A new species of *Ululodes* owlfly (Ascalaphidae: Ululodinae) from Cave Creek Canyon in the Chiricahua Mountains of Arizona

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ABSTRACT

A new species of *Ululodes* owlfly from the Chiricahua Mountains of southeast Arizona is described. Support for the evolutionary independence of the species from congeners is established along two lines of evidence: statistical measures of distances among COI sequences and comparative anatomy. The new species, *U. chiricahuensis*, is characterized via formal description and diagnosis, images, and a distribution map. A key to the owlfly species of Cave Creek Canyon is presented. Competing hypotheses for the biogeographic origins of *U. chiricahuensis* are discussed, as well as possible tests for their resolution.

INTRODUCTION

Despite being the most species-rich genus of owlflies in the Americas, *Ululodes* Smith, 1900, has had no new extant species described since the 1940s. In this paper we present the discovery of a new species of *Ululodes* narrowly distributed in southeast Arizona.

Ululodes is the largest of four extant genera currently recognized to constitute the subfamily Ululodinae (Jones, 2019). Its approximately 28 species (Jones and Oswald, 2013; Ardila-Camacho et al., 2019) occur from Canada to Argentina, at elevations from 0 to more than 2750

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masl in scrub habitat, in mixed grassland-scrub, and in and around forests, both at margins and along trails and natural flyways. Similar to many other, but not all owlflies, as members of the family Ascalaphidae are commonly known, *Ululodes* adults are crepuscularly active, obligatorily aerial predators of other flying insects. To filter prey from the air column, they rely on nearly holoptic vision expressing concentrated dorsal acuity in the ultraviolet intervals of the electromagnetic spectrum (Meglič et al., 2007; Belušič et al., 2013), agile volant dexterity, and complex and effective pedal and buccal specializations (Tjeder, 1992; Jones, 2014). Their flight acrobatics are rather well developed, on par with the much more ancient and generally somewhat larger Anisoptera, though owlflies are infrequently hawked by the latter during the evening changing of the guard, and some owlflies have been recovered from spiders' webs (all J.R.J., personal obs.). Owlfly larvae are equally capable predators, but rely on crypsis and thigmotactic, sit-and-wait strategies to capture prey.

Owlfly adults approximate Libellulidae (Odonata, e.g., *Leucorrhinia* sp. or *Sympetrum* sp.) in habitus, flight characteristics, and predation behaviors, and both spread specimens (fig. 1) and individuals in flight are often mistaken by nonspecialists for small dragonflies. To the unfamiliar observer, their most readily diagnosable feature is the greatly elongate antennae with terminal articles abruptly gathered into a symmetrical or subsymmetrical, pyriform club (Jones, 2019). These are two of many attributes differentiating members of the family from true antlions (Myrmeleontidae), giant mapped-wing antlions (Palparidae), and the owlflylike antlions (Stilbopterygidae), each a sister family in the Myrmeleontoidea (Jones, 2019; but see Machado et al., 2018, for an alternate classification) and in which the antennae and their constituent antennomeres are much shorter, and/or the clubs are clavate and more weakly differentiated. In *Ululodes*, the wings are frequently clear, or moderately to darkly fuscous, but sometimes are marked on the membrane with brownish, watercoloresque maculations formed into crescents, triangles, amorphic forms, and/or round spots, and considerable intraspecific variation may occur, with the membrane ranging from entirely hyaline to conspicuously maculated. Sexual dimorphism in varying degrees is standard: females are slightly larger, have shorter and plumper abdomens, particularly when gravid, and more often display patterning, especially on the hind wing; fuscosity of the wing membranes, when expressed, generally but not exclusively occurs in males.

Larvae are rigid, dorsoventrally flattened, and ovoid in dorsal profile, with the thorax and abdomen lateral margins bearing well-developed, marginally setose, scoluslike processes (Henry, 1976). The tegument is dull yellowish with brown freckling, but this pattern is generally obscured in live and dead specimens by a self-applied and often thick coating of environmental particles, usually sand or silt granules, but also dead prey parts, or whatever other useful items of proper size are found in the immediate vicinity (Henry, 1977; J.R.J., unpublished data). This opportunistic decorative behavior is commensurate with that seen in their distant cousins Chrysopidae and Hemerobiidae. The particles are affixed to a dense, dorsal pilosity of long and extremely fine filaments (Henry, 1976, 1977; J.R.J., unpublished data) that functions much as the weave portion of Velcro® (J.R.J., unpublished data). This apparently chitinous, not silken, fleece (J.R.J., unpublished data) is subtended by regular rows of specialized setae termed doli-

A

B

FIGURE 1. Images on all figures are of *Ululodes chiricahuensis*, n. sp. Scale = 10 mm. **A.** Habitus, male holotype, JRJ_02581. Note the antennae are straight. In sympatric *U. mexicanus*, the antennae are sigmoidally curved. **B.** Habitus, female, JRJ_02584. As in males of *U. chiricahuensis*, the antennae are straight. The diminutive distal wing maculae are also not seen in *U. mexicanus*.

TABLE 1. List of valid U.S. species of *Ululodes* Smith, 1900, and their distributions in the United States.

U. arizonensis Banks, 1907 [AZ]
U. bicolor (Banks, 1895) [AZ, CA]
U. chiricahuensis n. sp. [AZ]
U. floridanus (Banks, 1906) [widespread in U.S. south]
U. macleayanus (Guilding, 1823) [widespread in U.S. south and east]
U. mexicanus (McLachlan, 1871) [widespread in U.S. southwest and west]
U. nigripes Banks, 1943 [NM, TX]
U. quadripunctatus (Burmeister, 1839) [widespread in U.S. south, east, and northeast]

chasters; in *Ululodes* they are primarily club- or spindlelike. These dolichasters occur also on the head and on dorsal, ventral, and lateral body surfaces. The head capsule is quadrate, posteriorly bilobed in all instars (Jones, 2019; J.R.J., unpublished data), and sports seemingly inordinately long, curved jaws bearing three primary, spinelike teeth (Henry, 1976, 1977).

At present, approximately 435 valid species of owlflies are recognized in 100 genera and five subfamilies (Jones, 2019). True species-level diversity in the family—including in the Ululodinae—is higher, perhaps by a considerable amount. This conclusion is supported by descriptions of a score of new species of Haplogleniinae and Melambrotinae in taxonomic work by J.R.J. and colleagues (Jones, 2014; Jones and Badano, 2021; Jones et al., in prep.), other yet-undescribed specimens from all major owlfly subfamilies observed in research collections by the same, and images posted online in wildlife-imaging fora. As noted by Jones (2019), the ecology of adults directly contributes to their obscurity: cryptic patterning, rapid flight, and inconsistent attraction to light sources during evening collecting all result in only modest numbers of owlfly specimens, usually photophilic species, making their way into institutional collections. Evaluating, determining, and discovering diversity of *Ululodes* and other owlflies are key elements of ongoing research by J.R.J. and collaborators.

Here, we present *Ululodes chiricahuensis*, n. sp. (figs. 1–5), from and possibly endemic to the unique and vibrant Chiricahua Mountains of southeastern Arizona. Its addition brings the total species recorded from the United States to eight (table 1).

Discovery of this new species of *Ululodes* was made initially by J.R.J. via analysis of cytochrome oxidase I (COI) sequence data during laboratory work carried out for Jones (2019). A single specimen (α) collected by colleagues in a malaise trap a few miles southwest of the Southwestern Research Station in Cave Creek Canyon (CCC) of the Chiricahuas (see table S1: Material Examined in the online supplement: https://doi.org/10.5531/sd.sp.66), and subsequently stored in ethanol, exhibited slightly atypical anatomy to that of Cave Creek denizen *U. mexicanus* and the similar Texas-native *Ululodes nigripes* Banks, and was added to a batch of samples to be sequenced. Subsequent comparisons of barcode sequence data revealed considerable differences. This led to more careful investigations of the anatomy of the anomalous morphotype, and examinations of loan material from numerous arthropod research collections, including two of the most important in Arizona, the University of Arizona Insect Collection (UAIC), and the Arizona State University Insect Collection (ASUIC). Label data from two specimens at UAIC with matching morphotypes prompted several fieldwork expeditions by J.R.J. and associates (see Materials and Methods: Fieldwork, below) that culminated in the col-

lection of a short series of fresh specimens of the putative new species. Further examinations and comparisons of anatomy revealed unique suites of morphology that we interpret as corroboration and confirmation of our hypothesis of novelty.

To support our hypothesis of species independence, in this paper, we briefly quantify sequence differences of COI fragments for several U.S. species of *Ululodes*, and then present a full description for *Ululodes chiricahuensis*. We also present a key to the owlfly species of Cave Creek Canyon. We close with a discussion of the biogeography of *Ululodes* relative to the Chiricahua mountain range and other orogenies in the Arizona Sky Island Archipelago.

