Anaxipha hyalicetra sp. n. (Gryllidae: Trigonidiinae), a new sword-tailed cricket species from Arizona

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Abstract

A new *Anaxipha* species is described from a locality in southeastern Arizona adjacent to the border with Mexico. The species is unique among the North American fauna by virtue of the broad tegmina, distinctive male genitalia, and calling song phrased in an irregular chirp with a variable pulse train rate. The possibility that the behavioral repertoire of this species includes aggressive song as well as calling song is discussed.

Key words

aggressive song, calling song, mate recognition, Mexico, Neotropical, Sonora

Introduction

Anaxipha is a speciose genus of small crickets with a worldwide distribution (Walker and Funk 2014, Cigliano et al. 2018). The systematics of Anaxipha, and of the Trigonidiinae in general, are in a primitive state (Otte and Perez-Gelabert 2009). Regional systematic studies have revealed entire faunas of these crickets in recent years (Otte 2006, Otte and Perez-Gelabert 2009, Walker and Funk 2014), and numerous new species await description (e.g. Tan 2012, DHF unpublished data). A revision of the North American Anaxipha described two-thirds of the fauna as new to science (8 of 13 species; Walker and Funk 2014). All species known to date occur in the eastern portion of the continent (Walker and Funk 2014, Cigliano et al. 2018).

While engaged in general Orthoptera collecting in southeastern Arizona in 2013, the first author followed an unfamiliar calling song to discover an *Anaxipha* population. Apart from the highly disjunct locality, which is adjacent to the border of the United States with Sonora, Mexico, this *Anaxipha* immediately stood out as new to the North American fauna by virtue of the broad tegmina of males and the variable pulse train rate in the male calling song. Laboratory study revealed distinct genitalia and stridulatory file characteristics. No morphologically similar *Anaxipha* were found among specimens at the Academy of Natural Sciences of Drexel University (DHF pers. obs.). The species is described here as new.

Methods

Fieldwork was performed at dusk and at night during 15–16 July 2013, 23 July 2014, and 29–31 August 2014. Triangulation of calling songs, visual inspection, beating, and sweeping of vegetation were all employed to secure specimen series. Specimens are deposited at the Natural History Museum of Los Angeles County (LACM), at the Academy of Natural Sciences of Drexel University (ANSP), and at the University of Florida (UFL).

Habitus images (Fig. 1) were made at LACM using a digital microscope (model VHX-6000, Keyence Corp., Itasca, IL) with a 10× objective lens. With this microscope, a calibrated anchor point-based digital measurement function was used to obtain the following morphological measurements (in mm) for a subset of dried specimens deposited at LACM: body length (BL, measured from the front of the head to the end of the tegmina for males and to the end of the ovipositor for females), body width (BW, measured at the widest point of the tegmina immediately behind the hind trochanters), and hind femur length (HF). Measurements are reported as mean ± standard deviation (range) separately for each sex.

Male genitalia were removed from a pinned specimen that had been relaxed and cleared in hot 10% KOH. These were mounted in glycerin on a well slide and photographed using a trinocular microscope (Labophot, Nikon Inc., Melville, NY) equipped with a digital SLR (model T1i, Canon Corp., New York, NY) controlled with Canon EOS Utility software in Live View mode. Images taken at several focal points were composited in Adobe Photoshop CS3 software (Fig. 2A). Afterward, the genitalia were transferred to a genitalia vial with glycerin which now resides with the specimen.

The right tegmen of the above specimen was removed and slide-mounted in euparal. The tegmen was then photographed with the trinocular microscope (Fig. 2B). A single digital image was constructed from multiple fields using Adobe Photoshop. File counts were made from the photograph and, starting at the hind margin, a small red dot was added every 10th tooth to facilitate counting (Fig. 2C). Linear measurement was made from the first tooth (closest to hind margin) to the junction of the

PD

PTCF

stridulatory vein and the harp vein. This measurement was expressed as length of cell 5 (sensu Otte 1994) and tooth density was estimated from this region in order to minimize errors attributable to straight-line measurement of the (slightly curved) stridulatory vein.

