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Research

Phylogeny, Evolution, and Biogeography of the North American Trapdoor Spider Family Euctenizidae (Araneae: Mygalomorphae) and the Discovery of a New 'Endangered Living Fossil' Along California's Central Coast

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Abstract

We report here the discovery of a remarkable new monotypic mygalomorph spider genus, known only from one geographical location along the central coast of California. The single relict species comprising *Cryptocteniza kawtak* **n. gen. n. sp.**, is morphologically distinct and geographically isolated from other related genera, with its closest phylogenetic relatives found much further to the east in New Mexico and Arizona. Using a phylogenomic approach employing anchored hybrid enrichment, we reconstruct the evolutionary history of the family Euctenizidae Raven, 1985 to explore relationships among genera, affirmatively place previously undescribed taxa, explore rates of diversification, and reconstruct the group's biogeography. A biogeographic analysis shows that extinction likely played a significant role in shaping the observed disjunct modern-day distribution of *Cryptocteniza* and its sister taxa. Our extinction hypothesis is further bolstered by a diversification rate analysis identifying considerably higher rates of speciation in other euctenizid lineages like *Aptostichus* Simon, 1891. Consequently, changes in environmental conditions (or other related biotic and/or abiotic factors) may have spurred an adaptive radiation in related genera now widely distributed across the California Floristic Province biodiversity hotspot, with concomitant extinction in *Cryptocteniza* following the Miocene and establishment of a Mediterranean climate. Owing to its phylogenetic distinctiveness, incredibly narrow distribution and age, we show that *Cryptocteniza* meets all the criteria of an 'Endangered Living Fossil' and is consequently of grave conservation concern.

Key words: spider taxonomy, phylogenomics, extinction, Bipectina, Domiothelina

The trapdoor spider family Euctenizidae Raven, 1985 (Araneae: Mygalomorphae) comprises 76 nominal species placed among seven genera that are largely distributed throughout the United States, though a few species are known from Mexico. It ranks among the most diverse families of mygalomorphs (trapdoor and funnel web spiders, tarantulas, and their kin) in North America, with its closest rivals being the Halonoproctidae Pocock, 1901a (e.g., *Ummida* Thorell, 1875, estimated to have many undescribed species) and Theraphosidae (e.g., *Aphonopelma* Pocock, 1901b, with >50 described species). Although widespread across the continent, most of the euctenizid diversity is found in the American West and Southwest, with the genus *Myrmekiaphila* Atkinson, 1886 distributed in the Southeastern United States. Species-level diversity is relatively well known with most of the genera having had significant taxonomic effort allotted to them over the last 10–15 yr. For example, the genus *Aptostichus* Simon, 1891, revised by Bond (2012), is the most diverse with 41 species; *Eucteniza* Ausserer, 1875 and *Myrmekiaphila* were also recently revised (Bond and Platnick 2007, Bond and Godwin 2013) now comprising 14 and 12 species, respectively. The remaining genera are relatively small and contain either only two species (*Apomastus* Bond and Opell, 2002 and *Promyrmekiaphila* Schenkel, 1950) or are monotypic (*Neoapachella*

Bond and Opell, 2002). Unlike the other genera, *Entychides* Simon, 1888 is still in need of revision, but likely only contains a few species (J. Bond, personal observation). With the exception of *Apomastus*, which has an open burrow, all other members of the family cover their burrows with a silken-soil trapdoor that is relatively thin when compared to other Domiothelina taxa that tend to make thick cork-style trapdoors. *Myrmekiaphila* and *Promyrmekiaphila* share the unique habit of constructing burrows with side chambers that are often sealed with a subterranean trapdoor (Bond and Platnick 2007, Stockman and Bond 2008).

Euctenizids were originally considered a subfamily of Cyrtaucheniidae Simon, 1889; however, morphological (Goloboff 1993, 1995; Bond and Opell 2002) and molecular (Bond and Hedin 2006, Hedin and Bond 2006) studies over the past nearly three decades consistently failed to recover the family as a monophyletic group. Interestingly, the subfamily Euctenizinae was always recovered as an independent, monophyletic lineage (distantly related to 'true' cyrtaucheniids) and consequently was elevated to family level by Bond et al. (2012) on the basis of a total evidence approach using molecular and morphological characters. A recent phylogenomic-based treatment of all mygalomorph families resulted in a major relimitation of numerous family-level taxa (Opatova et al. 2020), but maintained strong support for the monophyly and composition of the Euctenizidae as previously circumscribed by Bond et al. (2012). Opatova et al. (2020) placed euctenizids in the inclusive Domiothelina clade, which includes four other families: Migidae Simon, 1889, Halonoproctidae, Idiopidae Simon, 1889, and the euctenizid sister group Ctenizidae Thorell, 1887 (also see Godwin et al. 2018). The euctenizid genera are parceled among two subfamilies (Bond 2012), Apomastinae Bond and Hedin, 2012 and Euctenizinae; the former comprising *Apomastus*, *Aptostichus*, and *Myrmekiaphila*, while the latter holds the remaining genera. The most recent genomic analysis by Opatova et al. (2020) does not support *Myrmekiaphila* as an apomastine but rather as the sister group to all euctenizids.

Since first collecting specimens of an unusual species at Moss Landing State Beach in Monterey County, California (Fig. 1), in 1997, the first author (JEB) has been aware of the possibility of a potentially new, monotypic euctenizid genus. At the time, and for many years thereafter, male specimens of this seemingly unique taxon remained elusive. As most students of mygalomorph spider systematics know, male mating clasper (modifications of the first walking leg) or pedipalp bulb morphology are often species and/or genus specific, causing male specimens to be highly sought after when describing new taxa. Not only did these newly discovered females seem unique, but they also lacked any of the characteristics considered diagnostic for all other euctenizine genera and thus it was impossible to confidently hypothesize their evolutionary placement. Without male specimens, we were hesitant to describe a new genus despite the fact that molecular phylogenetic analyses since 2006 have consistently failed to place the Moss Landing taxon within any of the known genera. However, its placement as the sister group to *Entychides*, along with its apparent monotypic status, did not entirely preclude inclusion in that genus; the Moss Landing taxon is likewise darker in color and has a few other characters (e.g., palpal coxae cuspule patterns), albeit plesiomorphic, that indicated some affinity with *Entychides*. Although morphologically similar, *Entychides* species all are known to have a unique male mating clasper morphology and are found a considerable distance to the east in Arizona and Mexico. Collecting a male specimen was imperative for genus-level placement.

Numerous attempts over 22 yr to collect mature males, either from a burrow (prior to dispersing) or out wandering, were unsuccessful. But in the early fall of 2018, a photograph of a single male specimen resembling the Moss Landing taxon was posted on iNaturalist (inaturalist.org). Equipped with a potential lead on when males might be active, we worked in collaboration with the California State Parks (Monterey District) to set pitfall traps at Moss Landing State Beach during the late fall season of 2019; finally, a male was collected in September of that year. As we report here, male morphology is highly distinctive and does not match *any* of the existing euctenizid genera including its close phylogenetic relative, *Entychides*. The discovery of a new monotypic genus with such geographically distant relatives and isolated on a single beach along California's coast raises a number of questions regarding euctenizid evolution and biogeography, as well the nature of higher taxa.

The aims of this study are threefold. First, using genomic scale data, we reconstruct the phylogeny of Euctenizidae. Our sampling includes representatives of all the genera, including the new genus. We especially sampled numerous species of *Aptostichus* to also assess the monophyly of that genus as well as the species groups proposed by Bond (2012). Second, to gain an understanding of the evolutionary patterns that led to such disjunct distributions, our newly derived phylogenetic framework was used to investigate rates of diversification across the family and reconstruct its biogeography. Third, we formally describe and diagnose the new monotypic euctenizid genus *Cyrptocteniza* **n. gen.** and describe its type species *C. kawtak* **n. sp.**

Materials and Methods

DNA Sequence Generation and Processing

We sampled a total of 28 taxa, 24 ingroup specimens representing eight euctenizid genera (Supp Table 1 [online only]), and two representatives of the closely related families Idiopidae and Ctenizidae as outgroups to root phylogenies. Sampling represents all of the nominal euctenizid genera and approximately one-third of all described species. All taxa included in this study were samples from a number of previous studies (Hamilton et al. 2016, Godwin et al. 2018, Opatova et al. 2020). Taxon sampling is summarized in Supp Table 1 (online only).