MATERIALS AND METHODS

Fieldwork

J.R.J., alone and with colleagues, made expeditions to various locations within the Chiricahuas in 2012 (August), 2017 (July), and 2018 (May [with J.B.J.] and August), in efforts to capture specimens of *U. chiricahuensis*. None, however, resulted in successful acquisition. In 2019, J.R.J. began living in residency at the Southwestern Research Station of the American Museum of Natural History (SWRS-AMNH) as a visiting scientist, and conducted nearly daily collecting from early July through mid-October at sites all over the range, but primarily in East Cave Creek Canyon. Collecting was carried out predominantly at dusk using portable light sheets illuminated by a combination of mercury vapor and ultraviolet light sources; other methods of acquisition included walking service roads at dusk and sweeping passing specimens with a long-handled aerial net, and inspecting boughs of trees and overhead vegetation for roosting individuals via headlamp after dark. A close-up image of the exact light sheet used during these collecting events and a sampling of the arthropod biodiversity in the Chiricahuas that frequents the area in midsummer, was documented by National Geographic during research at SWRS on declining global insect diversity (Kolbert and Liittschwager, 2020: cover photograph). See also fig. 10C.

Material Examined and Databasing

Over 1000 specimens of *Ululodes* were reviewed for this study. Approximately half were acquired via direct fieldwork, and currently reside in the personal reference collection of J.R.J. The remaining specimens were examined in situ or borrowed as loan material from several dozen arthropod research institutions. A full list of those museums and collections can be found in Jones (2014). Of those, a small subset was given special focus over the course of this project, as follows. As of 2019, specimens of *U. chiricahuensis* were known only from those marked with an asterisk (*).

ASUIC Arizona State University Insect Collection, Tempe, AZ
BYUIC Brigham Young University Insect Collection, Provo, UT
JRJC* Joshua R. Jones Research Collection, Laredo, TX
SWRS Southwestern Research Station Insect Collection, Portal, AZ
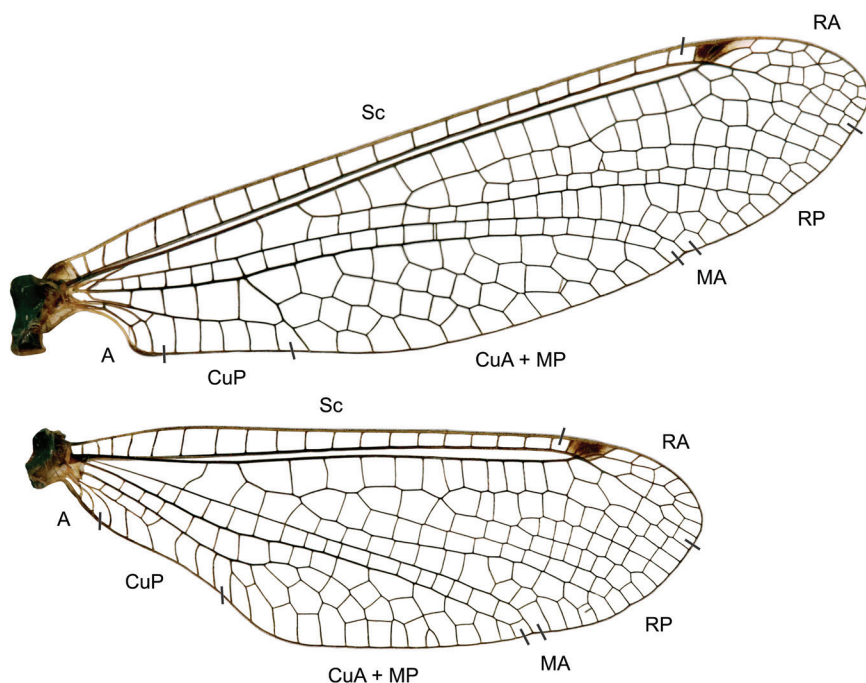UAIC* University of Arizona Insect Collection, University of Arizona, Tucson, AZ

FIGURE 2. *Ululodes chiricahuensis.* Wings diagrammed (male). Note the relative brevity and depth of the HW and the concavity along the margin of both wings in the CuP region.

The specimens examined for this work have been assigned and had attached to their pin a unique JRJC database number. These labels are recorded, along with other label information and metadata, in a comprehensive, DarwinCore-compliant database, as described in Jones and Badano (2021). The subset of this database containing specimens of the new species described in this study is presented in table S1 in the online supplement.

The holotype will be deposited in the UAIC, and other members of the type series are deposited in the UAIC, AMNH, and JRJC, as noted in table S1.

Specimen Preparation, Dissection, Examination, Comparative Anatomy

Pinned and dissected specimens were visualized under a Leica MZ6 dissecting microscope at magnifications of 6.3× to 40×. Abdomen removal and terminalia preparation followed protocols presented in Jones (2014) and Ardila Camacho and Jones (2012), but were slightly revised as follows, with the added steps marked in italics. Specimens were macerated overnight in a solution of 10% KOH at room temperature, cleaned in distilled water, *rinsed in a solution of 5% glacial acetic acid to neutralize the KOH, rerinsed in distilled water*, rinsed in 80% EtOH, and examined in glycerin. They are preserved in glycerin-filled microvials pinned beneath their proprietary specimens.
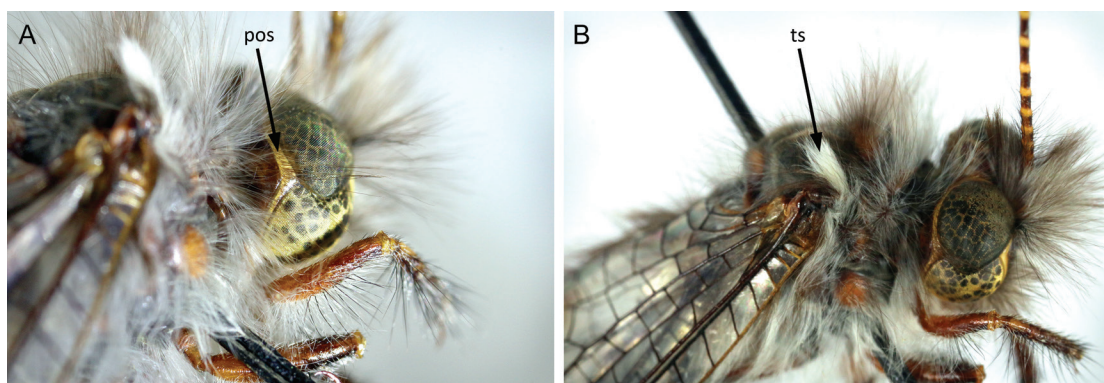
FIGURE 3. *Ululodes chiricahuensis.* **A.** Eyes and postocular sclerite setae, JRJ_03217. Note the fringe of erect setae on the sclerite. **B.** Tegular setal tuft, JRJ_03217. The tuft is erect and white in both sexes, different from that seen in sympatric *U. mexicanus.*

To enlarge the set of pinned reference specimens and improve characterizations of morphology, specimen α, JRJ_10038, was removed from its ethanol solution post-DNA extraction. It was first transferred to 100% acetone for several days, to reduce lipid residues on the tegument and recondition corporal setae that tend to mat out of alcohol. It was then carefully cleaned of detritus with forceps under a dissecting microscope and allowed to air dry for several minutes. Subsequently, while still pliable, it was pinned, carefully mounted on a spreading board, and allowed to air dry for a week in order to set. It is now included in the type series.

Photography and Illustrations

Habitus images of spread specimens were captured with a Canon EOS 80D body and a Canon EF 100mm f/2.8L Macro IS USM lens. Microscopic features were captured with a Canon MP-E 65 mm macro lens. Terminalia were photographed at the BYUIC with an Olympus SZX12 stereo fluorescence microscope and a Volpi V-Lux 1000 170 W 60 Hz fiber-optic light source, at magnifications of 10× to 25.6×. Images were stacked using Helicon Focus 7 software. Field site images were captured on an HTC U11 smartphone. All images were processed and prepared in Adobe Photoshop CS3. Measurements were made using 0.02 mm accurate vernier calipers, and are rounded off to the nearest millimeter.

Terminology

Anatomical terminology used in this study follows a number of sources, including Jones and Badano (2021), Jones (2014, 2019), Badano and Pantaleoni (2014), Tjeder (1992), New (1984), Penny (1982a, 1982b), Aspöck et al. (1980), Adams (1958), and the Torre-Bueno Glossary of Entomology (Nichols and Schuh, 1989). Wing venation follows Jones and Badano (2021) and Breitkreuz et al. (2017).
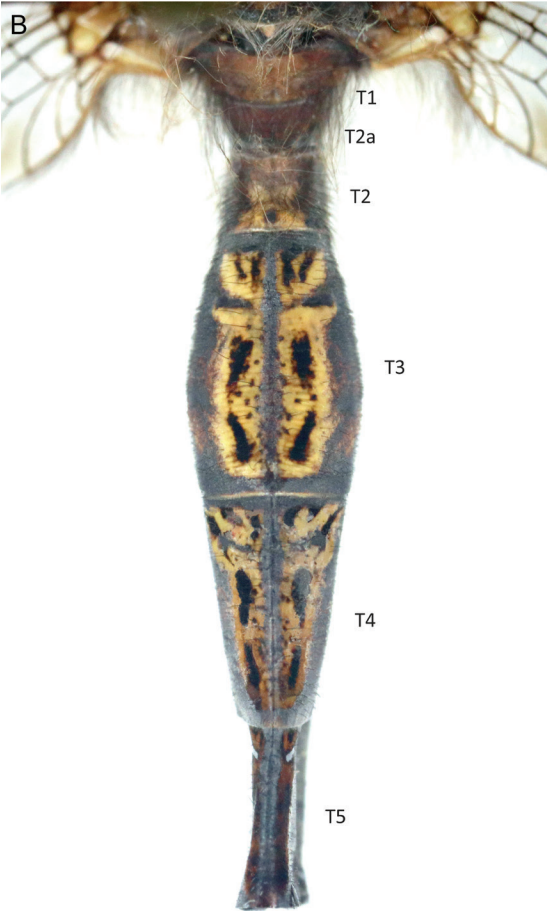
Abbreviations

