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A revision of the shield-backed katydid genus *Aglaothorax* (Orthoptera: Tettigoniidae: Tettigoniinae: Nedubini)

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Table of contents

Abstract . . . 4
Introduction . . . 4
Methods . . . 6
Results . . . 8
Morphology . . . 12
Genus ***Aglaothorax*** Caudell, 1907 . . . 12
Key to ***Aglaothorax*** species based on morphology, bioacoustics, and geography . . . 14
Systematic Treatment . . . 16
Ovatus Group . . . 16
Aglaothorax ovatus (Scudder, 1899) . . . 19
Aglaothorax giganteus (Rentz & Birchim, 1968) stat. rev. . . . 23
Aglaothorax tinkhamorum (Rentz & Birchim, 1968) stat. rev. . . . 25
Aglaothorax segnis Rehn & Hebard, 1920 comb. restored . . . 28
Aglaothorax armiger Rehn & Hebard, 1920 comb. restored . . . 30
Aglaothorax strobilion Cole, Weissman, and Lightfoot, sp. nov. . . . 32
Aglaothorax khioneos Cole, Weissman, and Lightfoot, sp. nov. . . . 34
Aglaothorax gurneyi (Rentz & Birchim, 1968) . . . 36
Morsei Group . . . 38
Aglaothorax morsei (Caudell, 1907) . . . 39
Aglaothorax costalis (Rentz & Weissman, 1981) stat. rev. . . . 43
Aglaothorax longipennis (Rentz & Weissman, 1981) . . . 47
Aglaothorax amathitis Cole, Weissman, and Lightfoot, sp. nov. . . . 50
Aglaothorax islandica (Rentz & Weissman, 1981) . . . 52
Aglaothorax hulodomus Cole, Weissman, and Lightfoot, sp. nov. . . . 55
Aglaothorax conistylus Cole, Weissman, and Lightfoot, sp. nov. . . . 57
Aglaothorax nesiazo Cole, Weissman, and Lightfoot, sp. nov. . . . 60
Aglaothorax bufonoides Cole, Weissman, and Lightfoot, sp. nov. . . . 62
Aglaothorax kelainops Cole, Weissman, and Lightfoot, sp. nov. . . . 64
Aglaothorax sphenosternum Cole, Weissman, and Lightfoot, sp. nov. . . . 67
Diminutiva Group . . . 70
Aglaothorax diminutiva (Rentz & Birchim, 1968) . . . 71
Aglaothorax constrictans (Rentz & Weissman, 1981) stat. rev. . . . 73
Aglaothorax dactyla (Rentz & Weissman, 1981) stat. rev. . . . 76
Aglaothorax acrolophitus Cole, Weissman, and Lightfoot, sp. nov. . . . 78
Aglaothorax oreibates Cole, Weissman, and Lightfoot, sp. nov. . . . 81
Aglaothorax poecilonotum Cole, Weissman, and Lightfoot, sp. nov. . . . 83
Discussion . . . 85
Acknowledgments . . . 100
Literature Cited . . . 101

Abstract

The Nearctic Shield-backed Katydid (Shieldbacks) genus *Aglaothorax* is revised. Species boundaries are delimited with molecular phylogenetics, morphology, bioacoustics, and cytogenetics. Five species are redescribed: *A. diminutiva* (Rentz & Birchim, 1968), *A. gurneyi* (Rentz & Birchim, 1968), *A. longipennis* (Rentz & Weissman, 1981), *A. morsei* (Caudell, 1907), and *A. ovatus* (Scudder, 1899). Eight described subspecific taxa are elevated to species rank: *A. armiger* Rehn & Hebard, 1920 **comb. restored**, *A. constrictans* (Rentz & Weissman, 1981) **stat. rev.**, *A. costalis* (Rentz & Weissman, 1981) **stat. rev.**, *A. dactyla* (Rentz & Weissman, 1981) **stat. rev.,** *A. giganteus* (Rentz & Birchim, 1968) **stat. rev.**, *A. islandica* (Rentz & Weissman, 1981) **stat. rev.**, *A. segnis* Rehn & Hebard, 1920 **comb. restored**, and *A. tinkhamorum* (Rentz & Birchim, 1968) **stat. rev**. Three described subspecies are made junior subjective synonyms: *A. ovatus* (Scudder, 1899) = *A. ovatus longicauda* (Rentz & Birchim, 1968); *A. dactyla* (Rentz & Weissman, 1981) = *A. diminutiva malibu* (Rentz & Weissman, 1981); and *A. islandica* (Rentz & Weissman, 1981) = *A. morsei santacruzae* (Rentz & Weissman, 1981). Twelve new species are described: *A. acrolophitus* **sp. nov.**, *A. amathitis* **sp. nov.**, *A. bufonoides* **sp. nov.**, *A. conistylus* **sp. nov.**, *A. kelainops* **sp. nov.**, *A. khioneos* **sp. nov.,** *A. hulodomus* **sp. nov.,** *A. nesiazo* **sp. nov.**, *A. oreibates* **sp. nov.**, *A. poecilonotum* **sp. nov.**, *A. sphenosternum* **sp. nov.,** and *A. strobilion* **sp. nov.** Evolution of songs and chromosomes, biogeography, rearing, and conservation are discussed in light of the updated and expanded systematics.