Songs were recorded in the field and in the laboratory using a digital linear PCM recorder with a built-in condenser microphone pair (model PCM-D50, Sony Corp., New York, NY). This device recorded .wav files at a 96 kHz sampling rate and a bit depth of 16 with a flat response range extending to 40 kHz. The temperature of laboratory recordings was controlled at 24.1 ± 0.7 °C (Table 1). Temperature was measured with a digital thermal sensor (model Trail Pilot 2, Highgear USA, Inc., Fletcher, NC).

Recordings were visualized (Fig. 3) with Raven Lite v. 2.0 (Cornell Laboratory of Ornithology, available from http://www. birds.cornell.edu/brp/raven/RavenOverview.html) and analyzed using BatSound (Pettersson Elektronik AB 2001). The Pulse Characteristics feature of BatSound automatically extracted pulse durations, intervals, and peak frequencies from the .wav files. Oscillogram thresholds for pulse characteristics extraction were set between -18 and -10 dB, with higher values necessary to avoid higher noise floors. Noise below 2 kHz was attenuated with a Butterworth high pass filter in BatSound before analysis. Spectrogram settings for peak frequency measurement were a Hanning Window employing a 256 Hz fast Fourier transformation. Song terminology follows that of Walker and Funk (2014). Abbreviations for song characters are reiterated here for convenience and are graphically shown in Fig. 3:

PΙ pulse interval PP pulse period (=PD+PI) pulse rate (=1/PP)PR Pdc pulse duty cycle (=PD/PP) РΤ pulse train PN number of pulses per train PTD pulse train duration PTI pulse train interval PTP pulse train period (=PTD+PTI) PTR pulse train rate (=1/PTP)pulse train duty cycle (=PTD/PTP) PTdc

pulse train carrier frequency

tween field and laboratory conditions.

pulse duration

Statistical analysis was performed in R (R Core Team 2015). Anaxipha songs are complex, and our analysis considered 12 song characters. Besides those characters that are mathematically re-

lated (see abbreviations above), additional correlations may exist among characters. To find statistically independent variables for analysis, we explored song character data structure with maximum likelihood factor analysis. The number of components to extract was determined by examining a scree plot generated with the nFactors package (Raiche and Magis 2015). A distinct inflection point ("knee") in the plot of eigenvalues vs. components indicates the number of components to extract. The number of components output by the nFactors scree plot was then input into the factanal function, with rotation set to varimax. The output of this function consists of statistically independent factors, together with the magnitudes and signs of the contributions of the song characters to each factor. A MANOVA compared song character means be-

Anaxipha hyalicetra Cole & Funk, sp. n.

http://zoobank.org/1CF3949F-F602-4AEA-ACB6-FF1195B2766D http://lsid.speciesfile.org/urn:lsid:Orthoptera.speciesfile. org:TaxonName:505367

Fig. 1: habitus and morphology; Fig. 2: male genitalia, tegmina, and stridulatory file; Fig. 3: songs, recording 140723_11, available as Suppl. material 1.

Holotype.—1 male. USA. ARIZONA: Santa Cruz County; Peña Blanca Canyon, Coronado National Forest, 31.38230, -111.09251, elevation 1203 m. 23-VII-2014. J.A. Cole leg. Recording number 140814_00. Prepared with tegmina raised. Right antenna missing most of the flagellum, otherwise complete (Fig. 1A, B). Deposited in LACM.

Paratypes.—3 males, 1 female (pinned), same data as holotype (ANSP); 5 males, 1 female, same data as holotype (FSCA); 4 males, 2 females (pinned), 4 males (DNA vouchers SING0518, SING0519, SING0520, SING0521 in 100% ethanol), same data as holotype (LACM); 2 males (pinned), same locality as holotype collected 31-VIII-2014 (LACM); 5 males (pinned), 2 males (DNA vouchers SING0453, SING0454 in 100% ethanol), same locality as holotype collected 15-16-VII-2013, J.A. Cole and J.F. Limón leg. (LACM).

