1 mile E junction Adobe Road, 34.164917°N, 116.038167°W, 550 m, 29 August 2011, one ♀, Wendell R. Icenogle, Alcohol Sprayed, DMNS (DMNS ZA.28409); Twentynine Palms, Amboy Road 1 mile E junction Adobe Road, 34.164917°N, 116.038167°W, 550 m, 17 October 2011, one ♀, Wendell R. Icenogle, Alcohol Sprayed, DMNS (DMNS ZA.28410); Twentynine Palms, Amboy Road 1 mile E junction Adobe Road, 34.164917°N, 116.038167°W, 550 m, 1 August 2009, one ♂, Wendell R. Icenogle, Alcohol Sprayed, DMNS (DMNS ZA.28411); Amboy Road, 8.5 miles E. of Twentynine Palms (at Adobe Road Junction), 34.1657°N, 115.903383°W, 81 m, 30 July 2009, one ♀, Wendell R. Icenogle, On pavement below lights on building, DMNS (DMNS ZA.29497); Junction Amboy Road and Utah Trail, 34.09915°N, 116.02208°W, 82 m, 21 July 2009, one ♂, Wendell R. Icenogle, DMNS (DMNS ZA.33730); Amboy Road just W junction Utah Trail, 34.16458°N, 116.0382°W, 472 m, 26 August 2017, one ♂, Wendell R. Icenogle, At lights, On sand drifts and pavement, DMNS (DMNS ZA.42121); Amboy Road just W junction Utah

Trail, 34.16458°N, 116.0382°W, 472 m, 26 April 2017, one ♂, Wendell R. Icenogle, At lights, On sand drifts and pavement, DMNS (DMNS ZA.42127); Amboy Road just W junction Utah Trail, 34.16458°N, 116.0382°W, 472 m, 3 September 2018, one ♂, Wendell R. Icenogle, At lights, On sand drifts and pavement, DMNS (DMNS ZA.42128); Amboy Road, 8.5 miles E of Twentynine Palms, Wonder Valley Community Center (Blower Road), 34.16567°N, 115.9038°W, 472 m, 9 May 2007, one ♂, Wendell R. Icenogle, At lights, DMNS (DMNS ZA.42176); Amboy Road, 8.5 miles E of Twentynine Palms, Wonder Valley Community Center (Blower Road), 34.16567°N, 115.9038°W, 17 May 2007, one ♂, Wendell R. Icenogle, At lights, DMNS (DMNS ZA.42177); San Diego County: Amboy Road, 8.5 miles E of Twentynine Palms, Wonder Valley Community Center (Blower Road), 34.16567°N, 115.9038°W, 3 June 2007, one ♂, Wendell R. Icenogle, At lights, DMNS (DMNS ZA.42178); Amboy Road, 8.5 miles E of Twentynine Palms, Wonder Valley Community Center, Blower Road, 34.16567°N, 115.9038°W, 2 May 2010, one ♂, Wendell R. Icenogle, At lights, DMNS (DMNS ZA.42179); Junction of Palm Canyon Road and Borrego Valley Road, Borrego Springs, 33.255782°N, 116.374497°W, 208 m, no date, three ♂, one ♀, W. Savary; R.M. Haradon, CAS (CASENT9033507); Ocotillo Circle, just N of junction Palm Canyon Drive, 33.25758°N, 116.385083°W, 279m, 27 August 2008, one ♂, Wendell R. Icenogle, Alcohol Sprayed, DMNS (DMNS ZA.25435); Ocotillo Circle, just N of junction Palm Canyon Drive, 33.257583°N, 116.385083°W, 195 m, 16 September 2009, one ♀, Wendell R. Icenogle, Alcohol Sprayed, DMNS (DMNS ZA.25436); Ocotillo Circle, just N junction Palm Canyon Drive, 33.257583°N, 116.385083°W, 7 m, 19 August 2010, one ♂, Wendell R. Icenogle, Alcohol Sprayed, DMNS (DMNS ZA.25440); Highway 78, Ocotillo Wells Ranger Station (State Vehicular Recreation Area), 33.155°N, 116.168°W, 195 m, 12 September 2008, one ♂, Wendell R. Icenogle, Alcohol Sprayed, DMNS (DMNS ZA.25441); Ocotillo Circle, just N junction Palm Canyon Drive, 33.25758°N, 116.385083°W, 7 m, 12 June 2008, one ♂, Wendell R. Icenogle, Alcohol Sprayed, DMNS (DMNS ZA.25438); Riverside County: 8 miles NW Palm Springs, 33.912332°N, 116.644096°W, 472 m, 1 May 1959, one ♂, M. Wasbauer, CAS (CASENT9033506); Dos Palmas Reserve (San Andres Palm Oasis) 5 miles E Salton Sea State Rec Area headquarters Highway 111, 33.51°N, 115.89°W, 3 April 2004, one ♂, Wendell R. Icenogle, path to Palm Oasis, DMNS (DMNS ZA.17210); Coachella Valley, Palm Springs Amtrak Station 1/2 miles S junction Indian Canyon Drive Highway I-10, 33.8974°N, 116.5483°W, 21 May 2006, one ♀, Wendell R. Icenogle, Sand dunes, DMNS (DMNS ZA.17213); Coachella Valley Palm Springs Amtrak Station 1/2 mile S junction Indian Canyon Drive and Highway I-10, 33.8974°N, 116.5484°W, 549 m, 21 September 2006, one ♀, Wendell R. Icenogle, Netted, Sand dunes nearby, on concrete walkway below yellowish lights, DMNS (DMNS ZA.17284); Coachella Valley Palm Springs Amtrak Station 1/2 mile S junction Indian Canyon Drive and Highway I-10, 33.8974°N, 116.5484°W, 107 m, 24 May 2006, one ♂, Wendell R. Icenogle, Sand dunes nearby, pavement below yellowish lights, DMNS (DMNS ZA.17285); Cottonwood Road, 1/10 mile S Junction Snow Creek Road, 33.8897725°N, 116.6841503°W, 545 m, 1 May 2011, one ♂, Wendell R. Icenogle, DMNS (DMNS ZA.42018); Coachella Valley Palm Springs, Amtrak Station 1/2 mile S junction Indian Canyon Drive and Highway I-10, 33.8974°N, 116.54584°W, 71 m, 24 May 2006, one ♀, Wendell R. Icenogle, DMNS (DMNS ZA.17235); Coachella Valley Palm Springs Nature Station 1/2 mile S junction Indian Canyon Drive and Highway I-10, 33.8974°N, 116.5484°W, 3 m, 4 September 2006, one ♀, Wendell R. Icenogle, Sand dunes nearby, on ground beside concrete walkway under yellowish lights, DMNS (DMNS ZA.17244); Utah: Washington Co.: West of Gunlock Road, ~160 feet, ~1.8 miles south of Gunlock State Park, 37.2297°N, 113.780503°W, 1056 m, 19 July 2020, one ♂, Zach J. Valois, At lights, DMNS (DMNS ZA.42397).