Whole genomic DNA was extracted using the DNeasy Blood and Tissue Kit (Qiagen), following the manufacturer's guidelines. Library preparation, enrichment, and sequencing were performed at the Center for Anchored Phylogenomics at Florida State University (http://anchoredphylogeny.com/) following the methods described in detail in Lemmon et al. (2012) and Hamilton et al. (2016); materials and methods are also extensively detailed in Opatova et al. (2020).

Following the targeting of the 585 loci within the Anchored Hybrid Enrichment (AHE) Spider Probe Kit v1 (Hamilton et al. 2016), 633 loci were recovered and assembled. Note that recovered loci numbers are higher than those targeted because long loci can be broken up into multiple loci during bioinformatic processing. All loci were aligned with MAFFT 7.402 (Katoh and Standley 2013) using the L-INS-i algorithm (--localprior and --maxiterate 1,000 flags). The alignments were scored for accuracy and ambiguously aligned positions were removed using the procedures outlined in (Hamilton et al. 2016). Individual loci were concatenated to yield a supermatrix; all alignments were visually inspected in Geneious 10.1.3 (Biomatters 2017).

Phylogenetic Analyses

Phylogenetic analyses were run on the Farm Community Cluster at the University of California, Davis. Maximum likelihood (ML) analyses were conducted in RAxML v8.2.6 (Stamatakis 2014) and

Fig. 1. The type locality and geographical distribution of *Cryptocteniza*. (A) Map inset of California showing approximate location of Moss Landing State Beach in Monterey County. (B–D) Aerial drone photographs of Moss Landing State Beach. (B) Overhead composite photograph. (C) Northward view. (D) View looking southward.

IQ-TREE 1.6.10 and 1.7.9b (Nguyen et al. 2015). For the RAxML analysis, the dataset was analyzed using the GTRCAT model. The best ML tree was selected from 1,000 iterations, each starting from an independently derived parsimony-based tree. Bootstrap support was inferred from 1,000 replicates. For IQ-TREE analyses, model selection for each partition was performed by ModelFinder Plus (Kalyaanamoorthy et al. 2017); support values were inferred via 1,000 replicates of ultrafast bootstrapping (Hoang et al. 2018) and SH-like approximate likelihood ratio test (SH-aLTR). Genealogical and sites concordance factors (gCF and sCF, respectively) were also calculated using IQ-TREE (Minh et al. 2018); gCF and sCF analyses are alternative measures of topological support and calculate the proportion of loci or sites from which a particular node in the preferred tree is inferred (Ane et al. 2006). As an additional estimate of gene tree species tree concordance, a species tree was also inferred from the 633 gene trees using ASTRAL-II v5.7.1 (Mirarab and Warnow 2015).

For ancestral state reconstruction analyses, a male mating clasper mid-ventral clasping spur armed with a spine(s) (a diagnostic character for some euctenizine taxa) was scored as present (1) or absent (0) for ingroup and outgroup taxa. Specifically, we are investigating a potential synapomorphy among euctenizine lineages. As discussed below, a number of taxa have a spine (or multiple spines) borne on a ventral tibial spur, whereas other genera have a distal lateral tibial spur bearing spines (e.g., *Entychides* and some outgroups); these two spurs are considered different characters for the purposes of our analysis of the former. Reconstructions were conducted using the R package corHMM (Beaulieu et al. 2013) on an ultrametric scaled tree with node.states=marginal. The R package ape (Paradis et al. 2004) was used to convert the preferred tree topology into a relative-rate scaled ultrametric tree ('chronopl' using an assigned lambda value of 0.1). This approach produces a tree whose branches are scaled to evolutionary rates, rather than a dated tree, and provides a means to understand evolutionary changes over relative 'time' in the group being investigated. Character optimizations using equal (ER) and all rates different (ARD) models were explored with the preferred model chosen by comparing AICc values calculated using corHMM.

Biogeographic analyses were conducted in Reconstruct Ancestral State in Phylogenies (Yu et al. 2015, 2020) using Statistical Dispersal-Vicariance Analysis (S-DIVA). Analyses were run with dispersal only possible between adjoining areas, allowing for extinction, and only two-unit areas in the ancestral distributions. The terminal taxa represented in the tree were assigned to four distribution ranges: (A) Eastern North America (NA; eastern Texas extending to east coast); (B) Southwestern NA (Western Texas, Arizona, New Mexico, and Mexico); (C) Southern California (CA); and (D) Northern CA (Fig. 4).

Similar to the approach employed by Garrison et al. (2016), we used BAMM—Bayesian analysis of macro-evolutionary mixture (Rabosky 2014)—to investigate shifts in diversification rates across the euctenizid clade. As above, outgroups were trimmed from the preferred tree and the topology was scaled to be ultrametric. As noted earlier, our topology includes approximately one-third of all the known nominal taxa, thus unsampled species were accounted for using clade-specific corrections based on numbers of species documented in the World Spider Catalog (World Spider Catalog 2019) and personal observations (J. Bond). The R program BAMM tools was used to set BAMM priors, and then BAMM was run using four independent runs comprising 100 million generations, sampling parameters every 1,000 generations; the expected number of rate shifts was set to (1). We discarded 10% of the burnin samples after convergence diagnostics were examined in R using coda (Plummer et al. 2006). BAMM tools was then used to plot the 95% credible set of rate shift configurations sampled and lineages through time.

All relevant run execution, control, script, and output files (RAxML, IQ-TREE, RASP, corHMM, and BAMM), data, DNA alignments, tree files, and Supp Table 1 (online only) Supp Figs. 1–4 (online only)/Supp Material (online only) are available online as supplementary materials.

Institutional Abbreviations

BME: Bohart Museum of Entomology (Davis, CA)
CAS: California Academy of Sciences (San Francisco, CA)

Quantitative Morphological Abbreviations

These features are explicitly defined and illustrated in Bond (2012).

ANTd: number of teeth on the anterior margin of cheliceral fang furrow.
Cl, Cw: carapace length and width. Carapace length taken along the midline dorsal-most posterior position to the anterior front edge of the carapace (chelicerae are not included in length). Carapace width taken at the widest point.
AME, ALE, PME, PLE: anterior median, anterior lateral, posterior median, and posterior lateral eyes, respectively.
LBl, LBw: labium length and width taken from the longest and widest points, respectively.
PTl, PTw: male palpal tibia length and width.
Bl: palpal bulb length from embolus tip to the bulb base, taken in the ventral plane at its longest point.
PTLs, TBs: number of female prolateral patella and tibial spines leg III.
STRl, STRw: sternum length and width. Sternum length from the base of the labium to its most posterior point. Width taken across the widest point, usually between legs II and III.
STC: superior tarsal claw.
PLS: posterior lateral spinneret.
TSrd, TSp, TSr: number of tibial spines on the distal most retrolateral, prolateral, and midline retrolateral positions.
ITC: inferior tarsal claw

Measurement, Characterization, and Illustration of Morphological Features

Format, descriptors, and morphological features measured/examined follow closely Bond et al. (2012). In some instances, anatomical terms may differ from previous works (e.g., palpal endites vs. previously used palpal coxae) owing to our attempt to follow, herein, the Spider Anatomy Ontology (Ramírez and Michalik 2019). Unique voucher numbers were assigned to all specimens (alphanumeric designations beginning with BMEA); these data were added to each vial and can be used to cross-reference all images, measurements, and locality data. All measurements are given in millimeters and were made with a Leica MC205 dissecting microscope equipped with the Leica Analysis Suite Software. Lengths of leg articles were taken from the mid-proximal point of articulation to the mid-distal point of the article (sensu Bond 2012, figures 11–16). Leg I and Leg IV article measurements are listed in the species description in the following order: femur, patella, tibia, metatarsus, tarsus. Carapace and leg coloration are described semi-quantitatively using Munsell Color

Charts (Windsor, NY) and are given using the color name and color notation (hue value/chroma).