Measurements.—Males (n = 7): BL = 7.63 ± 0.24 (7.38 - 7.95), BW = 3.38 ± 0.18 (3.13 - 3.73), HF = 4.20 ± 0.14 (4.00 - 4.35); females (n = 2): BL = 7.31 ± 0.27 (7.11 - 7.50), BW = 1.95 ± 0.06 (1.91 - 1.99), HF = 4.25 ± 0.23 (4.08 - 4.41).

Hind wings.—No specimens among the type series are macropterous.

Seasonal occurrence.—Available records suggest early summer to midsummer adult activity. Individuals were common from 15-23 July in two consecutive years. By 31 August 2014, males were scarce, and no females were found. Males collected 23 July lived in captivity until 19 August.

Habitat.—The population resides in a north-south trending canyon. Within the canyon, individuals are most common in the creek bed at the canyon bottom but extend a short distance up the canyon walls into mixed woodland. During both July collecting events monsoon rains had recently fallen in the canyon and humidity was high. Crickets were found on catclaw acacia (Senegalia greggii (A. Gray)), on stems of pointleaf manzanita (Arctostaphylos pungens Kunth), on Yucca, on bunch grass, and on oak leaf litter. Like other North American Anaxipha, individuals perched within 1 m of the ground (Walker and Funk 2014). Acoustic activity was observed in the field from 19:41 to 22:05 h. In July and August, A. hyalicetra was sympatric with Oecanthus californicus Saussure, an arboreal chirping Oecanthus rileyi Group sp., Gryllus ?personatus Uhler, and two undescribed Gryllus species. Cycloptilum sp. and Hoplosphyrum sp. scaly crickets (Mogoplistidae) were found in the same habitat during the August 2014 collecting event.

Diagnosis.—A. hyalicetra has a unique combination of morphological characters among the North American Anaxipha fauna. The

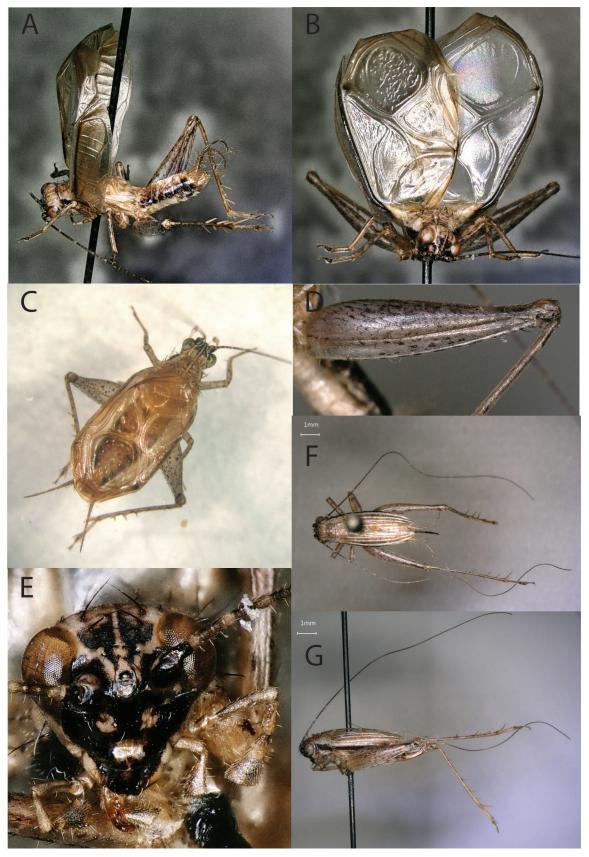


Fig. 1. A. Holotype male, dorsolateral view; B. Holotype male, anterior view; C. Paratype male, living habitus; D. Holotype male, left hind femur; E. Holotype male, face; F. Paratype female, dorsal view; G. Paratype female, lateral view.