Diagnosis

Chanbria regalis can be distinguished from *C. serpentinus* by the presence of fixed finger dentition on the male chelicerae and by a more robust base of the fixed finger. This species can be distinguished from all other *Chanbria* by a tapering sigmoidal male FF. Individuals are generally absent of dark pigmentation.

Measurements

All measurements are reported as averages, and ranges are in parentheses.

Males (n = 17): CL: 6.096 (3.154–7.829); CH: 2.060 (1.189–2.589); FFH: 0.587 (0.356–0.709); tip of MF to MM: 1.726 (1.078–2.407); tip of MF to MP: 2.041 (1.309–2.994); PL: 24.629 (20.880–29.289); LI: 12.506 (10.063–15.665); LIV: 21.618 (16.587–27.282); PPW: 4.079 (3.126–5.319); PPL: 3.014 (2.261–3.793); TL: 22.289 (17.467–27.841).

Females (n = 9): CL: 6.06 (3.367–7.354); CH: 2.154 (1.1555–2.612); FFH: 0.682 (0.333–0.939); tip of MF to MD: 1.644 (0.733–2.124); tip of MF to MP: 1.830 (1.384–2.596); tip of FF to FD: 0.905 (0.759–1.020); PL: 20.403 (17.190–23.738); LI: 11.633 (10.335–13.182); LIV: 21.268 (18.046–23.454); PPW: 4.385 (3.832–5.200); PPL: 2.977 (2.219–4); TL: 23.467 (19.818–26.549); GOL: 1.401 (1.244–1.557); GOW: 0.619 (0.492–0.746); GOD: 1.930 (1.7425–2.117).

Redescription: males

Coloration: Overall coloration light tan. Legs infuscate distally near ends of tibiae, femurs, and tarsi. Pedipalps darken near end of the tibiae. Palpal tibia, metatarsi, and tarsi darker reddish orange. Propeltidium darkens slightly along margins. FF and MF of the chelicerae darken distally.