Key words: California, Channel Islands, biogeography, bioacoustics, chromosome evolution, mitochondrial capture

Introduction

The genus *Aglaothorax* Caudell, 1907 contains the archetypal Shield-backed Katydids, (Shieldbacks) the males of the Ovatus Group bearing an exaggerated, broad, oval pronotum that conceals much of the head and abdomen (Fig. 1A). Taken together the wide pronotum, short hind legs, and small head lend a toad-like appearance to these katydids. *Aglaothorax* belongs to the Nearctic Nedubini along with *Neduba* and *Phymonotus* (Cole & Chiang 2016; Lightfoot *et al.* 2011; Rentz & Colles 1990). Presently, *Aglaothorax* is a small genus of five species known from arid Southern California and Nevada, USA (Cigliano *et al.* 2025; Walker 2025). Extrapolating from the numerous subspecies (Rentz & Birchim 1968; Rentz & Weissman 1981) and from song (Cole 2010) and genetic (Cole 2016) variation within described species, we hypothesized that the diversity of *Aglaothorax* has been underestimated as for other Nedubini, within which a new genus (Lightfoot *et al.* 2011) and several morphologically cryptic species of *Neduba* (Cole *et al.* 2021) have been described in recent years. This revision expounds upon that hypothesis by revealing five times the number of described species of *Aglaothorax*.

Biology. *Aglaothorax* species are thamnophilous katydids that inhabit coastal sage scrub, chaparral, desert scrub, pinyon-juniper and Joshua tree woodlands, and oak savanna. Like *Neduba* (Cole *et al.* 2021), some *Aglaothorax* hide in leaf litter or under tree bark during the day (JA Cole (JAC), pers. obs.), while others shelter in the interior of dense (Tinkham 1944) or thorny vegetation; desert species, for example, may receive ample protection within the spiny whorls of Joshua Tree (*Yucca brevifolia* Engelm.) leaves (Rehn & Hebard 1920) and Crucifixion Thorn (*Castela emoryi* (A. Gray) Moran & Felger; JAC, pers. obs.). *Aglaothorax* generally inhabit the understory, but inhabitants of pinyon-juniper (Rehn & Hebard 1920; Rentz & Birchim 1968; Tinkham 1944) and oak woodlands (Tinkham 1944) may be arboreal. Like other nedubines, *Aglaothorax* species are flightless: all individuals lack hindwings, and tegmina are absent in females and modified solely for sound production in males. The katydids are largely herbivorous and show no predatory or cannibalistic tendencies (Tinkham 1944; JAC & DB Weissman (DBW) pers. obs.), although individuals may scavenge dead animal matter (Fig. 1B). Aggression is limited to acoustical displays and to lateral pushing with the front and middle legs in territorial males of the Ovatus Group (JAC, pers. obs). Species of the Diminutiva Group and Morsei Group are tolerant of each other and may form aggregations while sheltering or while singing (JAC, pers. obs).