Digital images of specimens were made using a BKPlus Digital Imaging System (Dun Inc.™, Richmond, VA) where images were recorded at multiple focal planes and then assembled into a single focused image using the computer program Helicon Focus (Helicon Soft, Ltd., Ukraine). The female genital region was removed from the abdominal wall and tissues dissolved using trypsin; spermathecae were examined and photographed in the manner described above. Unless otherwise stated, scale bars = 1.0 mm.

Locality Data

Latitude and longitude for the collecting locality was recorded in the field using a Garmin Global Positioning System receiver (Garmin International Ltd., Olathe, KS) using WGS84 map datum. Detailed locality and associated GIS data as supplemental data files in spreadsheet and KML file format can be downloaded online Supp Material (online only).

Results

The concatenated AHE data set comprised 28 taxa, 632 loci, scored for 387,962 nucleotides. The proportion of gaps and undetermined/missing characters in the alignment was 22.13%. Figure 2A summarizes the preferred tree topology based on the IQ-TREE analysis (ln = −2674586.428); RAxML (ln = −2683888.063387) and ASTRAL produced trees with identical topologies (Supp Figs. 1–3, respectively, [online only]). Bootstrap values and SH-aLRT values were 100% for all but two nodes (Fig. 2A). The gCF and sCF values showed relatively consistent support among many loci and sites for most of the major nodes in the analysis (Supp Fig. 4 [online only]). Although bootstrap support was comparatively weak for the node uniting euctenizines and apomastines to the exclusion of *Myrmekiaphila*, the gCF analysis shows that ~71% of the loci support that grouping, a node that was also recovered in the ASTRAL analysis (Supp Fig. 3 [online only]). The morphologically distinct taxon collected from Moss Landing, California is a lineage falling between *Neoapachella* and *Entychides*. Based on these results, the monotypic genus *Cryptocteniza* **n. gen.** is newly described in the Taxonomy section below.

We scored a male tibial modification (ventral mating spur) for all 4 outgroup and for 24 ingroup taxa. Based on AICc values, the equal rates model (ER) produced the preferred reconstruction (AICc = 26.79642). Our ancestral character state analysis of male tibia mid-ventral spur/spine modification shows a less than definitive pattern owing to homoplasy and polymorphism across the taxa surveyed (Fig. 3). Generally speaking, having a tibial mid-ventral spur appears to be plesiomorphic for euctenizines (excluding *Myrmekiaphila*) with subsequent losses in *Promyrmekiaphila* and most *Entychides* species.

The biogeographic analyses results are summarized in Fig. 4. The ancestral distribution area for the family Euctenizidae is inferred to be widespread across the southeastern United States (area A) and across the American southwest (area B). Euctenizines are inferred to have an ancestral distribution extending throughout area B, followed by repeated patterns of dispersal and vicariance across the subfamily's history. The *Cryptocteniza* + *Entychides* lineage is inferred to have an ancestral distribution that extended across southern and northern California (areas C and D, respectively) with subsequent dispersal to the east, followed by vicariance between northern California and the more widespread southern California + American southwest distribution. *Entychides* likely had an ancestral distribution across southern California and the southwest (area B—Arizona, New Mexico, Texas) with extinction across the former, resulting in the present-day disjunct distribution between it and its sister genus, *Cryptocteniza*. Apomastinae is inferred to have an ancestral distribution originating largely in southern California, where most of the diversity is found today, followed by various dispersal and vicariant events throughout present day California. Closer to the tips, dispersal and vicariance events eastward towards the American Southwest are also observed (i.e., species of *Aptostichus* found in Arizona are derived).

The diversification rate shift analysis estimated one significant diversification shift across Euctenizidae (95% credible set); Fig. 2B shows the single best shift configuration. This rate shift, also reflected in the lineage through time plot (Fig. 2C), occurred within *Aptostichus*, shifting sometime after the split with *A. simus*; much lower rates of diversification are reflected across all the other lineages.

Discussion

General Overview of Relationships

Resolving relationships among the euctenizid genera has been a longstanding issue since the group was recognized as a potential family rank lineage. The first attempt to reconstruct euctenizid relationships relied entirely on morphological data scored by Bond and Opell (2002). In that analysis, they recovered the then subfamily Euctenizinae as monophyletic, but the intrafamilial relationships proposed therein have been consistently rejected by subsequent studies employing molecular data. Although the monophyly of the subfamily Euctenizinae has been reasonably stable in Sanger sequencing gene analyses based largely on rDNA data (28S and 18S), the composition of the Apomastinae, particularly with respect to *Myrmekiaphila*, has remained problematic. The total evidence phylogeny first proposed by Bond and Hedin (2006), recovered an orphaned phylogenetic grade of genera with *Apomastus* as the sister group to all euctenizids, followed by *Myrmekiaphila* and *Aptostichus* as taxa sister to euctenizines. Bond et al. (2012) first proposed Apomastinae as a subfamily, using broader taxon sampling and molecular data combined with morphology. The new subfamily was established to include all three of the 'orphaned' taxa, a result that had relatively strong support among all the data partitions.

The preferred phylogenetic hypothesis presented here provides robust support for euctenizid generic-level relationships (Fig. 2A). However, it appears to robustly reject inclusion of *Myrmekiaphila* in Apomastinae, with very strong support for its placement as the sister lineage to all other euctenizids, a result that was also not surprisingly recovered by Opatova et al. (2020) using the same AHE probe set. Although euctenizine relationships have shuffled around in previous analyses, the close affinity of the new genus *Cryptocteniza* with *Entychides* has been recovered before using other data (Bond et al. 2012).

Given the comparatively high rate of diversification (see discussion below) and remarkable habitat diversity among *Aptostichus* species, accurately resolving relationships among taxa attributed to this genus will be integral to understanding species pattern and process in this remarkably diverse group. Our results indicate that relationships among *Aptostichus* species remain unresolved particularly with respect to some of the species groups proposed by Bond (2012), which was based on a cladistic analysis using morphology. As in the cladistic analysis, we recover *Aptostichus simus*