Chelicera: FF sigmoidal, with dentition present ventrally. In some populations, dentition is reduced. Between three and four teeth present on MF. MP tooth largest, prominent, and recurved. When present, MSD tooth is smallest. Fondal notch absent. Fondal teeth vary in length.

Redescription: females

Coloration: Coloration as in males.

Chelicera: FF with seven to nine teeth. The following FF states were recorded among *C. regalis* females: seven teeth with FF formula FD-2FSD-FM-2FSM-FD, eight teeth with FD-2FSD-FM-3FSM-FP, or nine teeth with FD-3FSD-FM-3FSM-FP. The last two states are the most common. Moveable finger with four teeth. MP tooth largest, followed by MM tooth, with two smaller MSM teeth between them. Many of the chelicerae examined have FST and MST.

Operculum: Opercular morphology is highly variable between individual females. AMNH allotype with rounded opercular plates resembling isosceles triangles. Other morphologies present include elongate tapered lobes in specimen DMNS ZA.16442, broad anterior pillars with laterally curving lobes resembling an L-shape in specimen DMNS ZA.17213, or elongate, ovoid lobes as in specimen DMNS ZA.44238 (Fig. 7).

Distribution

Sonoran Desert. This species is wide ranging, occurring from the southwestern corner of Utah to the Sonoran Desert/Peninsular Desert in Baja California. It is restricted primarily to the eastern side of the Colorado River. One record is from the western side on the southern end of the distribution in Pima County, Arizona, suggesting that they might occur on both sides of the southern end of the river.

Discussion

Individuals of this widespread species are notable for a high level of intraspecific morphological variation in both the male chelicerae and the female genital operculum (Fig. 7A–D), and these structures have been used historically for species delimitation in eremobatids (Muma 1951, 1962). Such variability, especially in the relative lengths of the fondal teeth and general shape of the FF of the male chelicerae, challenges previous taxonomic assumptions about the usefulness of these 'sexually selected' structures for delimiting species within the genus. *Chanbria regalis* and *C. rectus* were differentiated by Muma (1962) based on the lack of curvature of the dorsal profile of the male FF (Supporting Information, Fig. S5) and the presence or absence of palpal scopula (papillae). However, the results of the PCAs from the SNP and mitochondrial dataset, the small K80 genetic distance, the relatively recent divergence time, and the lack of a distinct geographical barrier support the synonymization of these two species. More sampling from populations across the *C. regalis* range is necessary to determine whether the variable morphological traits we observed are stable across the geographical range or are aberrant traits. Given the little divergence in genetic data and inconsistent morphological traits, we are therefore in favour of a single-species hypothesis that maintains subtle variation of traits across populations.

Owing to this, our genetic results, and the level of intraspecific variation that we observe within this clade, in addition to our observation of the type material, we suggest the synonymization of *Chanbria tehachapianus* with *C. regalis*. This decision is motivated by the nearly identical morphology that *C. tehachapianus* shares with individuals of *C. regalis*, and the diagnostics used to erect the species [i.e. constricted base at the FF and lack of scopula (also known as papillae; Muma 1962)] are insufficient to maintain the species status confidently. Additionally, a lack of known specimens other than the holotype identified as *C. tehachapianus* and the lack of a distinct geographical barrier between its collection locality and the known range of *C. regalis* are evidence in favour of synonymizing these two species.

The high degree of variable morphology in the opercula of female *C. regalis* suggests that mating complementarity in *C. regalis* is not dependent on the shape of the genital opercular plate, and instead internal structures might be more important for facilitating mating complementarity than external structures, as noted in other studies (Garcia *et al.* 2024). Alternatively, this variation might simply be explained by the recent divergence and is an example of characters that have yet to reach fixation.

Chanbria serpentinus Muma, 1951

(Figs 6I, J, 7E, F)

Type material: Male holotype from Tucson, AZ, USA (AMNH). Examined.