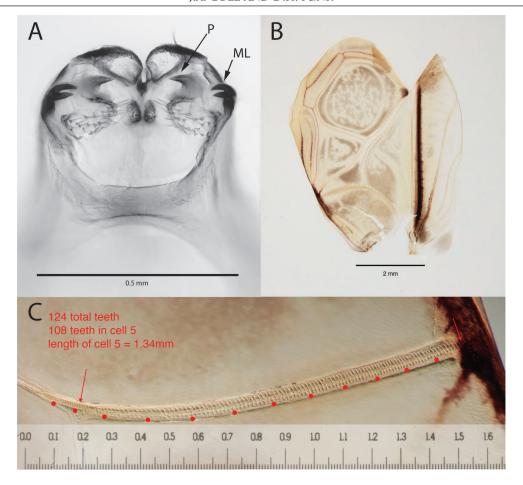


Fig. 2. A. Paratype male genitalia, oblique posterodorsal view, P = paramere, ML = median lophus; **B.** Paratype male excised left tegmen (recording numbers 140811_01 and 140723_15), posterior edge of tegmen at top of image; C. Paratype male, stridulatory file, same male imaged in B.

basal segment of the hind tarsus is longer than segments 2 + 3 combined, a feature that is also found in *A. imitator* (Saussure), *A. calusa* Walker & Funk, and many Neotropical species. The male tegmina in *A. hyalicetra* are broader than in every other *Anaxipha* species (Fig. 1B, C), although many Neotropical species have broad tegmina. With 124 teeth in the stridulatory file (Fig. 2C), *A. hyalicetra* overlaps in file characteristics only with *A. exigua* (Say), which is a fall species with narrow tegmina found in eastern deciduous forests. The male genitalia (Fig. 2A) are unique: the median lophi are bifurcate and hook inward, each paramere has a hooked tooth at the anterolateral corner, and the parameres slope anterolaterally from the midline (rather than a posterolateral slope or perpendicular orientation, cf. plate 13 Walker and Funk 2014). The variable PTR in male songs (Table 1, Fig. 3C) is unique among North American *Anaxipha* (see *Acoustic behavior* below).

Etymology.—l. hyalo (glassy) + cetra (a small light shield), referring to the broad, transparent male tegmina.

Acoustic behavior.—PR in A. hyalicetra is 45.4 s⁻¹ (Table 1, Fig. 3B), identical to that of A. fultoni Walker and Funk and close to that of A. imitator. Phrasing differs between these species. The calling song phrasing of A. hyalicetra is a series of PT of irregular length that may be termed a chirp (Fig. 3A, C). Phrasing in both A. fultoni and A. imitator is a broken trill rather than an irregular chirp. The calling song phrasing of the

new species is qualitatively similar to that of *A. litarena* Fulton from the beaches of the southeastern United States, except that the latter produces more regular PTR and PTD. The carrier frequency is 6 kHz. A series of harmonics extend to 43 kHz at 6 kHz intervals (Fig. 3A).

The scree plot (Fig. 4) has a distinct inflection point at n = 4 components. The four components extracted by maximum likelihood factor analysis (Table 2) may be interpreted as follows. Factor 1 describes PTR (together with mathematically related characters PTI, PTP, and PTdc). Factor 2 describes PTD, which is determined by PN. Factor 3 describes PR (with mathematically related characters PD, PP, and PI) and PTCF. Factor 4 describes pulse characteristics Pdc, PD, and PI, which contribute to PTD. The factor analysis model was rejected as a perfect fit for the data ($P = 4.64 \times 10^{-18}$); the four factors explain cumulatively 91% of variation. PTCF is the least classifiable character (i.e. highest uniqueness at 0.46).

Songs were significantly different between the field and the laboratory (MANOVA, $P = 9.32 \times 10^{-3}$). Notably, males produced more rapid PTR ($P = 3.65 \times 10^{-3}$) due to shorter PTD ($P = 8.06 \times 10^{-4}$) in the laboratory (Table 1). PTCF also differed between field and laboratory ($P = 1.21 \times 10^{-3}$; Table 1). Song character differences opposed relationships predicted by temperature: PR and PTR were faster and PD and PTD were shorter in the laboratory than in the field, despite a lower mean laboratory recording temperature (Table 1).