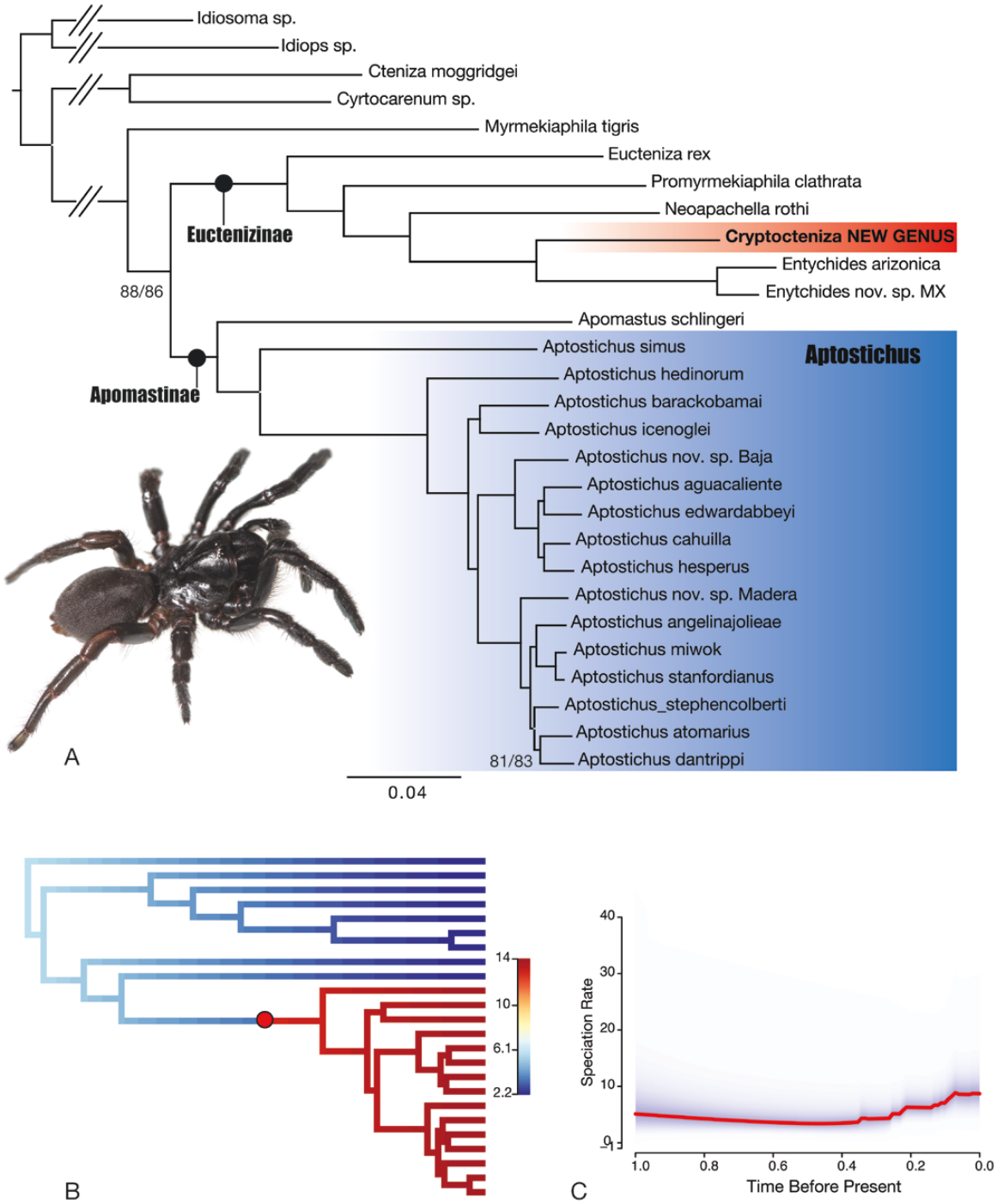

Fig. 2. Phylogenetic results using AHE data. (A) Preferred tree topology based on IQ-TREE maximum likelihood analysis; spider inset is photograph of live *Cryptocteniza* female. All nodes have 100% bootstrap/SH-aLRT values unless otherwise noted on tree (B) BAMM diversification rate analysis showing overall best rate shift configuration. (C) BAMM plot of rate-through-time curve.

Chamberlin 1917 as the sister group to all remaining members of the genus. Members of the Simus species group all share a number of unique morphological features. This morphological distinctiveness coupled with such deep divergence suggests that the Simus species group may warrant consideration as a separate genus; sampling of the remaining seven species attributed to the group would be needed before making such a determination. Compared to Bond (2012), we recover a paraphyletic Hesperus species group (i.e., the clade that includes *A. hesperus* (Chamberlin 1917); Fig. 1A) in light of the placement of *A. hedinorum* Bond 2012 as the sister to all remaining non-Simus group taxa. Furthermore, we fail to recover a monophyletic Atomarius species group given the alternative placement of *A. barackobamai* Bond 2012 and *A. icenoglei* Bond 2012 with respect to the lineage that includes *A. atomarius* Simon 1891 and the other closely related members of the Atomarius species group (Bond and Stockman 2008). The mismatch between the molecular-based phylogenetic hypothesis presented here and the morphological hypothesis proposed by Bond (2012) establishes a thought-provoking,

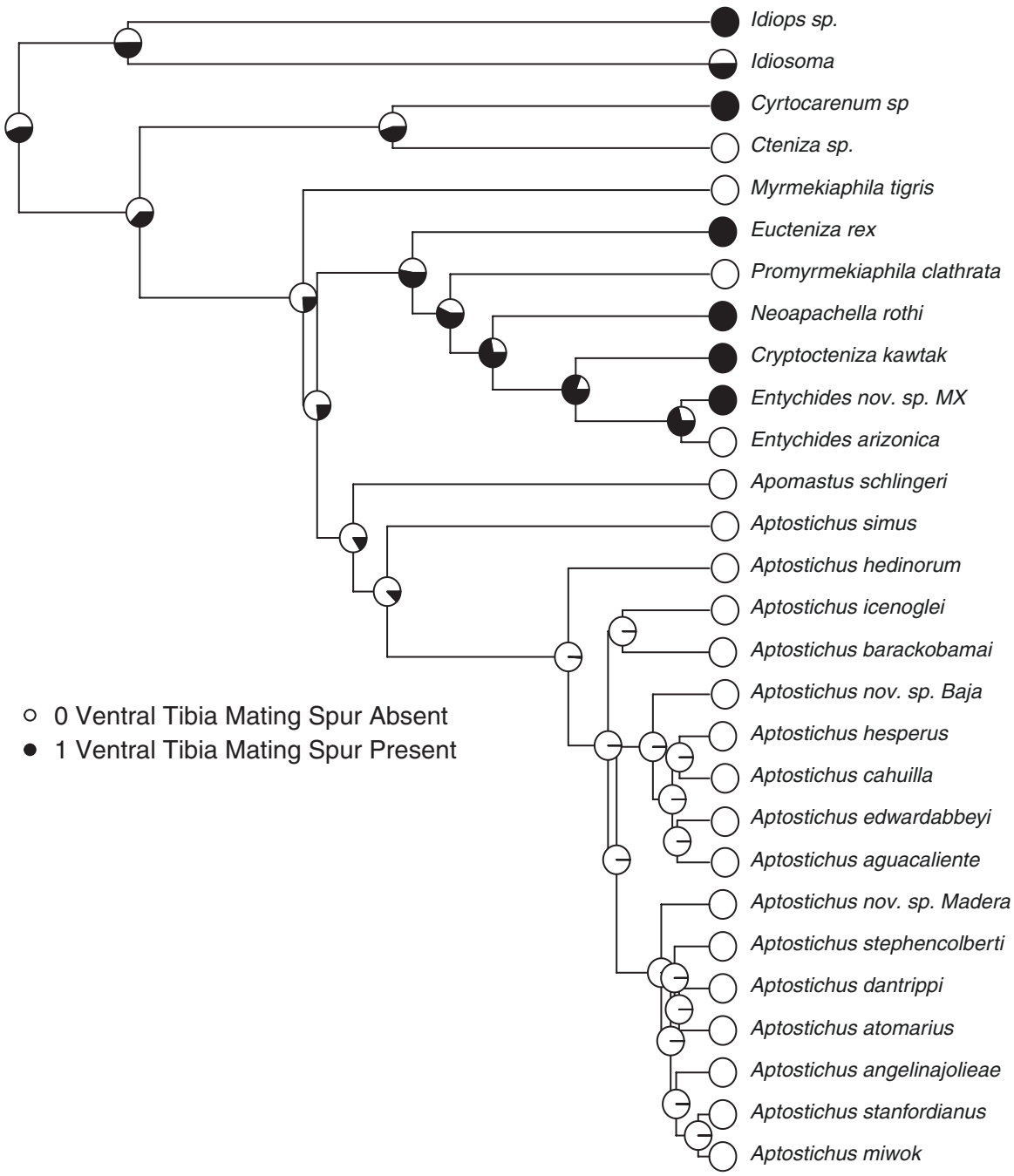

Fig. 3. Maximum likelihood ancestral state reconstruction of male tibia ventral mating spur with spine armature.

now well-established framework for investigating patterns of morphological evolution and adaptation across this diverse group of trapdoor spiders.