Other material examined: ***USA***: Arizona: Pima Co.: Posta Quemado Canyon 8 miles N Vail, came to UV light, 32.0543°N, 110.634°W, 1045 m, 30 May 1968, one ♀, F. Werner, DMNS (DMNS ZA.17735); Catalina State Park, 32.42445°N, 110.92271°W, 822 m, 27 April 2011, one ♂, P.E. Cushing; G. Selby, At Lights, DMNS (DMNS ZA.26433); Catalina State Park; Campsite A and B, 32.42445°N, 110.92271°W, 822 m, 4 June 2011, one ♀, P.E. Cushing; P. Casto; B.E. Trierweiler; C.G. Olds, Lantern Light, DMNS (DMNS ZA.26852); 4020 S Via del Pica Maderos, 31.8542°N, 110.9937°W, 886 m, 13 July 2011, one ♀, W.R. Savary, Casual, DMNS (DMNS ZA.28202); Catalina State Park, campsite A and B, 32.42445°N, 110.92271°W, 822 m, 6 Jun 2011, one ♂, C. Ho, Casual, DMNS (DMNS ZA.17648); Catalina State Park Campgrounds A and B; 32.42630 −110.92372, 32.4263°N, 110.92372°W, 825 m, 13 June 2018, five ♂, two ♀, P.E. Cushing; F. Channiago; L. Herrera; R.R. Jones, At lights, DMNS (DMNS ZA.38728); Catalina State Park Campgrounds A and B, 32.4263°N, 110.92372°W, 825 m, 13 June 2018, one ♂, P.E. Cushing; F. Channiago; L. Herrera; R.R. Jones, At lights, DMNS (DMNS ZA.38729); Catalina State Park Campgrounds A and B, 32.4263°N, 110.92372°W, 825 m, 12 July 2018, one ♂, P.E. Cushing; F. Channiago; L. Herrera; R.R. Jones, At lights, DMNS (DMNS ZA.38833); La Paz County: Ehenberg, Comber Boulevard at Colorado River, 33.61639°N, 114.52361°W, August 1974, one ♀, W.B. Warner, ASU (ASU_NoNumber).

Diagnosis

Chanbria serpentinus can be distinguished from other *Chanbria* species by the male chelicerae with an elongate sigmoidally shaped FF lacking dentition. It is also noticeably darker and smaller in overall body size compared with the geographically close species, *C. regalis*.

Measurements

All measurements are reported as averages, and ranges are in parentheses.

Males (n = 9): CL: 6.153 (5.164–7.829); CH: 2.03761 (1.641–2.589); FFH: 0.555 (0.443–0.694); tip of MF to MM: 1.658 (1.351–2.05606); tip of MF to MP: 2.262 (1.544–2.994); PL: 23.914 (20.800–29.217); LI: 12.980 (10.667–15.665); LIV:

21.755 (18.133–27.282); PPW: 3.957 (3.2–5.319); PPL: 2.797 (2.135–3.689); TL: 22.275 (18.4–27.840).

Females (n = 4): CL: 5.710 (5.171–6.498); CH: 1.957 (1.761–2.205); FFH: 0.636 (0.543–0.685); tip of MF to MD: 1.197 (0.925–1.386); tip of MF to MP: 1.969 (1.758–2.143); PL: 18.067 (15.916–19.733); LI: 10.584 (8.236–12.110); LIV: 19.360 (17.404–21.312); PPW: 2.577 (2.397–2.839);PPL: 3.701 (3.2–4.271); TL: 21.094 (19.385–24.933); GOL: 1.275 (1.122–1.499); GOW: 1.0547 (0.856–1.358); GOD: 1.681 (1.415–1.985).

Redescription: males

Coloration: Overall coloration sandy brown. Appendages darken distally near ends of tibiae and tarsi. Propeltidium with darker lateral margins. Cheliceral manus darkens proximally.

Chelicera: FF is sigmoidal, lacks dentition. Four teeth are present on MF. MP tooth largest, prominent, and recurved, followed by MM tooth, then posterior MSM tooth. Fondal notch absent. Fondal teeth reduced.

Redescription: females

Coloration: Coloration as in males.

Chelicera: FF with eight or nine teeth, formula FD-2FSD-FM-3FSM-FP or FD-3FSD-FM-3FSM-FP. Moveable finger with four teeth. MP tooth largest, followed by MD tooth, with two smaller MSD teeth between them.

Operculum: Two morphologies were observed in the opercular plates of *C. serpentinus* females. One is like those observed in some *C. regalis* females, with rounded plates that resemble scalene triangles, and the other consists of more broadly lobate plates with tapered anterior edges.

Distribution

Sonoran Desert. This species is apparently restricted to the eastern side of the Colorado River.

Discussion

Chanbria serpentinus females are nearly identical to *C. regalis* females, with *C. serpentinus* being distinguishable from *C. regalis* by the smaller size, darker coloration, and geographical location. Like *C. regalis*, the genital opercula of *C. serpentinus* females are intraspecifically variable and therefore not wholly informative for species identification.