The following abbreviations are used in the main text and figures: **bp,** base pairs; **C-Sc,** costal-subcostal field; **CuA,** cubitus anterior veins; **CuP,** cubitus posterior veins; **dv,** distivalve; **ep,** ectoproct; **ft,** feet; **FW,** forewing; **gon,** gonarcus; **GPC,** gonarcus-paramere complex; **HW,** hind wing; **id,** interdens; **KOH,** potassium hydroxide; **masl,** meters above sea level; **MP,** media posterior veins; **pa,** paramere; **pos,** postocular sclerite; **RA,** radius anterior veins; **RP,** radius posterior veins; **Sc,** subcosta veins; **S1, S2,…S9,** sternite 1, sternite 2,…sternite 9; **ts,** tegular setae; **T1, T2…,** tergite 1, tergite 2…; **T2a,** tergite 2 acrotergite; **YBP,** years before present; **YDE,** Younger Dryas Event.

DNA Sequence Analysis

Sequence data from region two (~800 bp) of the mitochondrial gene cytochrome oxidase I (COI) was selected for use in this study. COI is a fundamental gene in eukaryote systems, encoding the main subunit of an enzyme crucial in aerobic metabolism (Lunt et al., 1996). In recent decades, this marker has been shown in many groups of organisms to exhibit sequence basepair substitution rates concordant with species-level cladogenesis. As such, it has been tasked as a diagnostic "barcode" in numerous practical applications, including rapid identification for forensics (e.g., Boehme et al., 2012; Kim et al., 2020), geopolitical quarantines (e.g., Jordal and Kambestad, 2014; Guo et al., 2017; Lee et al., 2019; Cognato et al., 2020), and commercial applications (e.g., Sultana et al., 2018). It also has found a place in phylogenetic studies (Eliassen and Jordal, 2021; and many others), including of owlflies and other Neuroptera (e.g., Haring and Aspöck, 2004; Winterton et al., 2010; Jones, 2019).

Sequence fragments from six U.S. species of *Ululodes* were originally sampled, edited, and manually aligned in Sequencer (GeneCodes Corp.) and Mesquite (Maddison and Maddison, 2011) for Jones (2019), although not all of them were ultimately included in that study. For two, *U. mexicanus* and *U. nigripes*, redundant sequences were generated for separate male and female specimens, bringing the total dataset available for this study to eight specimens. Firstly, these redundancies corroborated and thereby confirmed species-marker identity. Secondly, the differences in the sequence identities of these species pairs were used as gamma values, serving as baselines from which to evaluate interspecific differences.

Within any particular genus, it is possible that the number of interspecific distances may not consistently exceed those of intraspecific differences, a problem laid out in detail early on in the delimitation of barcoding theory and tending to occur in nonmonophyletic taxa (Cognato, 2006). To ameliorate this potential concern, we carried out statistical tests to establish significance in the number of differences of the sequences examined.

FIGURE 4. *Ululodes chiricahuensis.* **A.** Abdomen, lateral aspect, male, JRJ_10038. Note the sparse, erect, dark, relatively long sagittal setae on both dorsal and ventral surfaces, a feature seen only elsewhere among species of the continental United States in *Ululodes quadripunctatus.* In that species, however, the males express a dense patch of black setae on T3, and the setae elsewhere on the tergum and on the sternum are only very short, as in other species. **B.** Tergal pattern, male, JRJ_02583. In males, the predominant dark maculation of T3 may be mesally interrupted or not. In *U. mexicanus,* the maculation is usually uninterrupted. **C.** Tergal pattern, female, JRJ_02584. In the two available specimens, the T3 maculation is mesally narrowed and uninterrupted.
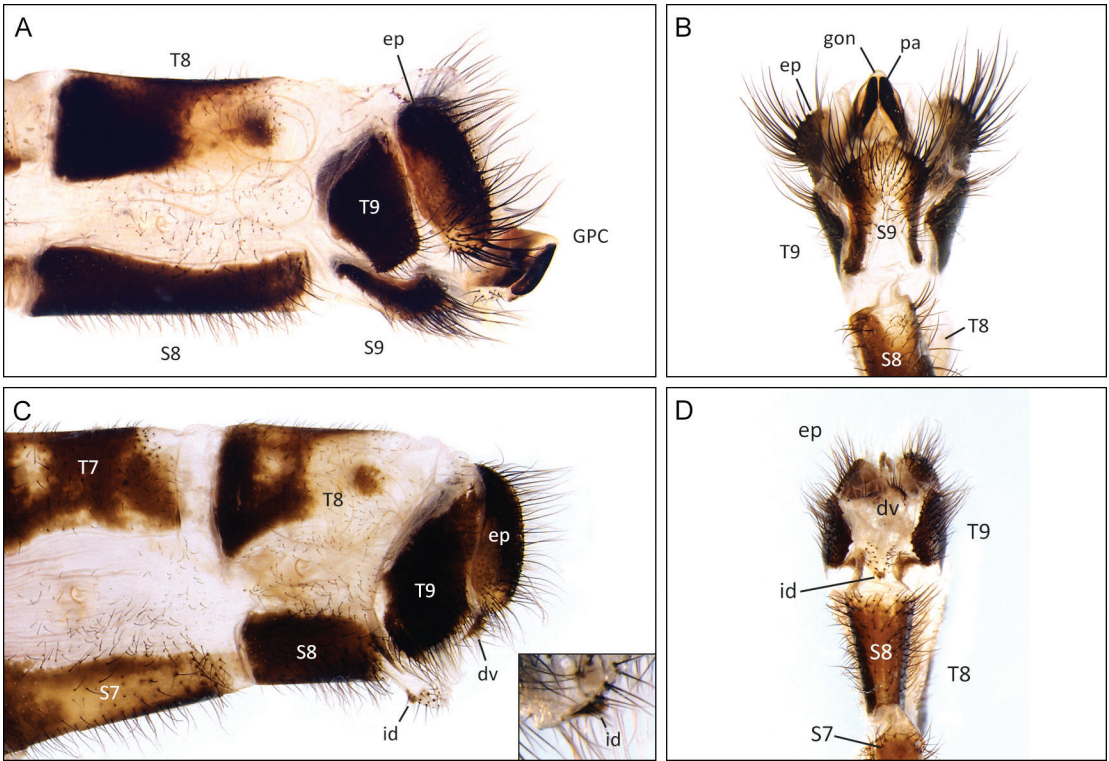
FIGURE 5. *Ululodes chiricahuensis.* **A.** Terminalia, lateral aspect, male, JRJ_10038. **B.** Terminalia, ventral aspect, male, JRJ_10038. **C.** Terminalia, lateral aspect, female. Inset: interdens, lateral aspect, JRJ_03217. **D.** Terminalia, ventral aspect, female, JRJ_03217.

Pairwise comparative analyses of the sequences were conducted in MEGA7 (Kumar et al., 2016) and constituted three analysis sets, as detailed below. Calculations of substitution rates among the sequences were measured firstly in order to infer phylogenetic relatedness and interpret biogeographic origins. Tree-building exercises will be carried out in future projects.

1. ABSOLUTE DIFFERENCES. These were measured as whole number counts of nonisologous basepair identities tabulated in pairwise comparisons.

2. TAMURA-NEI (T-N) EVOLUTIONARY DISTANCE ESTIMATION. COI sequence evolution can be quite rapid (Lunt et al., 1996), and there is always a concern of saturation, or overcycling, over time. Tests performed by Jones (2019) established that the COI dataset used therein, which comprised a diverse sampling of owlflies and outgroup taxa, was not saturated and that the raw sequences were therefore phylogenetically informative. However, the number of differences were a bit high relative to the sequence length, suggesting standard Jukes-Cantor (J-C) estimation might be low (Kumar et al., 2016). Further, J-C assumes no differences in rates between transversion (pyrimidines) and transition (purines) nucleotide substitution. By contrast, T-N, though still assuming site-to-site substitution rates are equal, applies different overall rates of change for pyrimidine and purine (Kumar et al., 2016), and so T-N values were calculated here.

3. MAXIMUM COMPOSITE LIKELIHOOD DISTANCE ESTIMATION. This method calculates the sum of log-likelihoods for a distance matrix of phylogenetically related sequence samples. Similar to T-N, it may yield even more accurate estimates of pairwise distances and substitution parameters by maximizing this sum (Tamura et al., 2004; Kumar et al., 2016). Equality of substitution rates among sites and of substitution pattern among lineages are assumed (Kumar et al., 2016).