Males sang in aggregations but did not settle into predictable chorus phase relationships, neither synchronous nor alternating

Table 1. Song character descriptive statistics. All means are reported \pm standard deviation with coefficients of variation (CVs) below. The *P* row shows *P*-value results from a MANOVA test that compared recordings between field and laboratory conditions. Temperatures between these conditions were compared with a 2-sample *t*-test.

		Temp	PR	PD	PI	PP	Pdc	PN	PTR	PTD	PTI	PTP	PTdc	PTCF
Combined mean		24.7 ± 0.9	45.4 ± 4.6	14.3 ± 2.3	7.9 ± 3.2	22.3 ± 2.3	64.4 ± 9.0	5.7 ± 1.8	3.5 ± 1.2	117.2 ± 43.4	223.4 ± 184.9	340.6 ± 194.0	37.7 ± 10.8	6.0 ± 0.4
	CV	0.03	0.46	0.38	1.33	0.23	0.01	0.55	0.40	16.10	153.06	110.46	0.03	0.03
Field mean		25.1 ± 0.8	44.1 ± 3.9	15.2 ± 2.1	7.0 ± 3.0	22.8 ± 2.1	66.8 ± 8.5	6.2 ± 1.7	2.9 ± 1.1	138.9 ± 42.7	278.2 ± 227.8	417.0 ± 225.4	37.8 ± 12.3	5.7 ± 0.3
	CV	0.023	0.351	0.282	1.319	0.196	0.011	0.462	0.436	13.141	186.597	121.789	0.040	0.019
Lab mean		24.1 ± 0.7	47.5 ± 5.1	12.8 ± 2.0	9.5 ± 3.2	21.3 ± 2.4	60.2 ± 8.6	4.8 ± 1.6	4.3 ± 0.6	86.9 ± 20.8	146.7 ± 34.9	233.7 ± 31.8	37.5 ± 9.0	6.3 ± 0.3
	CV	0.018	0.544	0.306	1.073	0.261	0.012	0.520	0.078	5.002	8.282	4.318	0.021	0.018
P			NS	0.015	NS	NS	NS	NS	3.60 × 10 ⁻³	8.06 × 10 ⁻⁴	NS	0.010	NS	1.21×10 ⁻³

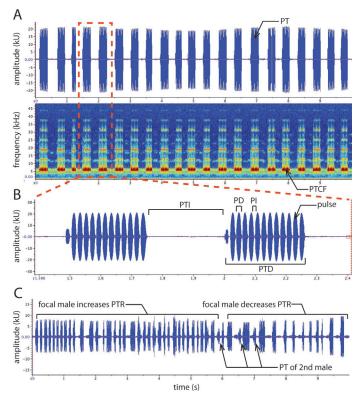


Fig. 3. A. Male calling song, field recording number 140723_11 , oscillogram (above) and spectrogram (below), 10 s window, $25.4 \,^{\circ}\text{C}$. PTR = $2.2 \, \text{s}^{-1}$, PTCF = $6.3 \, \text{kHz}$; B. $1 \, \text{s}$ window of same recording as in A, expanded from region surrounded by red box, showing pulse structure; C. $10 \, \text{s}$ oscillogram of interaction between two males in the field, recording 140723_09 , $23.9 \,^{\circ}\text{C}$. Changes in PTR of focal male are indicated.

(reviewed in Greenfield 2002). Males walked while singing, and, if on a stem, circled the stem (JAC pers. obs.). In the field, males were observed baffling by positioning themselves between twigs (JAC pers. obs.), a behavior that may improve broadcast by reducing destructive interference due to sound radiation to the rear of the insect (Forrest 1982, 1991, Greenfield 2002). When in close proximity in the field, one or both males may have increased their PTR by shortening their chirps (i.e. reducing PTD; Fig. 3C). To a human observer, the effect was a staccato chirp that reverted back to a lower PTR with longer PTD over time (e.g. Fig. 3A). PTdc remained unchanged during alteration of PTR.

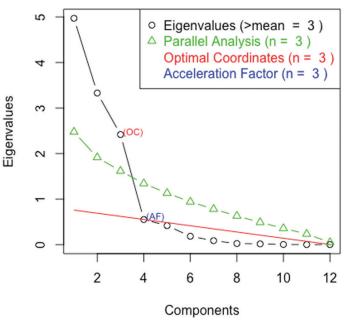


Fig. 4. Scree test results from the nFactors R package. The distinct inflection point of the eigenvalues plot at n = 4 components suggests extraction of that quantity of factors.