Chanbria brookharti Hansen & Garcia **sp. nov.**

(Figs 6M, N, 8)

urn:lsid:zoobank.org:act:5671F240-4BF6-4AA0-A56E-B05581A32440

Type material: Male holotype (*DMNS ZA.36968*) from Dalquest Desert Research Station, Brewster County, TX, USA. Examined. Type material at the DMNS with accession number DMNS 2009-110.

Etymology

The specific epithet is a patronym in honour of John (Jack) Odell Brookhart, who has dedicated >50 years of research to this arachnid order, profoundly contributing vast amounts of knowledge to the group. This dedication is also an expression of deep gratitude and appreciation of Jack's mentorship, training, advice, and unconditional friendship that he has given selflessly to any aspiring solifugologist who crossed his path. Jack is as rare a person as is this solifuge species is to science.

Diagnosis

Chanbria brookharti can be distinguished from other *Chanbria* species by the large protuberant structure on the FF tips of the male chelicerae. This structure is folded dorsodistally, laterally round, and FF is on a diagonal slope with respect to the manus, unlike the folded FF tip of *C. plicatus* male chelicerae.

Measurements

Male holotype: CL: 5.135; CH: 1.722; FFH: 0.426; tip of MF to MD: 1.561; tip of MF to MP: 1.986; PL: 17.291; LI: 13.245; LIV: 18.371; PPW: 3.602; PPL: 2.261; TL: 18.259.

Description: male

Coloration: Overall coloration very light tan, nearly translucent in some places, possibly owing to degradation in ethanol of the single known specimen. Propeltidium uniform in colour. Tibiae darken distally, femurs darken proximally, and palpal metatarsi darken distally. Palpal tarsi dark. Cheliceral manus uniform in colour. FF and MF darken distally into a red-orange. Protuberant structure on dorsal FF red-orange.

Chelicera: FF morphology unique among eremobatids. The most prominent feature is the modified tip, displaying a proportionally large, dorsodistally oriented, mesally folded protuberant structure. When viewed retrolaterally, this protuberance is anteriorly rounded and posteriorly tapered, with a pinhole near the distal margin. When viewed dorsally, the dorsal margin of FF extends straight near the manus before undulating in a sigmoidal ectally then mesally. Modified tip of FF folds to form distal parabolic cup-like structure. Ventral dentition on FF highly reduced. Dentition on MF is highly reduced and triangular, whereas in the other *Chanbria* they are strongly or subtly recurved. MP tooth is largest, recurved, and similar in stature to other *Chanbria* species. The proximal MM tooth is the second largest. There are MST present before the MM. The cheliceral manus is more ovular than in other *Chanbria*, lacking the dorsal hump observed in other species.

Pedipalp: Male. Approximately 10 pairs of enlarged moveable spines present on ventral surface of the palpal fibulae.
Females unknown.

Distribution

Distribution: Chihuahuan Desert. This species is known from only a single locality at Dalquest Research Station in Brewster County, TX, USA.

Discussion

Based on the male cheliceral morphology, this specimen is best placed in *Chanbria*. The specimen was collected serendipitously via a long-term pitfall trap from 2 August to 27 September 2007. We were unable to extract viable DNA for UCEs from this specimen, probably owing to its long-term exposure to solar radiation and changing environmental conditions. Several attempts, during different seasons, have been made to capture more representatives of this species, without success. This species is elusive and was found in a canyon near Alamo Springs and might be endemic to this canyon. Owing to the remote location where this specimen was found with respect to the other previously described *Chanbria* species, we believe the unique features and geographical location of this specimen merits new species status.

Chanbria mapemes **Garcia & Castillo sp. nov.**

(Figs 6O, P, 7H, 9)

urn:lsid:zoobank.org:act:203EC990-AF19-4255-BA04-3C8B09DBE62D

Type material: Male holotype (*IBUNAM CNANSO106*) from Sierra Mojada, Coahuila, México. Paratypes and allotypes (one ♂, two ♀) from the same locality, collected on the same date by D. Sissom, E. González-S., B. Hendrixon, S. Grant. Type and paratype material deposited at the Instituto de Biología, Universidad Nacional Autónoma de México (UNAM) arachnology collection with the accession numbers *CNAN-T01867* (holotype) and CNAN-T01868 (paratypes). Specimens were examined by the third author and photographs by the other two.