Acoustical activity of *Aglaothorax* occurs at night. Some males venture out of their daytime shelters onto the vegetation to sing, while others may remain in the center of bushes. Some species, particularly those of the Ovatus Group, produce frequently repeated high amplitude calling songs that may be heard at considerable distances (Fig. 1C), and may even be heard from vehicles traveling at highway speeds. Yet other species make high frequency (Fig. 1E) calling songs that may be difficult to hear at a distance and may sing only sporadically (Fig. 1D, E). Acoustical diel patterns vary among the species. As is typical for katydids, Ovatus Group species commence singing at sundown and continue through the first half of the night, depending on temperature. Acoustical activity of some other species,

such as *A. diminutiva* (Rentz & Birchim, 1968) and *A. longipennis* (Rentz & Weissman, 1981), peaks late in the night through the early morning (see Results). A comparison of song structure between the nedubine genera reveals that *Aglaothorax* calling songs consist of a single pulse train type in contrast to the songs of *Neduba* which consist of two alternating pulse train types (Cole 2010; Cole *et al.* 2021; Morris *et al.* 1975). *Phymonotus* males also produce a single pulse train type, but pulse trains occur in isolation (Lightfoot *et al.* 2011) whereas *Aglaothorax* group pulse trains into echemes or "chirps" (Cole 2010).

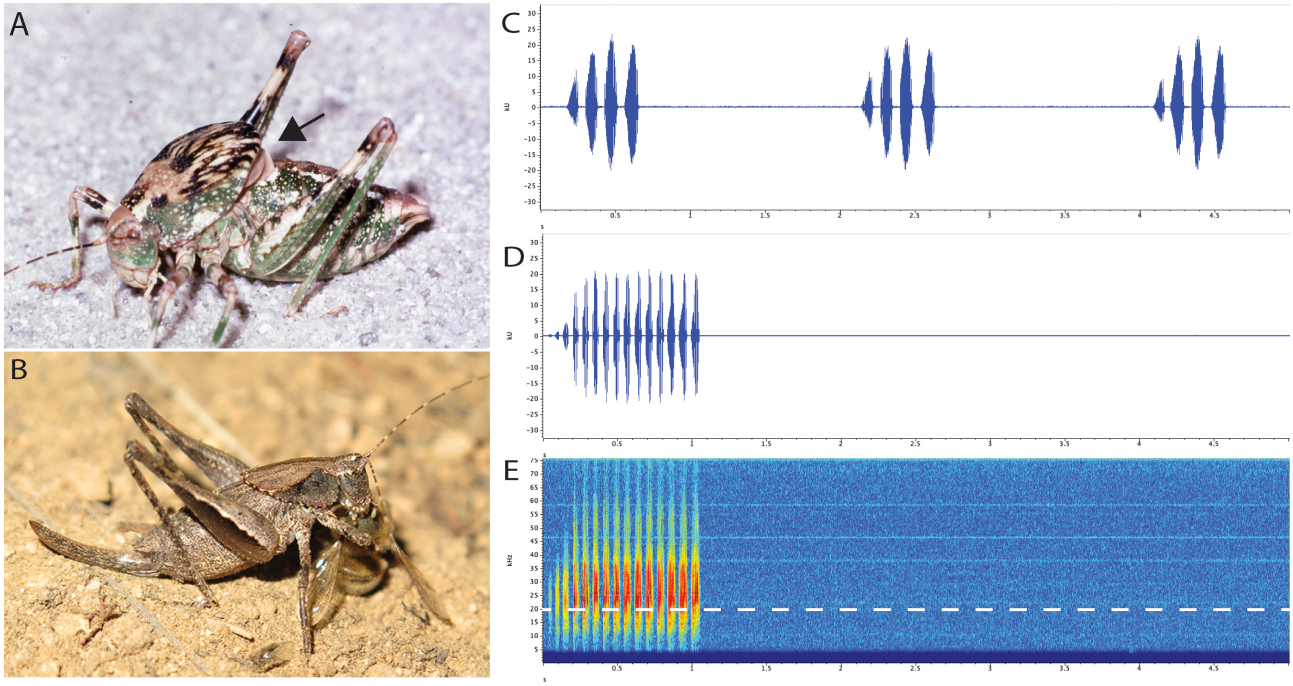


FIGURE 1. A. Habitus of *Aglaothorax giganteus* male, white tegmina (arrow) used in sound production visible below pronotum; B. *A. morsei* female scavenging a dead honeybee; C. Calling song of *A. ovatus*, Los Angeles County, California, 5 s oscillogram window showing three echemes consisting of four pulse trains each; D. Calling song of *A. morsei,* Los Angeles County, California, 5 s window showing one echeme consisting of 15 pulse trains; E. spectrogram of D: ultrasonic frequencies beyond human hearing range lie above white dashed line, warmer colors indicate higher sound energy, most of which is ultrasonic.