A New Monotypic Genus

The phylogenetic position of the newly discovered taxon in California presents a number of alternatives with respect to generic-level placement. One possibility is to place it within other genera (e.g., *Entychides* but see below), whereas a second alternative is to describe it as a new monotypic genus (*Cryptocteniza*). Bond and Opell (2002) diagnosed *Entychides* such that males of the genus are 'recognized by the presence of a group of spines that are borne on an apophysis on the distal most prolateral aspect of the tibia of leg I', a character state that *Cryptocteniza* males clearly lack (Fig. 5A and D). Interestingly, we have recently discovered males of a yet undescribed species of *Entychides* from Mexico that have a male leg I tibial spur, armed with a spine that appears to resembles the armature of other euctenizine genera (*Eucteniza*, *Neoapachella*, and now *Cyrptocteniza*); however, this species still retains the key *Entychides* diagnostic character described above (a distal mating spur positioned laterally). Our ancestral character state analysis (Fig. 3) shows that a tibial I spur and spine(s) modification may be plesiomorphic for the entire subfamily, but then is clearly lost in *Promyrmekiaphila*, as well as most known *Entychides* species. The argument could be made that on the basis of that single character,

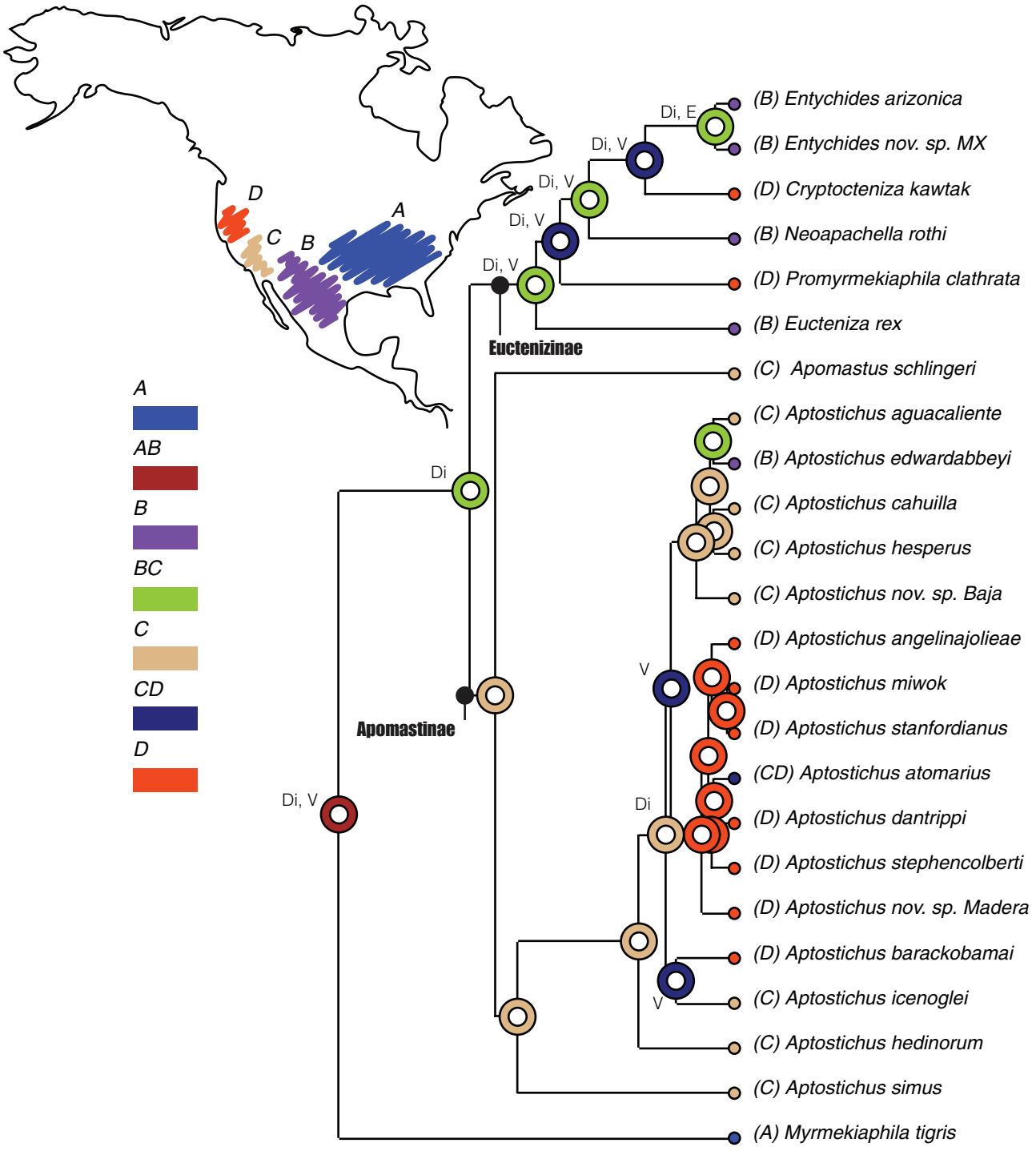

Fig. 4. RASP S-DIVA biogeographical analysis; Di = dispersal, V = vicariance, E = extinction.

collapsing all euctenizines into a single genus might be warranted, but that would create a morphologically diverse genus now lacking any single, obvious diagnostic feature. And, synonymizing all the genera save *Promyrmekiaphila* would render such a construct of *Eucteniza* paraphyletic. Given the morphological distinctiveness of all the euctenizine genera, we fail to see any advantage to creating a single highly polymorphic genus that lacks clear diagnostic features. Placing the new taxon in *Entychides* would be the least disruptive option from a nomenclatural perspective but, as discussed already, would compromise the diagnostic character shared by all previously described congeners attributed to that genus.

Based on all the evidence, we see little choice but to describe this enigmatic taxon as a new monotypic genus. Characterized as Gregg's Paradox (Gregg 1954), a monotypic taxon is generally rebuffed because it represents a taxonomic category of classification that is empty with respect to information content; that is, *Cryptocteniza* as a genus contains no diagnostic information that cannot already be attributed to the next level below (in this case a single species).