Etymology

This species epithet is inspired both by the indigenous Cocoyome word 'mapeme', meaning high rock or elevated hill, and by the Bolsón de Mapimí, a large internal basin surrounded by lower-elevation mountain ranges (Facio García, 2020). This basin is in the northwest of the Mexican Plateau, from which the type and paratype species were collected. The Cocoyome tribe was once a distinct indigenous group that inhabited this desert basin in present-day México.

Diagnosis

Chanbria mapemes is morphologically distinguished from the other *Chanbria* by not having the characteristic sigmoid-shaped FF as in *C. regalis* and *C. serpentinus* males. Instead, this species possesses an FF that is elongate, thin, and is virtually uniform in height along the extent of the length of the finger, except where it tapers towards the tip. Tip of FF is constricted. There are six teeth present on FF. Moveable finger, medial tooth (MM) is large and a similar size to the moveable finger, proximal tooth (MP), whereas in the other species it is reduced or absent. The geographical location of this species is remote from the other type localities and is the southernmost record for the genus.

Measurements

Male holotype: CL: 5; CH: 1.64; FFH: 0.3; tip of MF to MM: 1.42; tip of MF to MP: 1.84; PL: 15.13; LI: 12.3; LIV: 18.75; PPW: 3.2; PPL: 2.05; TL: 17.75.

Male paratype: CL: 4.45; CH: 1.4; FFH: 0.3; tip of MF to MM: 1.04; tip of MF to MP: 1.72; PL: 15.13; LI: 12.3; LIV: 18.75; PPW: 3.2; PPL: 2.05; TL: 14.88.

Female allotypes (2): CL: 4.15, 4.05; CH: 1.58, 1.55; FFH: 0.38, 0.2; tip of MF to MM: 1.02, 0.76; tip of MF to MP: 1.46, 1.20; PL: 11.65, 11.1; LI: 10.25, 9.4; LIV: 14.14, 13.2; PPW: 2.8, 2.75; PPL: 1.65, 1.25; TL: 13.875, 18.875.

Description: males

Coloration: Overall coloration is light beige with dark pigmentation. Propeltidium is predominantly dark, with anterior margins with dark pigmentation, light coloration in the centre that darkens distally towards the edges. Pedipalps are almost entirely dark, except for a light-coloured patch at the proximal end. Cheliceral manus uniform in coloration. FF and MF darken distally into a red-orange towards the tip. Legs I and II have no pigmentation. Legs III and IV have dark pigmentation on the distal ends of femora and proximal ends of metatarsi.

Chelicera: FF is long, slim, and nearly uniform in height. Tip of FF terminates in a sharp curved tip and is constricted, with a prominent indentation on the ectal side of the structure. Narrow line of stout setae on the mesal side of the FF along most of the length. Dentition present on FF, with six distinct teeth starting from the FP to FD. MF dentition is like that of *C. brookharti*, such that the MSD are triangular and there are MST present; however, the difference is that the MM is larger than any of the *Chanbria* species, and it is also slight recurved. Manus is ovoid like *C. brookharti*, with more of a dorsal hump, but less than that observed in the other species.

Pedipalp: Pedipalps are dark, with light coloration at the proximal end. Enlarged, moveable palpal spines are also present on the ventral side, as in *C. brookharti*. Papillae present in the males examined.

Ctenidia: Four 'stiletto-like' abdominal ctenidia.

Description: females

Coloration: Same as males.

Chelicera: Entire chelicerae are elongate and dorsoventrally slender. FF tooth formula is as follows: FST-FD-2FSD-FM-2FSM-FP, with seven principal teeth, not counting the teeth before the FD. Moveable finger dentition has four principal teeth, with the tooth formula MST-MM-2MSM-MP. Tips of chelicerae and tips of teeth darken at tips.

Operculum: Genital plates are scalene triangle shaped, with nearly horizontal sides at the posterior. The lateral side of opercula is the longest of the three sides.

Distribution

Chihuahuan Desert, Mexican plateau.

Discussion

This species is another *Chanbria* that is endemic to the Chihuahuan Desert; however, this species is the southernmost record for the genus thus far. Owing to the remote location, which is in a basin between two mountain ranges, coupled with the distinct morphology in comparison to the other species, we believe this evidence favours elevating this specimen to new species status.

Chanbria plicatus (Muma 1962), comb. nov.

(Figs 6K, L, 7G)

Therobates plicatus Muma 1962: 11.
Eremochelis plicatus (Muma): Muma 1970: 33.