Systematic history. Caudell (1907) proposed *Aglaothorax*, based on the type species *Tropizaspis ovata* Scudder, 1899, to contain North American shield-backed katydids with a greatly enlarged pronotum and short hind legs. Upon description of the genus, *T. castanea* Scudder and *T. diabolica* Scudder were transferred to *Aglaothorax* (Caudell 1907), with *diabolica* satisfying neither principal character called for in the genus description as it possesses a relatively narrow pronotum and long hind legs (see Cole *et al.* 2021). *Neduba morsei* Caudell was described in the same work (Caudell 1907). Soon after, *A. sierranus* Rehn & Hebard was described from California (Rehn & Hebard 1909), and *A. armiger* Rehn & Hebard and *A. segnis* Rehn & Hebard were described from Nevada (Rehn & Hebard 1920). Tinkham (1944) recognized *A. armiger*, *A. ovatus*, and *A. segnis* but did not correctly associate the latter two names with their species identities and type localities. Tinkham (1944) also transferred *diabolica* and *sierranus* to *Neduba* Walker, 1869 and kept *morsei* in *Neduba*.

In their North American Shield-backed Katydid revision, Rentz and Birchim (1968) treated *Aglaothorax* as a subgenus of *Neduba*, transferred *morsei* to *Neduba* (*Aglaothorax*), and *castanea* to *Neduba* (*Neduba*). *N. (A.) ovata* was treated as a complex of subspecies that included *armiger*, *segnis*, and three new subspecies: *gigantea* Rentz & Birchim, *longicauda* Rentz & Birchim, and *tinkhamorum* Rentz & Birchim. Two new species were described: *A. diminutiva* Rentz & Birchim and *A. gurneyi* Rentz & Birchim. Rentz and Weissman (1981) described *N. (A.) longipennis* Rentz & Weissman and eight subspecies: *N. (A.) diminutiva constrictans* Rentz & Weissman, *N. (A.) d. dactyla* Rentz & Weissman, *N. (A.) d. malibu* Rentz & Weissman, *N. (A.) morsei costalis* Rentz & Weissman, *N. (A.) m. curtatus* Rentz & Weissman, *N. (A.) m. islandica* Rentz & Weissman, *N. (A.) m. santacruzae* Rentz & Weissman, and *N. (A.) m. tectinota* Rentz & Weissman. *Aglaothorax* was reinstated to genus rank based on morphological

cladistics (Rentz & Colless 1990) and that rank has since been corroborated by morphological (Cole *et al.* 2021; Lightfoot *et al.* 2011), bioacoustical (Cole 2010), and molecular (Cole & Chiang 2016) evidence.

Methods

Collection, rearing, and preservation. *Aglaothorax* are secretive katydids that rely on crypsis and do not move frequently. Individuals may occasionally be discovered during the day hiding under bark or in leaf litter. The katydids are nocturnally active and usually inhabit vegetation strata close to the ground but are on occasion arboreal. Collecting series of *Aglaothorax* requires specialized techniques. Oatmeal trails are an effective collecting method, particularly for obtaining females. Males may be collected by triangulation of calling songs, a method that is effective for species that sing often or have loud (as perceived by human observers) signals. The high carrier frequencies of *Aglaothorax* songs means that observer age is negatively correlated with katydid detectability. Bat detectors set between a 20–30 kHz reception bandwidth may be used to locate singing males.

Substantial sampling for this study was obtained from rearing. Nymphs may be collected in larger numbers than adults and reared to adulthood in the laboratory. Nymphs may be found in the spring and early summer on flowers at night where they feed on pollen (JAC pers. obs.). *Aglaothorax* are not aggressive or cannibalistic towards one another and may be reared in groups. Captive katydids were fed a mixture of dry oatmeal flakes, rabbit pellets, bee pollen, and protein from fish or cat food, and provided with organic romaine lettuce or cut cabbage for moisture.