To determine the statistical significance of delta between the intraspecific and interspecific portions, once the distance values were generated, two-sample t-tests were performed on each distance dataset. The t-test was chosen because the population standard deviation is unknown and sample sizes were low (Thakur, 2022; Bobbitt, 2022a). A null hypothesis of nondifference between the means of the intra- and interspecific values for each dataset was inferred. For the alternative hypothesis, that the means are different and, specifically, that differences in the interspecific data subset are significantly higher, a one-tailed p-value of 0.05 was set (two-tailed = 0.1). Calculations were performed in Excel, using the following two-tailed t-test formula (Thakur, 2022).

$$t = (\overline{x}_1 - \overline{x}_2)/\sqrt{[(v_1/N_1) + (v_2/N_2)]}$$

Because of the considerable differences in sample size between the intraspecific and interspecific proportions of each respective dataset, and the discrepancy in variance, a slightly modified version of the two-sample t-test that accounts for such a gap was performed, the Welch's t-test. It assumes that: (1) populations of concern are normally distributed; and (2) observations are independent within and between samples (Bobbitt, 2022b). The essential modification of the latter's formula is the reduction from the smaller dataset of an assumed degree of freedom. For this latter test, a summary of the equation is given as (Bobbitt, 2022b):

$$t = (\text{estimate} - \text{value hypothesized})/\text{standard error}$$

The application of this latter formula had little impact on the outcome, as discussed below.

RESULTS

FIELDWORK

Of most relevance to the current study were the expeditions in 2019 to the Chiricahua Mountains. From these, over the interval of July 8 to August 24, over 50 owlfly specimens were captured in various canyons. Most of these were *U. mexicanus*; a few were *Ululodes bicolor* (Banks) and *Ascaloptynx juvenilis* (McLachlan). However, a single male (fig. 4B) and single female (fig. 1B) of *U. chiricahuensis* were collected (see the Key, below).

DNA SEQUENCE ANALYSIS

COUNTS AND DISTANCES VALUES: See tables 2 and 3.

TABLE 2. Differences among cytochrome oxidase I (COI) gene sequences of U.S. *Ululodes* species. The lower left trirant presents number of basepair differences. The upper right trirant gives Tamura Nei evolutionary distances and maximum composite likelihood distances, respectively.

	U. chir. ♂	U. flor. ♀	U. mac. ♂	U. mex. ♀	U. mex. ♂	U. nig. ♀	U. nig. ♂	U. quad. ♂
U. chir. ♂		0.149 / 0.159	0.133 / 0.147	0.094 / 0.091	0.090 / 0.088	0.079 / 0.079	0.081 / 0.081	0.123 / 0.125
U. flor. ♀	93		0.147 / 0.155	0.151 / 0.061	0.155 / 0.162	0.167 / 0.172	0.164 / 0.170	0.164 / 0.181
U. mac. ♂	85	92		0.122 / 0.134	0.122 / 0.134	0.130 / 0.143	0.129 / 0.144	0.150 / 0.174
U. mex. ♀	61	94	80		0.014 / 0.014	0.064 / 0.060	0.063 / 0.060	0.116 / 0.120
U. mex. ♂	59	95	80	11		0.055 / 0.052	0.054 / 0.052	0.110 / 0.114
U. nig. ♀	54	100	84	43	38		0.004 / 0.004	0.131 / 0.131
U. nig. ♂	55	99	84	43	38	3		0.125 / 0.125
U. quad. ♂	78	101	96	75	72	81	78	

Distances and t-test values: Differences between the intra- and interspecific populations were unambiguously significant. When the intraspecific mean distances were contrasted with the species-respective interspecific mean distances, the corresponding T-test values exceeded the t-test statistic threshold by factors of 6.76× to 7.49×, indicating a profound and conspicuous "barcode gap" (sensu Guo et al., 2017; Cognato et al., 2020). The enormity of the significance was such that reducing degrees of freedom had no discernible effect, and resulted in a reduction of only two hundredths. Thus, while informative, the application of Welch's t-test was ultimately superfluous.

However, sample size for the intraspecific pairs was low, rendering the statistical power of the test unsatisfactorily weak. Nevertheless, the test provides a quantifiable delta for side-by-side comparison of datasets that are inherently difficult to normalize. It seems clear that the sequence differences among sampled individuals of the included putative species of *Ululodes* are statistically much greater than among those of conspecifics.

SYSTEMATICS

Neuroptera Linnaeus, 1758 (Linnaeus, 1758)

Myrmeleontoidea Latreille, 1802 (Latreille, 1802)

Family Ascalaphidae Lefèbvre, 1842 (Lefèbvre, 1842)

Ululodinae van der Weele, 1909 (van der Weele, 1909)

Ululodes Smith, 1900 (Smith, 1900)

Diagnosis: Antennae extending beyond first fork of FW RA in spread specimens. Eyes bilobed. Face, including paraocular band, densely hirsute, with long, wispy setae. Pleurostoma present but poorly differentiated. Wing bases not appendiculate, margins usually

TABLE 3. Statistical significance of intraspecific vs. interspecific distances. Means and corresponding t-test statistical significance of intraspecific vs. interspecific distances at a cumulative probability (α) of 0.95 (p-value = 0.05). T-test threshold scores are given in the table.

	Absolute	T-N	MCL
Mean distance intraspecific	7.000	0.009	0.009
Mean distance interspecific	75.308	0.118	0.120
T-test value / t-table score	12.15 / 1.706	12.78 / 1.706	11.55 / 1.706
Welch's t-test value / t-table score	12.15 / 1.708	12.78 / 1.708	11.55 / 1.708

entire, HW posterior margin profile proximally concave in some species. Pterostigma short. HW CuA conspicuously sinuous. Wings sometimes maculated with patterning, membranes occasionally fuscous, particularly in males. T3 with conspicuous parasagittal patterning comprising dark longitudinal markings surrounded by a field of yellow pigment, generally consisting of an anterior set of small maculations, and a larger posterior maculation; this pattern continued, often in a slightly altered or reduced form, on T4 and T5, and occasionally in a very reduced manner on T6 and/or T7. Male ectoprocts weakly fingerlike, ventrad, produced portion variable, but not longer than height of main portion of ectoproct. Parameres simple, not extending beyond apex of gonarcus.

Ululodes chiricahuensis Jones and Jensen, sp. nov.

Figures 1–5

Diagnosis: Antennae with flagellum straight, flagellomeres dark with distal margins pale, club brown. Postocular sclerite with fringe of long, brown setae extending from vertex ventrad beyond ocular division. Tegular setae erect, long, white. Pterostigmata dark. Apical field cells arranged into two to three generally irregular rows. HW margin posterad of cubital area slightly but conspicuously concave, more so in males. Males with HW three-fourths the length of and slightly broader than FW. Female HW with a conspicuous triangular macula on posterior margin at bend in CuA, and smaller ones posterad of pterostigma and near terminus of MP; posterior margin maculae weakly expressed in males. Tergal maculae with bases of mesal setae marked with dark pigment. Metacoxa–sternite 1 membrane dark. Mesal setae along dorsal and ventral surfaces of abdomen slightly longer than in other species in genus.

Description

Size (mm): Male (N = 4): length of body 25–(26)–26; head + thorax 7–(8)–8; abdomen 17–(18)–19; forewing 22–(23)–25; hind wing 17–(18)–19; antennae 21–(23)–24; HW/FW 0.74–(0.76)–0.77; antennae/FW 0.91–(0.94)–0.96. Female (N = 2): length of body 22–(23)–23; head + thorax 7–(8)–8; abdomen 15–(15)–15; forewing 26–(27)–28; hind wing 22–(23)–23; antennae 22–(23)–23; HW/FW 0.82–(0.83)–0.85; antennae/FW 0.82–(0.83)–0.85.

Head: Occiput dark brown, with a diffuse, broad, ochre stripe running transversely in dorsal third, laterally narrowing and curving ventrad. Vertex brown, glossy, glabrous, parasagittal depressions paler or ochre, pigment at midpoint sometimes continuing laterad as a thin transverse ochre macula, depression sometimes bear a fringe of fine, pale yellow or white setae. Postocular sclerite pale yellow to ochre, bearing a narrow fringe of long, brown, slender setae running from dorsal surface ventrad to beyond ocular division, a few found along ventral reach of sclerite. Anterior extratorular sclerites dark brown. Antennal scape and pedicel ochre to brown; setae dense, otherwise as on frons and paraocular band; flagellum very straight, sigmoidal bend not expressed; proximal antennomeres pale cream to ochre, with long, slender, black verticils, these continuing but shortening along flagellum, remaining flagellomeres with dark brown, distal margins annulated with ochre; club ochre, with minute brown flecks densely distributed across mesal surfaces of each flagellomere, these roughly corresponding with the bases of numerous very short, stiff, black, adpressed and distally directed setae. Frons dark brown, mesally glabrous, a dense field of setae originating laterally and directed mesad, these predominantly grayish or pale yellow and white, with a few dark brown setae mixed in. Paraocular band concolorous with frons mesad, slightly paler laterad, starkly and thinly yellow along margin meeting ventral and dorsal lobes of eye; dorsally glabrous, mesally and ventrally with setae as on field on frons, and contiguous with it. Clypeus sagittally dull brown and ochre, dorsolaterally slightly swollen, dark brown and concolorous with frons, ventrolaterally dull pale yellow to cream; a dense field of setae as on frons, but slightly stiffer and more yellow. Labrum, maxilla, maxillary palps, labial palps various shades of amber-brown, from pale to dark. Labrum setae stiff, slender, curved, golden. Mandibles amber-brown basally, darkening distally. Labium yellowish brown; labium apex laterally with a small clawlike cluster of four to five mesally directed, medium-length, stiff, dark, mesodorsally curving setae; whorls on palps black. Ligular setae somewhat dense, long, slender, white.