Type material: Holotype male from Mercury, NV, USA, 15 July 1960, coll. Elden Beck (AMNH). Allotype female from Mercury, NNV, USA, on 6 July 1960, coll. Elden Beck (AMNH). Examined male holotype from images, but unable to examine female allotype.

Non-type material examined: ***USA***: Nevada: Churchill Co.: Sand Mountain, 22 miles SE of Fallon, 39.291389, −118.415556, 1–8 July 2011, one ♂, W.B. Warner, Pitfall Trap Array, ASU (ASU_NoNumber); Soda Lake ~1 mile NW Fallon, 39.518885, −118.868331, 23 July 1965, one ♂, T. Briggs; K. Hom; V. Lee, CAS (CASENT9033966); Clark Co.: trail off Calico Basin Road, 36.144061, −115.4088627, 1060 m, 1 June 2021, one ♂, one ♀, E.L. Garcia, DMNS (DMNS ZA.41887); Lincoln County: Corrola Dunes, ~23 miles South US-93 on old Alamo Road, 37.02029, −115.19195, 1006 m, 24 May 2014, one ♂, Zach J. Valois, Wind-blown dune field/high dunes, DMNS (DMNS ZA.33144); Corrola Dunes, ~23 miles South US-93 on old Alamo Road, 37.02029, −115.19195, 1006 m, 24 May 2014, one ♂, Zach J. Valois, Wind-blown dune field/high dunes, DMNS (DMNS ZA.33145); Mineral Count: junction of Highways 95 and 360, 38.27833, −118.1025, 1340 m, 26 June–20 July 2018, one ♂, one juvenile, M.E. Irwin; G.R. Ballmer, Malaise Trap, CAS (CASENT9094952); Nye County: Mercury in can trap in Rock Valley, 36.633, −116.313, 870 m, 10 July1965, one ♂, M.H. Muma, DMNS (DMNS ZA.16071); Nevada Test Site, Mercury, Jackass Flats, off Jackass Flats Road, 36.63619, −116.0756, 878 m, 30 June 2011, one ♂, P.E. Cushing, DMNS (DMNS ZA.27726); 12 miles NW Tonopah Crescent Dune, 38.229722, −117.335, 30 April–7 July 2011, one ♂, W.B. Warner, Pitfall Trap Array, ASU (ASU_NoNumber).

Diagnosis

Chanbria plicatus can be distinguished from other *Chanbria* by the distinct mesally folded tip of the male cheliceral FF that forms a concavity on the mesal side and by the presence of a deep, thin, proximally upturned fondal notch. *Chanbria plicatus* is the only *Chanbria* species in which the male chelicerae have a fondal notch and flagellar groove. It is also noticeably darker in coloration than *C. regalis* and *C. brookharti*.

Measurements

All measurements are reported as averages, and ranges are in parentheses.

Males (n = 5): CL: 4.057 (3.701–4.739); CH: 1.854 (1.619–2.285); FFH: 0.413 (0.378–0.457); tip of MF to MM: 1.412 (1.294–1.614); tip of MF to MP:1.487 (1.440–1.534); PL: 18.114 (16.116–21.553); LI: 10.671 (9.753–11.411); LIV: 18.070 (16.159–20.240); PPW: 3.115 (2.856–3.744); PPL: 2.240 (2.030–2.789); TL: 16.713 (14.423–18.735).

Females (n = 2): CL: 4.969 (4.716–5.222); CH: 1.702 (1.599–1.80531); FFH: 0.555 (0.504–0.608); tip of MF to MP: 1.7485 (1.695–1.802); tip of MF to MM: 1.859(1.695–2.079); PL: 15.096 (14.481–15.711); LI: 9.239 (8.024–10.455); LIV: 17.220 (15.442–18.997); PPW: 3.372 (3.165–3.578); PPL: 2.175 (2.060–2.290); TL: 18.382 (17.729–19.037); GOL: 1.362 (1.359–1.367); GOW: 0.700 (0.643–0.756); GOD: 1.518 (1.515–1.523).

Redescription: males

Coloration: Dorsally sandy brown, ventrally light tan. Femurs and tarsi uniform sandy brown, tibiae lighten proximally. Propeltidium with darker anterior margin. Cheliceral manus sandy brown with lighter margins. FF and MF darken distally.