More recently, DBW has reared adults from eggs laid by field collected adult females. These females were offered dry, sterilized sand for oviposition while being housed in 1 L glass jars, a section of which was sprayed with water to create a moisture gradient. Females were maintained at room temperature and exposed to natural photoperiod. The sand was examined every two weeks for eggs that, once discovered, were removed with soft forceps. Recovered eggs were then placed on moist, sterilized sand in 60 x 20 mm polystyrene petri dishes and covered with 5 mm of additional sand. The sand was kept continually moist with the addition of water throughout the 12–18-month study period. Eggs from four taxa *(A. islandica*, *A. nesiazo* **sp. nov.**, *A. oreibates* **sp. nov.**, and *A. poecilonotum* **sp. nov.**) were obtained and all hatched successfully. But because the eggs from different taxa were treated somewhat differently, the results from these efforts will be discussed under each of the four species. Additionally, we give specific timing details since different species may have different requirements to get eggs to hatch.

Specimen preservation was aided by taxidermy. Gut contents were removed with fine-point forceps inserted through the cervical membrane or from a ventral abdominal incision cut along the pleural membrane. Loose cotton was then inserted to re-shape the abdomen and to absorb liquid. Colors, particularly greens, were preserved by freeze-drying in a frost-free freezer, with or without taxidermy. Freeze-drying was judged to be complete when legs were immoveable, a process which generally took several months.

DNA extraction, gene sampling, and sequencing. Molecular laboratory methods were similar to those used for *Neduba* (Cole *et al.* 2021). Right middle or hind legs were removed from molecular voucher specimens and stored in 100% EtOH or frozen directly. DNA was extracted using commercially available extraction kits (DNEasy Blood and Tissue Kit, Qiagen, Valencia, CA, USA) according to manufacturer instructions, or by using custom ethanol precipitation chemistry based on earlier versions of this kit.

Gene sampling included six gene regions previously used for Nedubini: the entire *internal transcribed spacer 2* (*ITS2*), a fragment of the *28S rDNA* gene (*28S*), a 444 bp fragment of *arginine kinase* (*AK*), a 384 bp fragment of *wingless* (*WG*), an 816 bp region of the 3' end of *cytochrome oxidase I* (*COI*), and a 498 bp fragment of *cytochrome oxidase II* (*COII*). Gene regions were PCR amplified with primers and thermocycling profiles used for Nedubini (Cole 2016; Cole *et al.* 2021). The first four gene regions are nuclear (referred to hereafter as nDNA) and the last two are mitochondrial (mtDNA).

Most PCR products were Sanger sequenced from 2013 to 2014 at California State University Northridge, and from 2015 to 2022 by a commercial provider (Laragen Inc., Culver City, CA, USA). Gene sampling was completed 2023–2024 using multiplexed nanopore sequencing. Nanopore library preparation began with ligation (kit LSK-109, Oxford Nanopore Technologies, Oxford, UK) of unique sequence tags (kit EXP-NBD196, Oxford Nanopore Technologies, Oxford, UK) onto ~130 ng of pooled PCR products for each specimen according to manufacturer instructions. A pooled library quantity of 10–20 fmol was sequenced on a nanopore sequencer (model Mk1C, Oxford

Nanopore Technologies, Oxford, UK) fitted with R9.4.1 or R10.4.1 flow cells, and set to demultiplex and basecall ('fast' setting) in real time with Guppy v. 6.3.8 (available from www.nanoporetech.com), with .fastq file output.

Contig assembly and alignment. Sanger trace files were assembled into contigs and edited in Geneious v. 2023.0.4 (www.geneious.com).Trace files from previous *Aglaothorax* accessions (Cole 2016; Cole & Chiang 2016) were reassembled, quality checked and edited. Amplicon pools were separated using Cutadapt v. 4.0 (Martin 2011), which searched for and trimmed primers, adapters, and other sequence 5' and 3' to adapters in both forward and reverse orientation ('revcomp' option) while discarding superfluous reads that were not trimmed ('discard-untrimmed' option).

Consensus sequences for length-variable nDNA regions were generated with NGSpeciesID v. 0.1.3 (Sahlin *et al.* 2021). This application searched Cutadapt-trimmed .fastq amplicon pools, subsetted to 300 reads ('sample_size 300'), for products within 50 bp of target amplicon length and minimum quality score of 12, and clustered with kmer count 13 and window size 20 ('ont' option). Consensus sequences were polished with Medaka v. 0.11.5 (available from https://github.com/nanoporetech/medaka) and checked with pairwise or local MUSCLE alignment in Geneious, particularly when multiple consensus sequences were generated. Consensus sequences for protein coding *COI* and *COII* nanopore reads were generated with ONTbarcoder v. 0.1.7 (Srivathsan 2021) set to find exact expected amplicon lengths, consensus by length limited to 50 bp deviations from expected amplicon length, consensus by similarity based on coverage of 100 reads, and a consensus sequence acceptance threshold of N-free sequence above a proportion of 0.3.