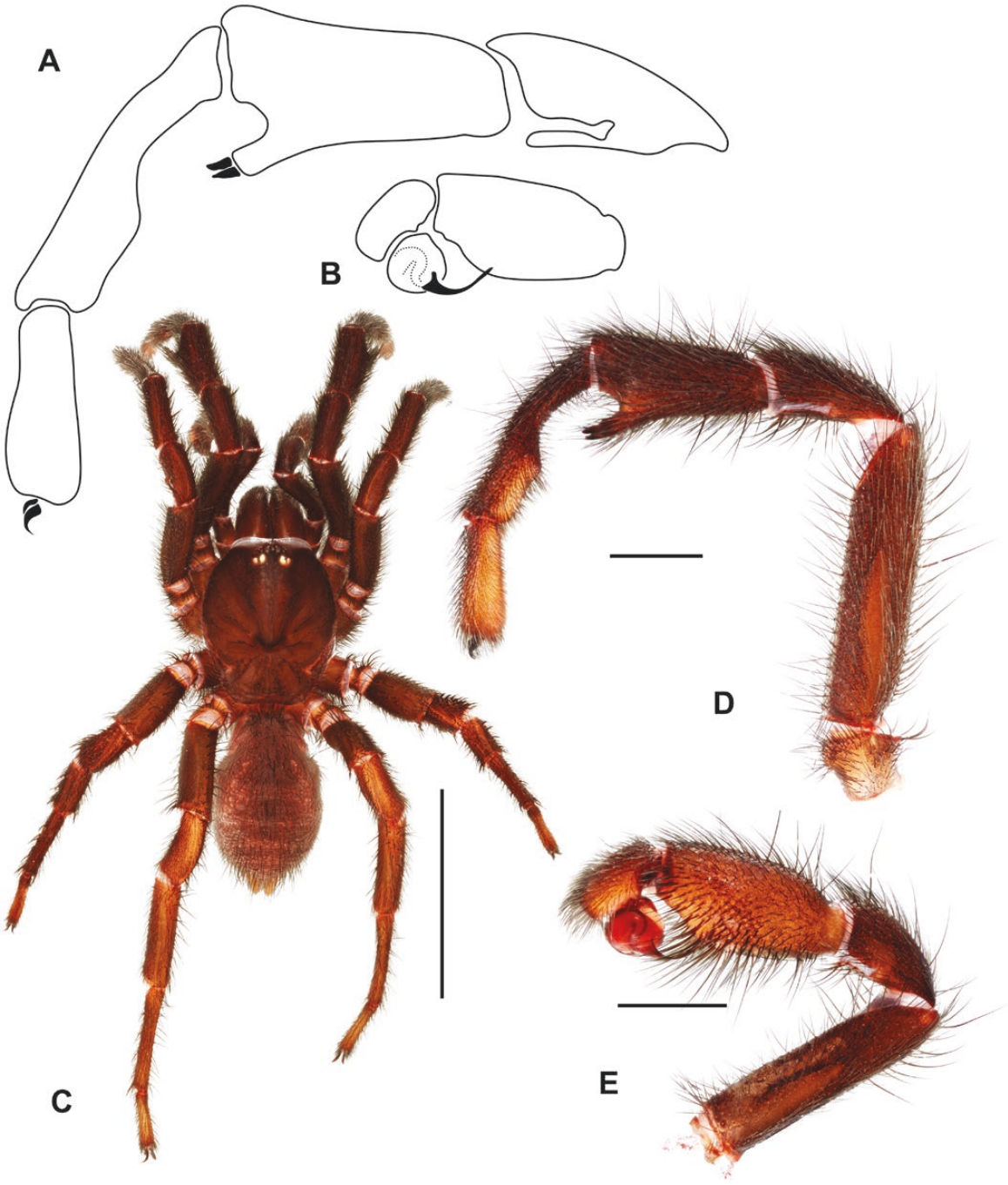

Fig. 5. *Cryptocteniza kawtak* **n. sp.** male HOLOTYPE. (A, B) Line drawings, retrolateral view. (A) Leg I, patella, tibia, metatarsus, tarsus showing ventral mating spur. (B) Pedipalp. (C) Habitus, scale bar = 5 mm. (D) Retrolateral view of Leg I. (E) Retrolateral view of pedipalp.

As noted in the paragraph above, we feel that the alternative harm to nomenclatural stability and abandoning well-established diagnosable genera in favor of a more inclusive polymorphic taxon does not seem warranted. And, taken together with our biogeographic and diversification analyses, we would suggest that a far more informative narrative that better reflects the evolutionary history of the group may apply.

Cryptocteniza kawtak **n. sp.** is clearly separated geographically from its closest relatives (Fig. 4). Isolated on a single beach along California's central coast (Fig. 1), it lacks any contemporary connection with *Entychides* and *Neoapachella*, both which have distributions much further to the east in Arizona and New Mexico. Given the putative extremely low vagility of most mygalomorph taxa, long-distance dispersal seems highly implausible. Moreover, the depth of divergence, inferred by branch length, between *C. kawtak* and its sister taxa (Fig. 2A) also indicates recent long-distance dispersal (to include human mediated dispersal) is highly unlikely. Our biogeographic analysis (Fig. 4) supports an ancestral distribution throughout California and the American Southwest followed by extinction in California at the *Entychides* ancestral node. In short, these analyses support the already obvious hypothesis that an *Entychides*/*Cryptocteniza* ancestor was once far more widespread

across the American west with extinction leading to the disjunct distribution pattern observed today.

Patterns of diversity, numbers of species, and breadth of geographic range across most of the euctenizine genera are generally much lower when compared to *Aptostichus*. Diversification across the American southwest, estimated to have occurred during the late Cretaceous/early Tertiary (127-109 mya; Opatova et al. 2020) shows a complex pattern of dispersal, vicariance, and extinction (Fig. 4) likely reflecting the complex and dynamic geology of the region during that time period. The BAMM diversification analysis lends support to the hypothesis of extinction across euctenizine lineages as evidenced by the downturn in the lineage through time plot prior to increased diversification in *Aptostichus* (Fig. 2C). Changes in environmental conditions (or other related biotic and/or abiotic factors) after the Miocene and establishment of a Mediterranean climate (Rundel et al. 2016) across the California Floristic Province biodiversity hotspot may have spurred an adaptive radiation in *Aptostichus* along with concomitant extinction in *Cryptocteniza*—leaving a lone lineage persisting in this unique habitat. We acknowledge that any of these results taken alone might be criticized as speculative. But together, they support a compelling hypothesis that *Cryptocteniza* is the remaining relict of a much more broadly distributed taxon, effectively displaced when *Aptostichus* radiated across California.

A monotypic genus, ecologically stranded on an isolated beach little over 24 hectares in area, along the central California coast, raises the notion of a relict taxon, or even the specter a 'living fossil'. Although the concept of living fossils is somewhat contentious (Turner 2019), a recent characterization of such putative relict taxa has been reworked to include phylogenetic criteria and conservation related goals. Termed 'Endangered Living Fossils', such taxa are defined as having the qualities of being very narrowly distributed, evolutionarily distinct, and anciently diverged, typically having a stem age predating a major environmental change or geological epoch (Vargas et al. 2020). Interestingly, a number of spider genera (e.g., *Archoleptoneta* Gertsch, 1974, *Trogloraptor* Griswold et al., 2012) in California meet these criteria and are often characterized by the retention of ancestral character states (Ledford and Griswold 2010, Griswold et al. 2012). The single relict species comprising the new genus *Cryptocteniza*, in our opinion meets these criteria: it is 1) morphologically distinct, 2) geographically isolated from other congeners, with its closest phylogenetic relatives found much further to the east in New Mexico and Arizona, and 3) is the product of an ancient divergence prior to major ecological changes during the Miocene. Owing to this phylogenetic distinctiveness, incredibly narrow distribution and age, *Cryptocteniza* meets all the criteria of an 'Endangered Living Fossil' and is consequently a lineage of grave conservation concern (see Conservation Status details below).

Summary

Our results provide a robust and well-resolved phylogenetic framework for investigating speciation pattern and process across the North American Euctenizidae. We update euctenizine relationships, confirming previous hypotheses that the southeastern genus *Myrmekiaphila* is the sister group to all other euctenizids. While biogeographic reconstructions show a complex pattern of vicariance, dispersal, and extinction across Euctenizinae, southern California representing the cradle of apomastine diversity is empirically demonstrated for the first time. We document the discovery of a new monotypic genus, known only from a coastal California sand dune habitat and provide data analyses that support its status as an 'Endangered Living Fossil'. Although we openly acknowledge that a monotypic genus is far from ideal, it is quite plausible that this genus was once likely far more widespread across California and the American Southwest, with potentially greater past species diversity throughout its larger hypothetical ancestral range. As noted by Rix et al. (2017), the higher-level taxonomic status of a lineage (i.e., treatment of genera) becomes somewhat 'academic' in instances like this and thus we can only hope to have made a decision that best recognizes phylogenetic diversity, while maintaining the diagnostic clarity of all of the other euctenizine genera. Regardless, *Cryptocteniza kawtak* **n. sp.** is an evolutionary lineage of considerable significance. We strongly advocate that efforts must be made to evaluate its population size and health, as well as plead that an immediate conservation strategy be formulated to protect this unique and critically endangered taxon.