Chelicera: FF with distinct tip that folds over to the flagellar groove (FG) on mesal side. Height of FF greater than in other *Chanbria*. FF lacks dentition. Dorsal margin of the FF is shaped like an elongate, sigmoidal wave. The proximal tooth on MF is large, prominent, slightly recurved. distal teeth on MF present in each specimen but highly reduced, with fondal notch deep, thin, upturned dorsally. Fondal teeth prominent, with tooth I in both ectal and mesal row longest. Shape of cheliceral manus is unique among *Chanbria* species, being less dorsoventrally compressed and with a more prominent dorsal hump from base of FF and subsequently tapering near posterior portion of manus.

Redescription: females

Coloration: Same as in males.

Chelicera: FF with seven teeth, with formula FD-2FSD-FM-2FSM-FP. Moveable finger with four teeth. MP tooth is largest, followed by MM tooth, with two smaller MSM teeth between them. A diastema, a wide gap between two teeth, exists between first and second fondal tooth in each row.

Operculum: Opercular plates in the shape of elongate tapered lobes. Plates are tapered anteriorly and lobed posteriorly.

Distribution

Nevada, USA. Mojave Basin and Range (Great Basin) Province, occurring on the east side of the Colorado River.

Discussion

This species is similar in size and has dark pigmentation on the propeltidium, pedipalps, and legs, as in *C. serpentinus*. Collection records indicate that this species has affinities to dune-like or sandy habitats in the Mojave Basin and Range. Owing to the similarities in habitat preference, dense setation on pedipalps, strongly procurved MF in males, and elongated chelicerae in females, we suggest that *Eremochelis plicatus* Muma, 1962 should be moved into *Chanbria* as *Chanbria plicatus*. This new combination is strongly supported by phylogenomic and morphological evidence, and this species is likely to be the earliest diverging member of *Chanbria*.

Key to males of the species of *Chanbria*

1. Fixed finger sigmoidal in shape 2
- Fixed finger non-sigmoidal in shape 3
2. Dentition present on the fixed finger beginning at approximately half the length of finger. Fixed finger height is robust proximally, then tapers distally .... *Chanbria regalis* Muma, 1951
- Dentition absent or reduced on the fixed finger .... *Chanbria serpentinus* Muma, 1951
3. Fondal notch and flagellar groove present. Tip of fixed finger folds mesally over flagellar groove .... *Chanbria plicatus* (Muma, 1962)
- Fondal notch absent and fixed finger extending upwards 4
4. A prominent, round protuberance present on the tip, accompanied by a miniscule hollow cavity when viewed dorsally. Protuberance is folded ectally when viewed dorsally. Large moveable ventral spine-like structures on pedipalps .... ***Chanbria brookharti* sp. nov.**
- Uniform in fixed finger height, except at tip, where it tapers. Tip is constricted laterally. Six prominent teeth present on fixed finger .... ***Chanbria mamepes* sp. nov.**

Key to females of the species of *Chanbria*

1. Fixed finger with seven to nine teeth. Operculum plates simple, in the shape of triangulate lobes or elongate diagonal pillars 2
- Fixed finger with seven teeth following a tooth formula of FD-2FSD-FM-2FSM-FP. Operculum plates are tapered anteriorly, with distal diagonal ovoids. Dark coloration on propeltidium and legs .... *Chanbria plicatus* (Muma, 1962)
2. Operculum plates triangulate lobes with diagonal posterior edges 3
- Operculum plates scalene triangulate shaped, with virtually horizonal posterior edges. Propeltidium and legs with dark pigmentation .... ***Chanbria mapemes* sp. nov.**
3. Specimen comparatively small and dark in coloration, specifically on the propeltidium and legs .... *Chanbria serpentinus* Muma, 1951
- Specimen comparatively large and light in coloration .... *Chanbria regalis* Muma, 1951

SUPPLEMENTARY DATA

Supplementary data is available at *Zoological Journal of the Linnean Society* online.

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CREDIT STATEMENT

Erika L. Garcia (Conceptualization, Methodology, Data Collection, Data Analysis, Imaging, Visualization, Writing, Supervision, Data Curation), Quincy G. Hansen (Data Collection, Imaging, Writing), and Jaír R. Castillo (Data Collection, Imaging)
Conflict of interest: None declared.

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DATA AVAILABILITY

Raw sequences used for UCEs are available through the Sequence Read Archive (SRA; BioProject PRJNA982881). *COI* matrices and tree files are available on Figshare under the project name 'A phylogenomic approach to a taxonomic revision: a combination, new synonymies, and a description of two new species within the camel spider genus *Chanbria* Muma 1951 (Solifugae: Eremobatidae)' https://doi.org/10.6084/m9.figshare.24894948.v1.

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