Thorax: Pteronotum base color dark brown to dull black; mesoprescutal lobes diffusely orangish to yellow, bearing a somewhat dense field of long, slender, wispy mixed white and pale brown setae; mesoscutum with sublateral, distinctly triangular orange to yellow maculations, surfaces with sparse, long, slender, mixed pale yellow and brown setae, denser antero- and posterolaterally; mesoscutellum sagittally and posterolaterally with orange or yellow maculations, setae densest posteriorly. Tegula bearing a small, dense tuft of dorsally erect, long, slender, predominantly white setae, a small posterolateral portion dark brown. Metascutellum mesally orange or yellow. Pleuron concolorous with notum, mesopleuron with anepisternum and katepisternum diffusely orange, all surfaces sometimes covered in pruinescence; setae moderately dense, long, slender, wispy, white, except brown between wings and along margins of wing bases.

Legs: Femora brown proximally, darkening to almost black in distal third to half, dorsal surfaces sometimes not completely darkened, particularly on profemora, femurotibial joints paler; surfaces bearing adpressed short, stiff, white setae, these become long and wispy on posterior faces, posteroventral faces bearing long, slender, stiff, black filtering setae. Tibiae more or less completely but unevenly dusky brown to black, distal and

proximal portions of dorsal surfaces sometimes not darkened; protibial antennal comb a dense field of short, stiff, golden setae on ventral face; antero- and posterolateral surfaces of all tibiae with stiff, short to medium-length white setae, these intermixed with numerous long, slender, stiff, black filtering setae. Tarsi overall concolorous with tibia, but each pale yellow or brown proximally, darkening to dark brown or black distally, distal tarsomere sometimes paler; ventral setae short, stiff, black.

Wings: Basal sclerites and membranes cream to yellow. Costa light brown along foremargins, becoming yellow along posterior margins near wing base, all other veins and crossveins brown to dark brown. In males, membranes frequently fuscous, and HW approximately three-fourths length of FW, conspicuously shorter and slightly broader. *Forewing.* C-Sc field slightly expanded anterad in basal third, narrowing in distal two-thirds, comprising approximately 20–25 cells, Sc veinlets perpendicular to Sc. Pterostigmata with three to four veinlets, stigma membrane basement pigment dark cream to brown overlain with very dark brown to black pigment, veinlets sometimes margined with darker brown pigment. Apical field cells arranged in two to three somewhat irregular rows. Deltus devoid of pigment. Pre-RP field with three crossveins. RP with five forks. CuA fork acute. CuA-MP field with approximately six to eight irregular rows. CuA-CuP field with four to five prefork crossveins, one postfork crossvein. CuP field with cells undivided. *Hind Wing.* As in FW, except: Pre-RP field with one crossvein. MP fork ill formed. CuA conspicuously but only moderately arcuate, less so in males. Pre-CuP disk swollen, translucent yellow. CuP short, continuing approximately only 2 crossveins distad of anal veins. Posterior margin in proximal third of wing concave, more so in males. Female with a moderately large, triangular, brown maculation on posterior margin at bend in CuA, and small, round maculae posterad of pterostigma, and near terminus of MP on wing margin; both posterior margin maculae weakly expressed in males.

Abdomen: Ground color of all sclerites dark brownish gray, concolorous with that of metathorax. *Tergum.* Sclerotized portions of T1 bearing numerous long, wispy, brown setae, becoming dense and white on posterolateral surfaces; dorsomesal membrane pale brownish, concolorous with metanotum, setae sparse. Sclerotized portions of T2 acrotergite bearing numerous long, wispy, mixed brown and white setae, becoming denser and whiter laterad. T2 dorsum pale, anterior two-thirds cream colored, sometimes appearing whitish with pruinescence, posterior third yellow except for a posterosagittal, small, disk-shaped area, setae dorsally only moderately dense, medium-length, somewhat stiff, dark, laterally becoming dense, long, wispy, white. T3 dorsum with anterior yellow pigment field subtriangular, containing a pair of longitudinal, irregular, thin, black maculae, lateral macula sometimes only poorly expressed; posterior yellow field longitudinally subrectangular or slightly arcuate, length approximately 3× that of anterior field, anterior margin of pigment straight where it meets dorsoventral depression, posterior margin rounded, black macula elongate narrow, irregular, thinning, and sometimes discontinuous mesally, particularly in males; sagittad, margin of posterior yellow field adjacent to black macula with tiny black spots, each marking a setal base; setae dorsally medium length, stiff, slender, black, more densely distributed sagittally and elsewhere outside of posterior yellow field,

laterally dense and short in males, largely glabrous in females. T4 with similar patterning, but anterior yellow field broader, width two-thirds length of posterior yellow field, anterior field with three black maculae; setae as on previous tergite, but lateral distribution less dense. T5 patterning as on T4, but reduced in size; setosity similar, but sparser. T6 and T7 with small, diffuse, irregular markings of yellow and dark pigment, setae as on previous, but sparse. T8 mostly evenly dark brownish gray, laterally pale brown or orangish to cream in distal half, pale portion surrounding a circular black macula. *Pleuron.* Pleural membrane, if visible, concolorous with ground color of tergites, dark, and marked with longitudinal, irregular, thin streaks of orangish or otherwise pale pigment, pale pigment also narrowly circumscribing each spiracle. *Sternum.* Metacoxa–sternite 1 membrane dark brown, concolorous with metacoxae, sometimes covered with pruinescence. Sternite base color concolorous with that of sternum and pleuron, posterior margins of S1–S7 sometimes narrowly orangish or pale. S1–S4 sometimes pruinose, S2–S3 setae dense, wispy, white. S4–S8 with a sparse covering of medium-length, thin, golden-brown setae. Mesal setae along length of dorsum and venter slightly longer than in other congeners.

Male terminalia: *Unmacerated.* Sclerites mostly dark gray and/or brown, concolorous with ground color of abdomen and thorax, colors sometimes obscured by body oils. T9 mostly recessed under T8 and glabrous, dark brown, distal margin very thinly paler in dorsal two-thirds, ventral half bearing a sparse fringe of long, slender, curving, dark and golden setae. Ectoproct with ventral margins only weakly produced, surfaces dark, proximal margin mesally with a diffuse, semicircular pale area, all surfaces bearing long, stiff, curving, dark setae, these densest and longest along distal margin. S9 dark, diffusely paler sagittodistad, surfaces with long, slender, dark setae. *Macerated.* Pulvillus unproduced, membranous, bearing approximately 8 short, slender, stiff, dark setae. Gonarcus dorsum evenly curved in lateral view, apex extending slightly past posterior margin of parameres, slightly pigmented proximolaterally, glabrous; ventral patch somewhat rough in texture, not obviously setose. Paramere with pigment of mesal margin sclerotization longitudinally covering approximately half of total surface.

Female terminalia: *Unmacerated.* Ground color and oiliness of sclerites as in male. T9 as in male. Ectoprocts approximately semicircular in lateral view as in all females in the genus, but ventrally slightly abrupt, otherwise very similar to that of male in color and setosity. T8 dark, membranous distal third orangish or yellow; interdens dark brown. *Macerated.* Interdental membrane bearing 20–25 short, stiff, slender, dark setae; interdens a longitudinal carina or blade, short, thin, somewhat evenly curved in lateral view, but posteriorly more abrupt, length more than twice height, flanked by a few small setae.

Variation: In one male (JRJ_10038), the wing membranes are only very weakly fuscous along the posterior margins. The HW posterior margin maculae are essentially unexpressed in another (JRJ_02581). In one female (JRJ_03217), only the triangular CuA maculae are expressed in the HW.

Remarks: C. Henry (personal commun.) recounted identifying *Ululodes* owlflies in Cave Creek as *U. mexicanus* by matching the triangular CuA macula in the HW of females to the

image in van der Weele (1909: fig. 78). As observed in the present study, *U. chiricahuensis* females also share this feature. It is possible that Henry encountered some female specimens of *U. chiricahuensis*, whose wings aren't as conspicuously different as are those of males, and simply didn't recognize them as new. We only now understand that *U. chiricahuensis* exists, and can be differentiated by numerous features, e.g., tergal setae color, shape of antennae and HW, HW length, number of cell rows in the apical field, additional smaller maculae on wing membranes, etc., but several of these characteristics are quite subtle, particularly in females, and discovering them and formulating a differential diagnosis would have required extensive comparisons with other *Ululodes* species.

New Species Registration

The new species name *Ululodes chiricahuensis* Jones and Jensen has been registered with ZooBank under LSID EA8E5BEF-769C-46E0-A143-2727E7F37E0C (https://zoobank.org/).