The *L-INS-i* algorithm in MAFFT v. 7.471 (Katoh *et al.* 2002; Katoh & Standley 2013) was used to align *28S*. *ITS2* sequences were aligned by simultaneously considering nucleotide sequences and positions in secondary structures. Precise start and endpoints of *ITS2* were located using a hidden Markov model (Eddy 1998) implemented through the *ITS2* Database (Koetschan *et al.* 2010). A minimum free energy (MFE) RNA secondary structure model was estimated using the RNAfold Server (Lorenz *et al.* 2011) available through the Vienna RNA Websuite (Gruber *et al.* 2008). A preliminary MAFFT alignment of *ITS2* was then realigned according to the MFE secondary structure model using RNAsalsa (Stocsits *et al.* 2009). Protein coding *COI* and *COII* genes were aligned according to amino acid sequence in Geneious.

Model selection and phylogenetic analysis. Phylogenetic matrices were edited and concatenated in Mesquite v. 3.61 (Maddison & Maddison 2015). Appropriate substitution models were selected using PartitionFinder 2 (Guindon *et al.* 2010; Lanfear *et al.* 2012, 2016). Bayesian consensus trees were estimated in MrBayes v. 3.2.7 (Huelsenbeck & Ronquist 2001; Ronquist *et al.* 2012; Ronquist & Huelsenbeck 2003) via the supercomputer resources at the CIPRES science gateway (Miller *et al.* 2010). PartitionFinder 2 results were incorporated directly into MrBayes blocks in concatenated Nexus files. *ITS2* indels were coded as binary characters with 1 = presence of nucleotide and 0 = presence of a gap at a given alignment position and analyzed as restriction data with variable coding. Four runs of four MCMC chains proceeded for 3×10^7 generations.

Morphology. The authors collected the bulk of specimens that were examined in the revision. Specimens were examined in the collections of the Bohart Museum of Entomology, UC Davis (BMED), the California Academy of Sciences (CAS), the California State Collection of Arthropods (CSCA), California State University, Northridge (CSUN), the Natural History Museum of Los Angeles County (LACM), and the personal collection of the senior author (JAC). For new species, all specimens collected by us as well as others with associated metadata (i.e. songs, karyotypes, DNA) were designated as paratypes. Historical museum specimens without additional lines of evidence were often relegated to Material Examined.

Our specimen code system remains the same as used in *Neduba* (Cole *et al.* 2021), and is repeated here for convenience:

S = DBW stop, i.e. collecting event, e.g. S82-37, the 37th collecting event in 1982
A (adult) = eclosion date of adult reared from nymph
JAC = specimen barcode, 9-digit number
R = DBW recording number
JCR = JAC recording date_[underscore] number, e.g. 160729_03, the 3rd recording on 29-VII-2016
T = DBW testes preparation for karyotyping
JCT = JAC testes preparation for karyotyping
D = number associating DBW voucher specimen with tissue, usually right middle leg
DNA = number associating JAC voucher specimen with tissue

SING = DNA extraction, numbered sequentially

Male internal genitalia were removed from specimens that were relaxed by immersing the tip of the abdomen in boiling water for a few min. The genitalia were excised with fine forceps and cleared in 10% KOH for 0.5 d followed by neutralization in distilled white vinegar for 0.5 d. Internal genitalia were stored in glycerol in microvials pinned under the voucher specimen. Tegmina removed for counting of file teeth were enclosed in a gelatin capsule pinned under the voucher specimen.

Habitus images were captured with a digital camera (model TG-5, Olympus, Center Valley, PA, USA) set to focus stacking in microscope mode. Micrographs were made with a C-mount digital camera (model MU1803, AmScope, Irvine, CA, USA) attached to a trinocular zoom microscope (model SM-1T, AmScope). Figures and plates were assembled in Adobe Illustrator (www.adobe.com). Anatomical orientations in images are designated 'R' = dorsal and 'V' = ventral.

Specimen locality data without GPS coordinates were georeferenced using the GEOLocate batch client (available at geo-locate.org). Maps were generated using the 'rnaturalearth' package (Massicotte & South 2023) in R v. 4.1.3 (www.r-project.org) interfaced through RStudio v. 2022.02.3+492 (available at www.rstudio.com).