Nomenclature

This paper and the nomenclatural act(s) it contains have been registered in Zoobank (www.zoobank.org), the official register of the International Commission on Zoological Nomenclature. The LSID (Life Science Identifier) number of the publication is urn:lsid:zoobank.org:pub:D2E45766-742E-4A94-BBD9-8AD181CFB4DC

Taxonomy

Family Euctenizidae Raven 1985

Subfamily Euctenizinae Raven 1985

urn:lsid:zoobank.org:act:C27FB688-5D8E-4E77-ABCC-FD108DC4C22D

Type Genus: *Eucteniza* Ausserer, 1875

Included Genera: *Entychides* Simon, 1888; *Eucteniza* Ausserer, 1875; *Neoapachella* Bond and Opell, 2002; *Promyrmekiaphila* Schenkel, 1950; *Cryptocteniza* **n. gen.**

Genus *Cryptocteniza* n. gen. Bond & Hamilton

http://species-id.net/wiki/Cryptocteniza

Figs. 1, 5, and 6

(urn:lsid:zoobank.org:act:B801C7CF-E4F5-42C0-8DC1-4D148B483B16)

Etymology: The verbal adjective 'hidden secret' is prefixed to *Cteniza*, which is the Greek feminine noun 'comb'. The latter in reference to the comb-like rastellum common in taxa formerly assigned to the family Ctenizidae (e.g., *Eucteniza*); the prefix in reference to both the diminutive form of the rastellum and the seemingly 'hidden in plain sight' nature of the genus.

Type Species: *Cryptocteniza kawtak* Bond & Hamilton

Diagnosis: Males of this genus can be recognized by having a leg I mating clasper tibia that is armed ventrally with a slender, forward curved, anterior mating spur bearing two stout spines (Fig. 5A and D); tibia I lacks a distal, mid lateral spur found on closely related *Entychides* males. *Neoapachella* and *Eucteniza* males both have large leg I tibial prolateral spines that lack a prominent forward curved apophysis but are typically positioned on a low mound or spur. *Promyrmekiaphila* male tibia lack altogether similar armature but rather have a cluster of spines. Females are similar in general appearance but are dark in coloration and have a faint abdominal banding pattern (Fig. 6A) that is lacking in *Entychides*. Spermathecal

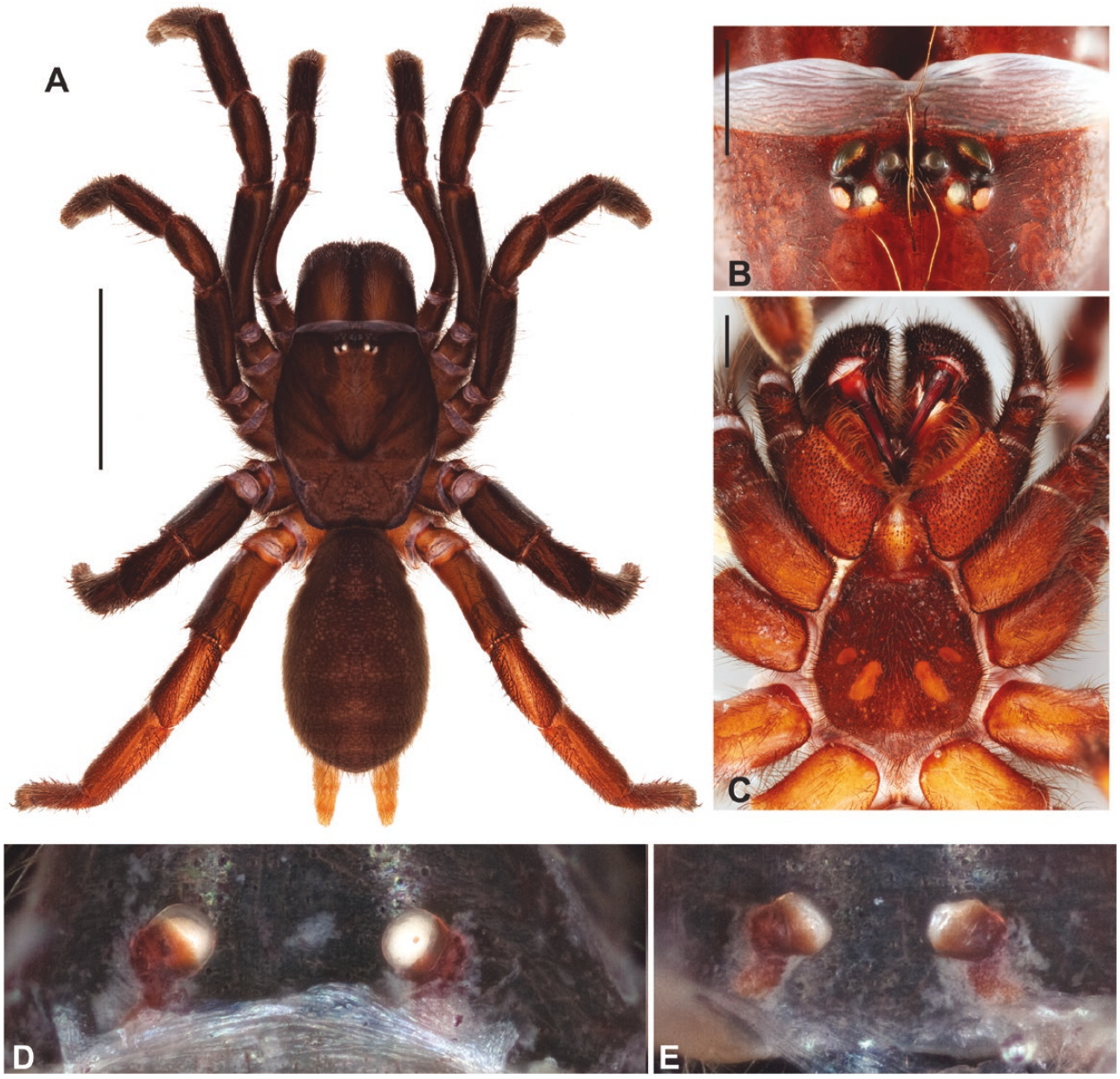

Fig. 6. *Cryptocteniza* **kawtak n. sp.** female. (A) Habitus female PARATYPE; scale bar = 5 mm. (B, C) Detailed anatomy of eye group (B) and ventral aspect of prosoma. (D, E) Cleared spermathecae of paratype (D) and other paratype from the type locality (E).

morphology is subtly unique—anterior bulb receptacula are short, unbranched, heavily sclerotized, and angled inward (Figs. 6D and E), whereas other genera have a long lateral base (*Entychides*), are much shorter (*Eucteniza*), or angled laterally (*Promyrmekiaphila*). *Neoapachella* females have a straight thoracic fovea and a unique patch of spines on the retrolateral surface of tarsus IV, whereas *Cryptocteniza* females have a procurved thoracic fovea and lack the tarsal spine patch.

General Description: Small- to medium-sized trapdoor spiders. Cephalothorax longer than wide, sloping posteriorly but nearly flat, lacks pubescence. Carapace sclerotization equal across its length. Thoracic fovea intermediate to wide, procurved (Figs. 5C and 6A) and deep. Carapace of males fringed with stout black setae (Fig. 6A). Eyes on a low tubercle, slightly raised in males (Fig. 5C), not so in females (Figs. 6A and B). AME and PME subequal diameter. PME row slightly recurved or straight, AME row nearly straight (Fig. 6B). Caput moderately high. Carapace of ethanol preserved specimens appears dark brown. The coloration of living spiders tends to be nearly black. Female and male abdominal coloration distinctive, very dark brown to black with faint transverse banding.

Sternum widened posteriorly, sometimes wider than in other euctenizids, tapering anteriorly. Posterior sigilla large and positioned mid-posteriorly (Fig. 6C). Anterior margin of sigilla has a somewhat rounded margin but are not entirely oval. Palpal coxae longer than wide with cuspules distributed across entire surface (Fig. 6C). Labium wider than long, with a few, to a moderate number of cuspules. Chelicerae dark brown. Rastellum consists of two to three spines not borne on a distinctive mound. Fangs long but heavily built. Cheliceral furrow promargin with row of large teeth. Retromarginal row consists of a patch of denticles.