Key to the Owlfly Species of Cave Creek Canyon and the Chiricahuas

1. Eyes entire, formed of a single, spherical orb; wings conspicuously narrowed at their bases . . . . *Ascaloptynx juvenilis* (McLachlan)
– Eyes divided, formed of a dorsal and ventral lobe; wings not conspicuously narrowed at their bases (*Ululodes* Smith) 2
2(1). Postocular sclerite glabrous posterad of dorsal ocular lobe; antennal flagellomeres predominantly pale, anterior margins annulated with darker pigment; occurring primarily in open areas at lower elevations, including mouths of canyons . . . . *Ululodes bicolor* (Banks)
– Postocular sclerite with a fringe of dark setae posterad of dorsal ocular lobe; antennal flagellomeres predominantly dark, anterior margins annulated with paler pigment; occurring at higher elevations of canyons in the range 3
3(2). Tegular setae dark, wispy; antennae sigmoid at rest; HW margin convex posterad of curve in CuA . . . . *Ululodes mexicanus* (McLachlan)
– Tegular setae forming a white, erect tuft; antennae straight at rest; HW margin concave posterad of curve in CuA, more so in males . . . . *Ululodes chiricahuensis*, n. sp.

DISCUSSION

Knowledge of *Ululodes* Owlflies and Cave Creek Canyon

A detailed ecology for most species of owlflies is essentially unknown. In fact, our biological knowledge of owlflies as a group is largely a set of generalizations assumed for all members based on focused studies of a mere handful of species, contrasted with an absence of contrary data—due to a lack of formal investigations or published observations—to suggest deviations from these null models. At present, most of our information thus is taxonomic and its quality has been, in several cases, questionable. But this situation is changing.

This paucity of ecological information and questionable nature of taxonomic information have been true for the Nearctic fauna, which includes many species that are only very poorly known. In stark contrast, however, the fauna also includes a small handful of the most biologically well-understood owlflies. In particular, *Ululodes mexicanus* (McLachlan) is perhaps the most comprehensively characterized of all owlfly species, both morphologically and ecologically, due to important works by Henry in the 1970s, in which he described in great detail the anatomy of all life stages, and characterized the life cycle and various other ecological attributes of the same (Henry, 1972, 1976, 1977). Nevertheless, for several decades now, the taxonomic status of *U. mexicanus* has been somewhat in doubt, due to nearly coincident but unpublished revisionary work on the Nearctic owlflies by Shetlar (1977), who did not recognize the species as valid, and the subsequent species catalog of North American Neuropterida of Penny et al. (1997), who, without consulting representative material, accepted and validated Shetlar's conclusions. Our view here, based on our ongoing studies of U.S. species, is that *U. mexicanus* is, in fact, an independent and valid species (table 1) well distributed in the United States.

Fieldwork by Henry was carried out at SWRS, where he spent three summers during his doctoral program. *Ululodes mexicanus* frequents this area, along with *Ascaloptynx juvenilis* (McLachlan) (determined as such by Jones, 2014) and, at lower elevations near the mouth of Cave Creek Canyon, *Ululodes bicolor* (Banks). As with *U. mexicanus*, the canyon and environs where it occurs are exceptionally well researched and characterized, due to the presence of the field station and the considerable influx of professional and avocational scholars it has attracted annually from all over the world since its establishment by the American Museum of Natural History in the 1950s. Many visiting researchers regularly run light sheets to attract nocturnal, photophilic arthropods—a generally effective method for attracting at least some *Ululodes* spp. and other Western Hemisphere owlflies—all summer long. Thus, it is no small surprise to discover a new species of *Ululodes* owlfly occurring in the same areas where so many others, including Henry, have meticulously collected for nearly three-quarters of a century.

Of U.S. *Ululodes* species, *U. chiricahuensis* is morphologically most similar to *U. mexicanus* and *U. nigripes*. *Ululodes mexicanus* is widespread throughout the western United States, with records as far north as Oregon (Lyons and Ross, 2012), south and east through California, Nevada, and Utah, and eastward across Arizona; its easternmost reach is southwestern New Mexico. *Ululodes nigripes* is described from western Texas. Its westernmost reach is recorded to southeastern New Mexico, though it may extend slightly further west, possibly into central New Mexico, where it may even enter into narrow sympatry with *U. mexicanus*.

Ululodes mexicanus is widespread throughout the Chiricahuas (fig. 6) and is frequently collected in Cave Creek Canyon (figs. 7–10). Until this study, it was thought to be the only species of *Ululodes* occurring at SWRS. We now know that both *U. bicolor* and *U. chiricahuensis* also occur in various parts of the drainage.

Chiricahuas and Sky Islands

Figures 6–10

The Chiricahua Mountains are an isolated orogeny on the southeast border of Arizona formed chiefly of volcanic rhyolite discharged by the Turkey Creek Volcano eruption 26.9 million years ago (Pallister et al., 1997). Stretching approximately 48 km (30 mi) from north to south and 32 km (20 mi) from east to west, they rise from a valley floor elevation of ~1190–1372 masl (3900–4500 ft) east to west (Cahalane, 1939; figs. 6, 8). Their highest point, Chiricahua Peak, overlooks the surrounding valleys from more than 1800 m (6000 ft) above, at 2976 masl (9763 ft – Moore et al., 2013).

The Chiricahuas are an important link in a chain of related but more or less similarly isolated orogenies connecting the Sierra Madre Occidental of northwestern Mexico to the southern reach of the Colorado Plateau, the Mogollon Highlands of central Arizona (Heald, 1951). This rugged "Madrean archipelago" (Lowe, 1992; Van Devender et al., 2013) of "Sky Islands" (Heald, 1951; Van Devender et al., 2013) serves as a crucial biogeographic bridge between the subtropical latitudes of the south and the temperate latitudes of the north, which otherwise would be physically and climatically separated by lowland deserts (Tennessen and Zamudio, 2008). Coupled with the elevational gradients of each range, the island bridge collectively supports five biomes: hot desert, grassland, chaparral, deciduous forest, and coniferous forest (Van Devender et al., 2013). Correspondingly, they host an incredible diversity of life: over half of the North American avian species (Warshall, 1995; Foreman et al., 2000; Spector, 2002), the most diverse assemblages of mammals, reptiles, and ants in North America, and the greatest bee species richness on Earth (Foreman et al., 2000; Spector, 2002). The archipelago is likewise a key corridor for migration, particularly that of birds, and a distributional sorting mechanism for species at the margins of their natural range. Within this transition zone, for example, seven and four avian families occur at the southernmost and northernmost limits of their distributions, respectively (Warshall, 1995; Foreman et al., 2000; Spector, 2002). Similarly, the Islands host numerous Neotropical plant species from 14 families (Warshall, 1995; Foreman et al., 2000; Spector, 2002) found elsewhere only to the south.