Song terminology, recording, and analysis. To remain consistent with existing song terminology for Nedubini, we term the sound unit that results from a complete movement of the tegmina, and thus the unit that consists of a complete series of pulses (toothstrikes), as a pulse train (Cole *et al.* 2021; Morris *et al.* 1975) rather than as a syllable (Baker & Chesmore 2020). Per Baker & Chesmore (2020), we hereby correct erroneous song terminology in which the *Aglaothorax* pulse train was incorrectly termed a pulse despite having clear toothstrikes (Cole 2010).

DBW laboratory recordings were made under varied temperatures (24.5±2.3, range 20.5–29.0°C) with a reel-to-reel tape recorder (model 4000 Report LC, Uher, Munich, Germany), running at 19 cm/s, and a condenser microphone (model ME40 with K34 power module, Sennheiser Corp., Wedemark, Germany). DBW analog recordings were digitized with a firewire interface (model Cakewalk FA-66, Roland Corp., Los Angeles, CA, USA) into a MacBook Pro computer running Logic Pro v. 10.3.3 (Apple, Inc.). JAC laboratory recordings prior to 2009 were made in a semi-anechoic chamber maintained near 25.0°C (24.9±0.3°C, range 23.0–25.5°C) with the following signal chain: 1/2 inch measurement microphone (model M51, Linear-X, Tualatin, OR, USA) into a custom amplifier, then into a PC computer sampling at 151.5 kHz. This equipment recorded frequencies up to 75 kHz with flat response between 10–40 kHz. JAC field and laboratory recordings since 2009 were made with linear PCM recorders (models PCM-D50 and PCM-D100, Sony Corp., USA) set to 96 kHz sampling rate, bit depth 16, and low frequency cutoff engaged, recording frequencies up to 48 kHz.

Song .wav files were prepared for analysis by batching through a custom macro in Audacity v. 2.4.2 (available from www.audacityteam.org) that converted stereo files to mono, applied a high pass filter below 5 kHz with a 48 dB rolloff, and normalized to -3 dB SPL. Song analysis was accomplished with the warbleR package (Araya-Salas & Smith-Vidaurre 2017). Pulse trains were temporally delimited with automatic detection (*autodetec* function) with the following settings: *ssmooth*=300, *mindur*=0.01 ms, and *maxdur*=0.9 ms. Detailed spectral parameters (*specan* function) were calculated from the upper and lower frequency limits (*frange* function) of the *autodetec* output through a bandpass filter (*flim* function) set between 5 and 40 kHz, between which most acoustic energy occurs.

Karyotyping. Methods used for *Neduba* (Cole *et al.* 2021) apply here with the following addition. Since 2019 (when EWS replaced the retired NU), after excision, testes were soaked in 0.9% trisodium sodium citrate for 30–45 min, then immersed twice in a 3:1 solution of 100% ethanol:glacial acetic acid. Karyotypes are reported in the manuscript as counts of chromosomes classified by centromere position: m=metacentric and t=telocentric. For example, 2n♂=20(4m+14t+XtYt) is a karyotype from an adult male that has a diploid number of 20 chromosomes including 4 metacentric autosomes (or 2 pairs), 14 telocentric autosomes (7 pairs), and telocentric X and Y sex chromosomes.

Results

Phylogenetic Analysis. Data and GenBank accession numbers for specimens included in the phylogenetic analysis are reported in Supplementary Table 1. Alignment lengths were 596 bp for *ITS2*, 1118 bp for *28S*, 444 bp for *AK*, 384 bp for *WG*, 816 bp for *COI*, and 498 bp for *COII*. PartitionFinder results are shown in Table 1. Bayesian analyses



FIGURE 2. Bayesian consensus tree of nDNA matrix. Nodes with less than 85% posterior probability are collapsed. Terminals in red show mitochondrial capture in Fig. 3.