Apical PLS article short, domed. Spinnerets mostly with pumpkiniform spigots with several articulated spigots interspersed on apical and median articles of PLS and the PMS. Two to three large, articulated spigots on apical most aspect of the PLS. PMS article robust. See Bond and Opell (2002) for more detailed descriptions of these spigot types.

Anterior leg articles slender relative to posterior. Tarsi short and robust. Female scopulae long, dense, symmetrical, extending full length of tarsus and metatarsus I–II scopulae extend no further than the tarsus of the pedipalp. Posterior legs lack distinct scopulae. Pedipalp claw with many teeth. Male tarsi I and II with relatively dense scopulae similar to females. Basal palpal tooth and STC I–IV basal tooth not elongate, positioned on the median keel, not bifid. STC IV with five or more teeth. Female anterior legs with few ventral spines. Prolateral surface of female patella III covered in numerous thick spines. Distal ventral aspect of tarsus IV with short, sparse spine patch. Preening combs absent. Tarsal trichobothria arranged in a zigzag pattern with typical base. Spermathecae with a short base and posteriorly heavily sclerotized.

Male tibia I with a distal ventral apophysis (clasping spur) bearing two stout distal spines. Metatarsus I with proximal ventral to prolateral excavation bordered distally by a low distal swelling. Palpal cymbium lacks spines. Palpal bulb normal, similar to other euctenizid species (Fig. 5B and E), embolus long. Palpal femur short, lacks spines.

Distribution: The genus is monotypic and known only from the type locality of the type species (Fig. 1).

Cryptocteniza kawtak n. sp. Bond & Hamilton

(urn:lsid:zoobank.org:act:B4C8E972-0C1F-431C-BE6B-A613FE8426D3)
http://species-id.net/wiki/Cryptocteniza_kawtak

Type Material: HOLOTYPE MALE (BMEA101070; deposited in the BME) and two FEMALE PARATYPES (each deposited in the BME and CAS) from United States, California, Monterey County Moss Landing State Beach, vegetated dunes between roadway and beach, N 36. 80876 W -121.78902, coll. by J. Bond 2005–2019.

Etymology: The specific epithet is a noun in opposition from the Amah Mutsun inflected form of the word for seashore, *kaw*. The name was constructed to honor the Amah Mutsun Tribal Band and reflects the occurrence of this species along the coast (seashore). Prior to the arrival of the Spanish in the 1700s, the Amah Mutsun had lived for thousands of years on lands in the Monterey Bay and Moss Landing region. Like many of the native indigenous tribes of California, the Amah Mutsun suffered oppression and slavery under Spanish and Mexican rule, followed by near extermination at the hands of the United States and California State governments. With their lands stolen, the first governor of California, Peter Hardemann Burnett (1807–1895), actively promoted the extermination of California's native peoples, which included the Amah Mutsun. Over the past few decades, there have been substantial efforts to revitalize the language of the Mutsun people; its last fluent speaker, Ascension Solarsano, died in 1930 (Warner et al. 2016). Formation of the specific epithet herein referenced the Mutsun-English dictionary published by Warner et al. (2016). A detailed history of the Amah Mutsun Tribal Band, its culture and language can be found at http://amahmutsun.org/.

Diagnosis: The species is distinguished in the generic diagnosis.

MALE HOLOTYPE: *Specimen preparation and condition.* Specimen preserved in 70% EtOH. Pedipalp, leg I removed, stored in vial with specimen. *General coloration in alcohol.* Carapace black 2.5Y 2.5/1; abdomen same with faint dusky banding. *Cephalothorax.* Carapace 3.29 long, 3.28 wide, glabrous, pars cephalica elevated. Fringe with heavy setae extending to midline. Thoracic fovea groove deep, procurved. Eyes on slightly raised tubercle. AER, PER slightly recurved. PME, AME, subequal diameter. Sternum moderately setose, STRl 2.19, STRw 1.88. Posterior sternal sigilla large, oval, not contiguous; anterior sigilla pair smaller, placed at margin. ANTd comprising five large teeth; posterior margin with patch of ~14 smaller teeth. Palpal coxa, numerous cuspules across entire surface, labium with six cuspules, LBw 0.695, LBl 0.402. Rastellum five stout spines not on a mound. *Abdomen.* Moderately setose; apical segment of PLS short, triangular in shape. *Legs.* Leg I: 3.26, 1.72, 1.82, 2.11, 1.21; leg IV: 3.01, 1.33, 2.54, 2.51, 1.33. Moderately dense scopulae on tarsi I, II and distal half of metatarsi I, II. Tarsus I with thin band of ~6 trichobothria. ITC small, gently curved. Leg I spination pattern (Fig. 5A and D); TSp 0, TSr 0, TSrd 0. *Pedipalp.* PTw 0.864, PTl 1.689, Bl 0.825. Embolus arises sharply from copulatory bulb, long thin tapered (Fig. 5B and E).

Variation: Males known only from the holotype specimen.

FEMALE PARATYPE (MY3460): *Specimen preparation and condition.* Specimen preserved in same manner as male holotype. *Color.* Same as male. *Cephalothorax.* Carapace 5.58 long, 5.23 wide, glabrous. Lacks fringe. Thoracic fovea groove deep and procurved. Tubercle absent. AER nearly straight, PER straight to slightly recurved. AME, PME subequal diameter (Fig. 6B). Sternum moderately setose, STRl 3.19, STRw 2.92. Posterior sigilla large, widely separated sub-oval in shape; medial anterior sigilla relatively small, positioned laterally. ANTd with five teeth with posterior margin comprising denticle patch. Palpal coxae, numerous cuspules, spread evenly across; labium with many cuspules, LBw 1.09, LBl 0.87. Rastellum comprises four spines not on a tubercle. *Legs.* Leg I: 4.35, 2.35, 2.46, 2.45, 1.42; leg IV: 3.88, 2.56, 3.36, 3.12, 1.60. Dense scopulae tarsus/metatarsus of Legs I/II, tarsus/tibia of pedipalp. Tarsus I with ~10 trichobothria arranged a relatively tight staggered row. PTLs >30, TBs 12. ITC small, gently curved. Preening combs absent. Anterior spermathecae short, heavily sclerotized, unbranched (Fig. 6B and C). Apical segment of PLS short, domed.

Variation (n = 5): **Cl** 4.71–5.58, 5.24 ± 0.16; **Cw** 4.3–5.23, 4.76 ± 0.19; **STRl** 2.67–3.3, 3.05 ± 0.11; **STRw** 2.55–3.08, 2.8 ± 0.09; **LBw** 0.95–1.15, 1.03 ± 0.04; **LBl** 0.76–1.03, 0.88 ± 0.04; **Leg I:** 11.27–14.12, 12.69 ± 0.46; **ANTd** 4–6, 5 ± 0.32; **PTLs** 21–27, 22.6 ± 1.12; **TBs** 4–11, 7.2 ± 1.39.

Additional Material Examined: Numerous female specimens collected at the type locality, deposited in BME and CAS.

Distribution: Known only from the type locality at Moss Landing State Beach, Monterey County, California.

Natural History: *Cryptocteniza kawtak* individuals build moderately deep (compared to syntopic *Aptotichus simus* and *A. stephencolberti*) burrows that are often >30 cm in depth. Their heavily silk-lined burrows have unbranched entrances and are covered with a thin silken-sand trapdoor. Based on limited data, males likely disperse in late August through November.

Conservation Status: Using NatureServe (Faber-Langendoen et al. 2012) Conservation Status Rank criteria, we consider the status of *Cryptocteniza kawtak* to be CRITICALLY IMPERILED because of

its high risk of extinction due to a very restricted range (only a single population/occurrence is known). Like other coastal dune taxa, *C. kawtak* faces other threats as a consequence of sea-level rise and invasive plant species (Nicholls et al. 2008, Nicholls and Cazenave 2010, Sarmati et al. 2019).

Supplementary Data

Supplementary data are available at *Insect Systematics and Diversity* online.

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