Endemism and Biogeography in the Sky Islands

Figures 6–10

While biodiversity in the Islands is high, species-level endemism appears to be low (McLaughlin, 1995; Van Devender et al., 2013). As examples, of the 600+ species of plants and 187 species of ants present in the Chiricahuas (Moore et al., 2013), many are rare or sporadic, but few if any are known to occur there and nowhere else. Exceptions to nonendemism include a handful of noctuid moths so far recorded only from the Santa Rita, Huachuca, and Chiricahua Mountains (Walsh, 2009; Crabo and Lafontaine, 2009; Schmidt and Anweiler, 2010), but
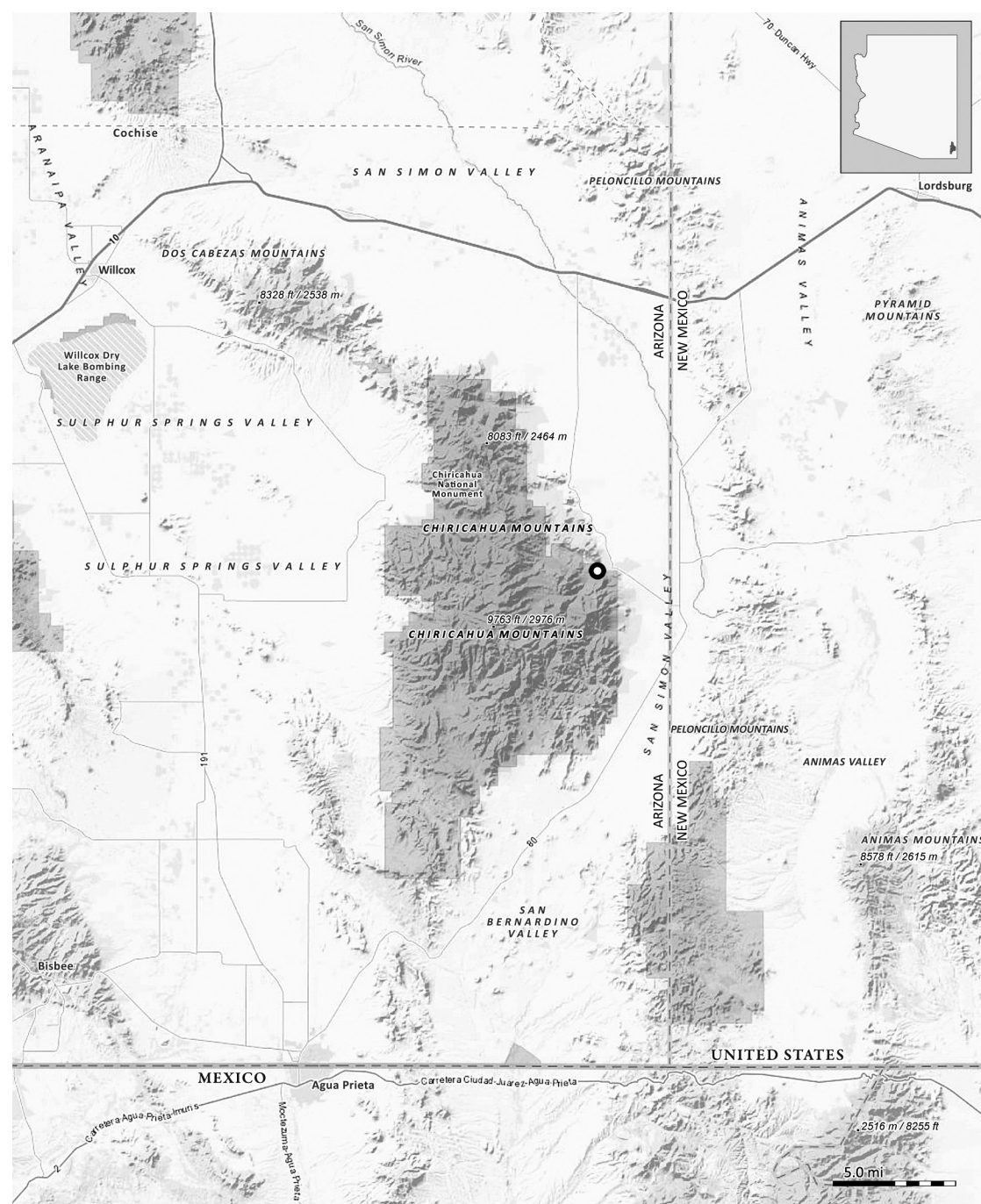
FIGURE 6. Chiricahua Mountains. The black circle marks the town of Portal near the mouth of Cave Creek Canyon. Inset, top right: the range sits in the southeast corner of Arizona, near the borders of New Mexico and Mexico.
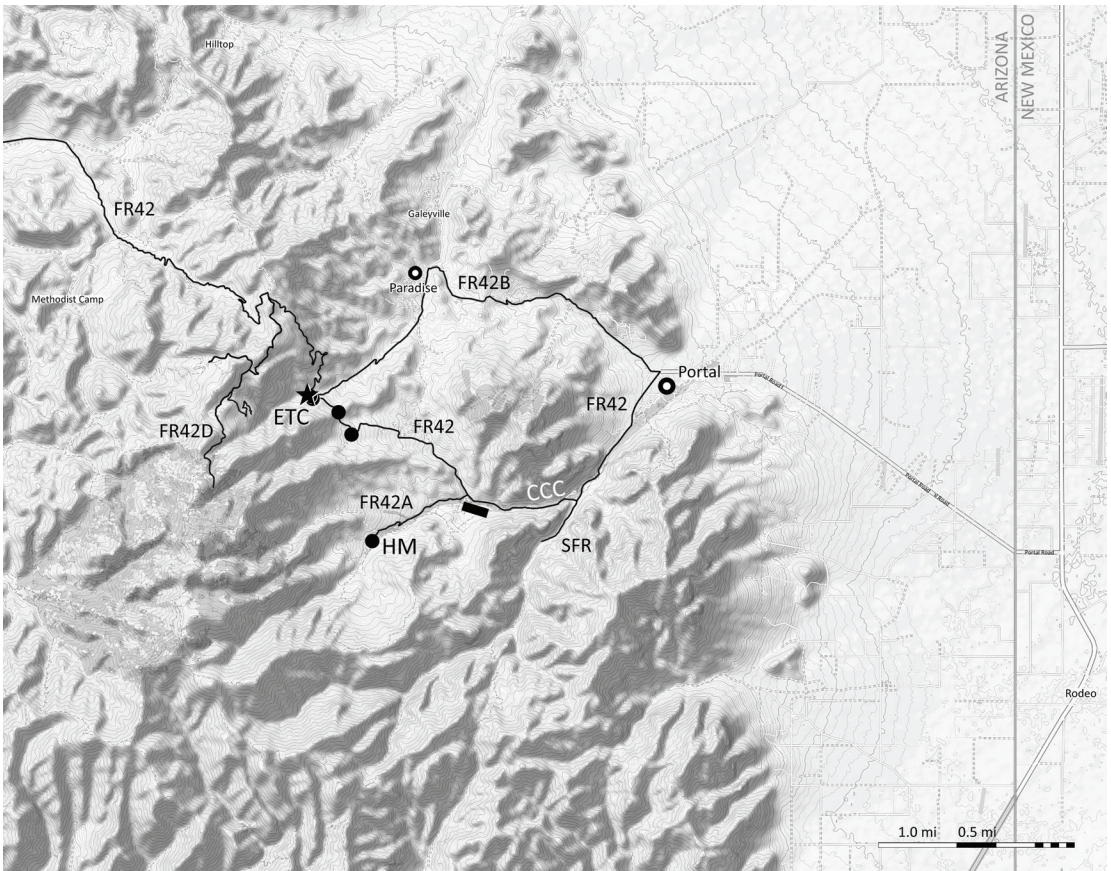
FIGURE 7. Collection localities for *U. chiricahuensis*, Cave Creek Canyon. The larger black circle to the east marks the town of Portal, and the smaller circle to the northwest marks the intermittently occupied hamlet of Paradise. The black rectangle indicates the Southwestern Research Station main campus. Black circles indicate paratype localities. The black star is the holotype locality. Abbreviations: **CCC,** Cave Creek Canyon; **ETC,** East Turkey Creek; **FR,** Forest Road; **HM,** Herb Martyr Campground; **SFR,** South Fork Road.

at least one of these may occur across the southern border in the Sierra Madre. The reasons for low Madrean endemism are likely biogeographic factors, namely the duration of stable climatic conditions, the sequence and timing of prehistoric isolation events, and periodic perforation of intrinsic barriers.

Despite low reports of endemism, multiple lines of data from Sky Island species suggest that differentiation of isolated populations is an ongoing and widespread phenomenon in the archipelago. Analyses of Madrean *Sceloporus* lizard populations have shown high genetic variation among isolated ranges but low variation within them, apparently indicating that no gene flow has occurred between populations from nearby canyons for hundreds of thousands of years or longer (Tennessen and Zamudio, 2008). The authors (Tennessen and Zamudio, 2008), who examined this question in some depth, noted that similarly deep intraspecific divergences in mitochondrial DNA sequences have been observed in other sky island species including treefrogs (Barber, 1999), jumping spiders (Masta, 2000), longhorn beetles (Smith and Farrell, 2005), and flies (Dyer and Jaenike, 2007). They

FIGURE 8. Chiricahua Mountains. **A.** The Chiricahua Mountains from NM Hwy 9 near its junction with NM Hwy 80, view of the east flank. **B.** Cave Creek Canyon from Foothills Rd., view southwest into canyon mouth.

further point out that for the first three taxonomic groups, many haplotypes from different islands are reciprocally monophyletic. Additionally, from other taxa they report that on separate mountain ranges, considerable differences have been measured for allozymes of sweat bee populations (Packer and Taylor, 2002), and for morphology of populations of ground beetles (Ball, 1966), land snails (McCord et al., 1995), and plants (Slentz et al., 1999; Boyd, 2002; all cited in Tennessen and Zamudio, 2008). Each of these examples contributes to a trend of isolation one would expect to result in speciation and endemism. Thus, we are left to wonder why more full-blown endemics are not present to be counted in the Sky Islands. It simply may be that the genetic and other biochemical changes discovered in phylogenetic studies have not yet manifested as conspicuously novel external morphologies that tend to promote recognition by taxonomists writing most descriptions.