Table 2. Loadings of song characters onto four factors as returned by maximum likelihood factor analysis.

Character	Factor 1	Factor 2	Factor 3	Factor 4
PTR	-0.75	-0.48		
PTI	1.00			
PTP	0.98			
PTdc	-0.70	0.50		
PTD		0.91		0.37
PN	0.83			
PR		-0.99		
PP		0.99		
PD		0.47	0.53	0.70
PI		-0.47	0.46	0.63
Pdc		0.49		0.87
PTCF		-0.44	-0.50	

Discussion

A trickle of new species discoveries shows that there is still much to learn about the orthopteran fauna of Arizona, despite much historical systematic attention (Rehn 1908, Hebard 1935a, b, Ball 1942) and the popularity of the state as a destination for insect collectors and hobbyists. Mass collecting methods employed by general entomologists such as beating, sweeping, and light trapping are not comprehensive sampling strategies for orthopteran diversity and were not effective in collecting this new species. Macropterous Anaxipha are attracted to lights, especially in the tropics, but such sampling is not effective for micropterous species. Seasonality is also a consideration. Collectors generally sample Arizona after the onset of the monsoons in August, and thus may overlook species that are active early in the season such as the Anaxipha described here. Two southern Arizona katydids described in recent years: Bucrates weissmani Walker (Walker 2014) and Microcentrum latifrons Spooner (Spooner 1988), are also active as adults early in the season, the latter being sympatric with A. hyalicetra.

Collecting in the Atascosa and Pajarito Mountains in Santa Cruz County, Arizona, failed to find this cricket outside of the type locality. Collecting in adjacent Sonora, Mexico, may prove more fruitful. *Anaxipha hyalicetra* is evidently part of an incursion of Neotropical *Anaxipha* into North America. Once alpha diversity and higher level taxonomic relationships are better known, the species with long first hind tarsal segments may be transferred to a new genus. This set includes *A. hyalicetra*, *A. calusa*, and *A. imitator* among the North American fauna together with the majority of Neotropical species.

As we observed song character differences between field and laboratory conditions that oppose those predicted by temperature, the possibility that A. hyalicetra male behavior includes an aggressive chirp is worth investigating. Specialized aggressive songs in crickets are brief chirps that may be produced more frequently and at higher amplitude than calling song chirps (Alexander 1962, Brown et al. 2006). A staccato chirp characterized by fast PTR and short PTD (Table 1, Fig. 3C) was observed in field situations where two males were in close proximity. We have not performed controlled experiments to determine whether these song changes function in aggression, but it is possible that unintentional artificial crowding in the laboratory may have induced aggressive acoustic behavior, where these same changes to PTR and PTD were also observed. Aggressive songs signal competitive potential (Brown et al. 2006) should an encounter escalate to physical combat (Jang et al. 2008, Bertram et al. 2011, Bertram and Rook 2012), a behavior that is often observed in crickets that defend burrows or shelters (Jang et al. 2008, Bertram and Rook 2012). As A. hyalicetra is a vegetation-inhabiting cricket that has not been observed fighting, aggressive signaling behavior may function instead to regulate male spacing or increase male attractiveness (Mhatre and Balakrishnan 2006, Chamorro-R et al. 2007). An intriguing hypothesis worth testing in A. hyalicetra is that when aggregated, males may increase energy expenditure to appear more attractive to listening females (Jia et al. 2001, Mhatre and Balakrishnan 2006). PTR adjustments do not alter PTdc, which has among the lowest CV of any of the 12 measured song characters (2-4%; Table 1). PTdc may be a signal component that permits mate recognition (Mendelson and Shaw 2012) despite behavioral adjustment of PTR during intrasexual competition.

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Supplementary material 1

Authors: Jeffrey A. Cole, David H. Funk

Data type: WAV file

Explanation note: Male calling song supplementary file.

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