For at least some of these species, however, inadequate recent diversification time may be another explanation. During the prolonged episode of the Pleistocene, the climate of North America was cooler, and the corridor lowlands and mountain arroyos of southeast Arizona were occupied by the same dense woodlands (Van Devender, 1977; Brusca et al., 2013). Presumably, the generally contiguous habitats of this temperate regime counteracted many isolation effects, except in pockets of specialized habitat such as at the highest elevations, keeping most dispersed populations in contact and supporting at least periodic gene flow between valleys and canyons (Vinegar, 1975; Van Devender and Spaulding, 1979; Van Devender, 1990;
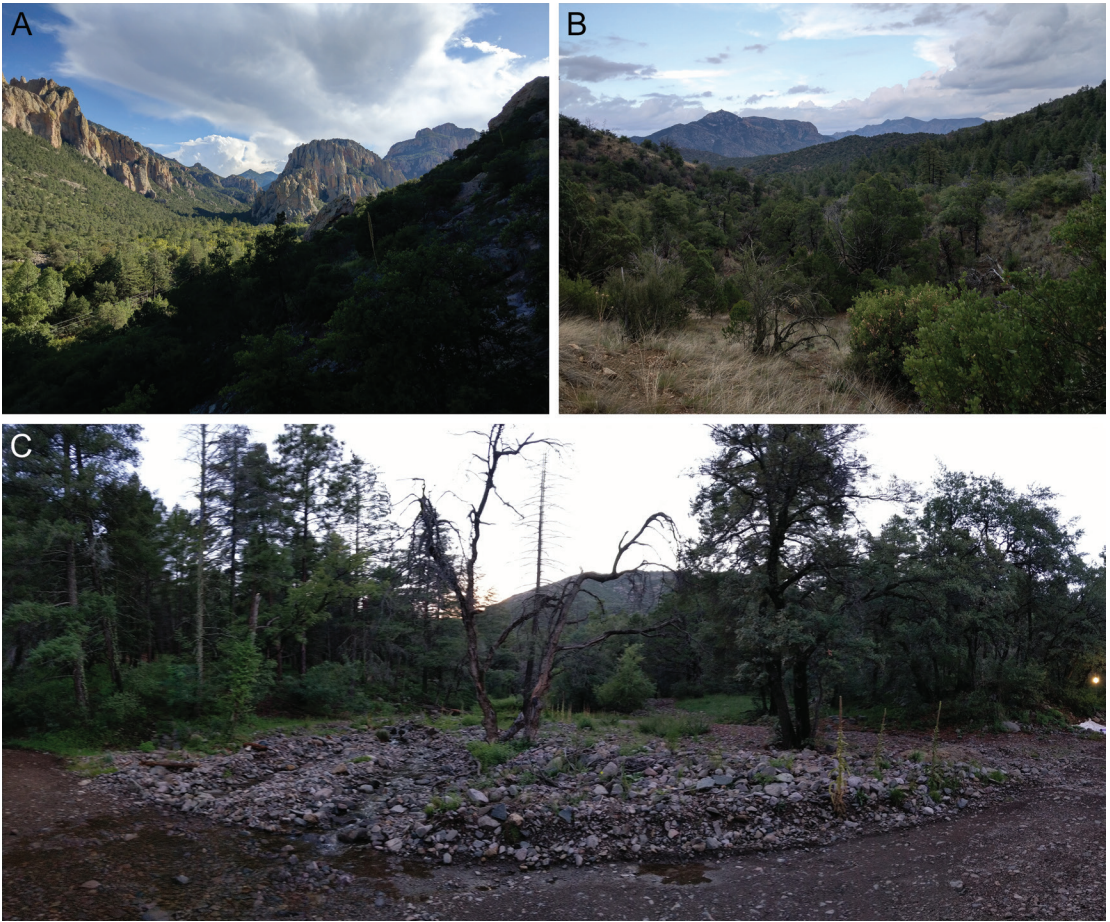
FIGURE 9. Cave Creek Canyon localities. **A.** Lower Cave Creek Canyon, view south-southwest. Exposed cliffs of rhyolite rise above the valley floor. **B.** View northwest toward Paradise from FR42, just north of its junction with FR42B and East Turkey Creek, Upper Cave Creek Canyon, showing scrub oak-juniper habitat typical of the area. **C.** Holotype locality for *U. chiricahuensis*: "Hippy Hollow," at the East Turkey Creek crossing of FR42 near the road's junction with FR42B, Upper Cave Creek Canyon. See figure 7.

De La Ru´a et al., 2001; Estoup and Clegg, 2003; Tennessen and Zamudio, 2008). But around the termination of the Pleistocene and advent of the Holocene, a series of far-reaching environmental changes, apparently triggered by the Younger Dryas Event (YDE) circa 12,900–11,800 YBP, wiped out lowland habitat and its associated macro- and microflorae and faunae (Tennessen and Zamudio, 2008; Fayek et al., 2012; Andronikov and Andronikova, 2016; Powell, 2022). By approximately 8000 YBP, a dramatic floral conversion associated with prolonged warming and drying had taken place in the lowlands surrounding the Sky Islands, to desert scrub in the west and desert grassland in the east (Van Devender, 1977; Brusca et al., 2013). Presumably the Pleistocene species that remained and survived have been adapting to the novel climatic and associated floral regimes and ecological webs in the YDE postliminary span, but this interval yet may be too brief to effect perceptible cladogenesis for many organisms.

FIGURE 10. Cave Creek Canyon localities (continued). **A.** Herb Martyr Recreational Area, Upper Cave Creek Canyon, view southwest, representative of habitat in all areas where specimens of *U. chiricahuensis* thus far have been collected. **B.** FR42A at Herb Martyr Campground, where specimen JRJ_02584 was collected. **C.** Greenhouse Trail parking lot on FR42, where specimen JRJ_02583 was collected, using the light sheet setup shown.

BIOGEOGRAPHY AND POSSIBLE ORIGINS OF *ULULODES CHIRICAHUENSIS*

Ululodes chiricahuensis, a U.S. isolate known only from upper Cave Creek Canyon in the Chiricahuas (figs. 9, 10), poses thus a bit of a conundrum. Our distance analyses indicate greater genetic proximity between *U. chiricahuensis* and *U. nigripes* than *U. chiricahuensis* and its Cave Creek companion *U. mexicanus* (table 2), and *U. chiricahuensis* and *U. nigripes* likely are sister species. This close relationship suggests (1) that one species split from the other and (2) current or (3) former geographic proximity/sympatry. At present, *U. chiricahuensis* and *U. nigripes* populations are not contiguous within the U.S. *Ululodes nigripes* is widespread in west Texas and appears to occur on the southeastern margins of New Mexico, whereas *U. chiricahuensis* is known only from Cave Creek Canyon, a divide of 245 km (150 mi). Sympatry of *U. chiricahuensis* and *U. nigripes* may occur further south in Mexico, however. This is the case for at least one other owlfly endemic to Arizona, *U. arizonensis*, which in the United States occurs

TABLE 4. Competing biogeographic hypotheses. Alternate hypotheses explaining the current isolation of *Ululodes chiricahuensis*, n. sp., in the East Turkey Creek environs of Cave Creek Canyon, Chiricahua Mountains, southeastern Arizona.

Hypothesis	Current Distribution	Former Distribution	Evolutionary origin	Emergence Interval
1	CCC and Mexico	CCC, U.S., and/or Mexico	U.S. or Mexico	Pleistocene or earlier
2	CCC	CCC, U.S., and/or Mexico	U.S. or Mexico	Pleistocene or earlier
3	CCC	CCC	CCC	Holocene or earlier

only in the Huachucas and Santa Ritas, but for which a handful of specimens are now known from recent field studies in Sonora, Mexico (unpublished data from Van Devender).

If *U. chiricahuensis* and *U. nigripes* are not currently sympatric, what can explain their highly disparate distributions? One of the following biogeographic hypotheses may hold the answer (see summary in table 4):

1. 1. The actual current distributions of *U. chiricahuensis* and *U. nigripes* extend far south into the northern Sierra Madre Occidental of Mexico, where they are sympatric, and where they originated coincident with or antecedent to the Pleistocene. Cave Creek Canyon is the northernmost distribution of *U. chiricahuensis*, and west Texas/southeastern New Mexico are the northernmost range of *U. nigripes*. Climate fluctuations following the YDE, or perhaps other environmental factors, allowed newly dispersing populations of *U. chiricahuensis* and *U. nigripes* to make their way northward until a fragment of *U. chiricahuensis* marooned itself in Cave Creek Canyon.

2. 2. *Ululodes chiricahuensis* is Pleistocene in origin or earlier, and formerly had a much greater distribution extending far outside of Cave Creek Canyon, where its populations were sympatric with those of sister species *U. nigripes*. Holocene fluctuations, or other environmental factors following the YDE, then fragmented once contiguous populations of each species into isolated patches until, for *U. chiricahuensis*, only the Cave Creek Canyon population now remains.

3. 3. *Ululodes nigripes* formerly had a much greater distribution, extending across New Mexico and eastern Arizona and into Cave Creek Canyon. Environmental and/or other factors, perhaps the YDE at the end of the Pleistocene, caused its distribution to recede far east and possibly south, leaving an isolated population trapped in Cave Creek Canyon. Over time this fragment evolved in the canyon to become *U. chiricahuensis*.

Possible Tests

New data could help determine the best explanation. Any specimens of *U. chiricahuensis* collected outside of Cave Creek Canyon would immediately disprove hypotheses #2 and #3 above. Specimens of both *U. chiricahuensis* and *U. nigripes* collected south of the U.S.-Mexico border likewise would lend credence to hypothesis #1, particularly if sympatric or proximate. In the absence of the discovery of novel specimens of *U. chiricahuensis* outside Cave Creek

Canyon, phylogenetic analysis of North American *Ululodes* and estimation of divergence times via molecular clocking could lend support for hypothesis #2 or #3. Specifically, a cladogenesis event timed considerably earlier than the Pleistocene-Holocene transition would lend support to hypothesis #2, whereas one timed to the Pleistocene-Holocene transition or later (more recently) could be explained by post-Younger Dryas Event climate changes, and provide strong support for hypothesis #3.

CONCLUSIONS

Further comparisons of the morphology and nucleic acid composition of *U. chiricahuensis* to those of other *Ululodes* species are needed to verify phylogenetic relationships and evaluate the various biogeographic hypotheses proposed here. More extensive sampling and sequencing of fresh material also could avail exploration of haplotype networking, gene flow, and other population-level attributes. And deeper analysis of the historical biogeographic conditions of the regions east and south of the Chiricahuas may also shed additional light. For now, it is satisfying to learn that *U. chiricahuensis* exists.

This study adds a fascinating new taxon to the Cave Creek fauna. It also highlights both the canyon's wonder as a setting for rare and beautiful marvels, and its value as a refuge of unique biodiversity. For future taxonomists and hobbyists who are fortunate enough to capture this rare species, the Cave Creek owlfly will represent yet another token of the spectacle and profound capacities of evolution in island biogeographic settings.

ACKNOWLEDGMENTS

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