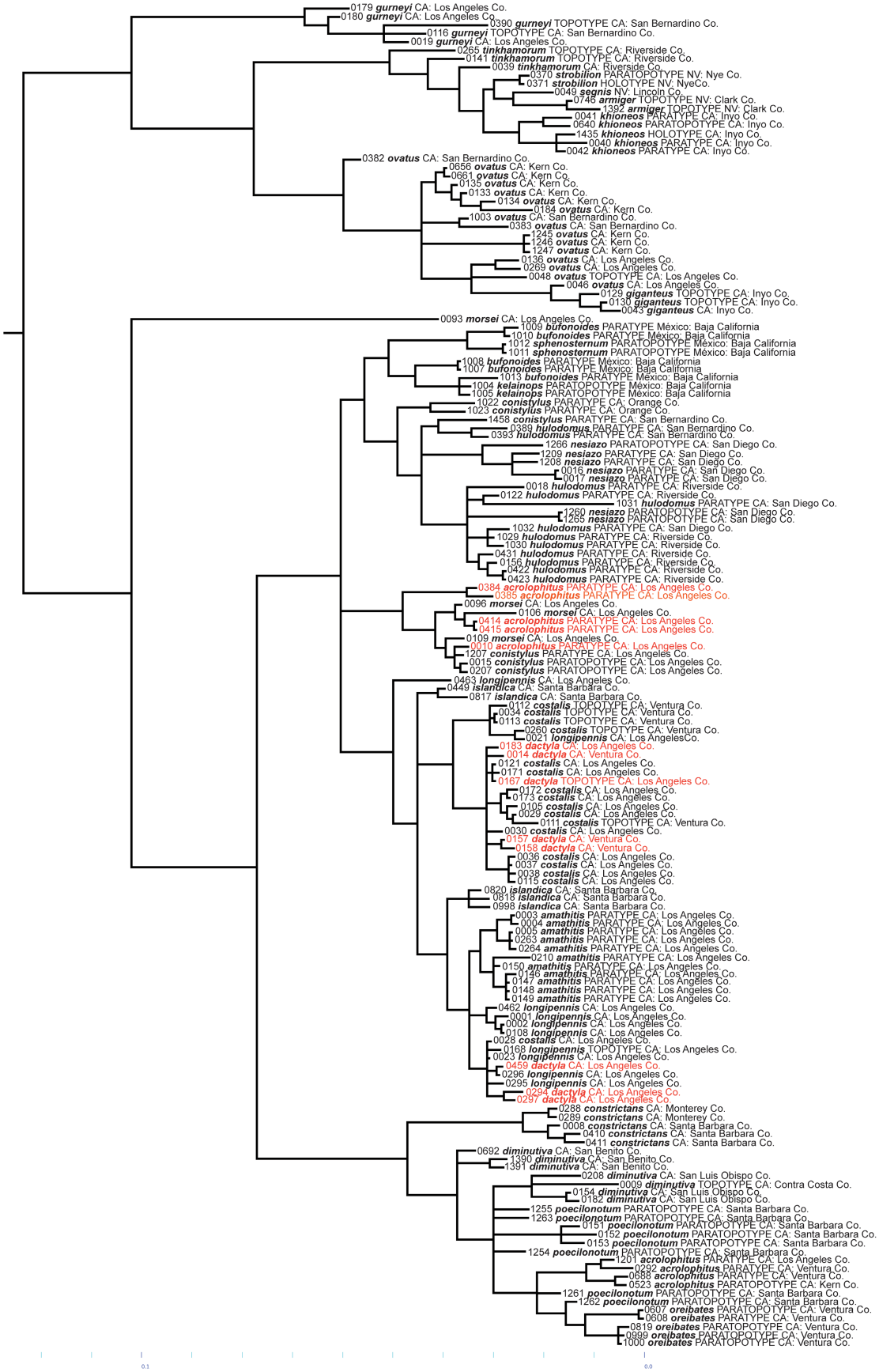


FIGURE 3. Bayesian consensus tree of mtDNA matrix. Nodes with less than 85% posterior probability are collapsed. Terminals in red are Diminutiva Group exemplars that experienced mitochondrial capture into the Morsei Group.



FIGURE 4. Bayesian consensus tree of concatenated matrix. Terminals in red show exemplars involved in mitochondrial capture.

terminated in the following standard deviations of split frequencies: concatenated dataset = 8.75 $\times 10^{-2}$, nDNA = 7.45 $\times 10^{-2}$, mtDNA = 4.14 $\times 10^{-3}$. Only the mtDNA analysis converged below the 0.02 threshold (Huelsenbeck & Ronquist 2001).

TABLE 1. Data partitions and substitution models selected by PartitionFinder 2.

Subset	Partition	Model
1	*COI* 1st codon position, *COII* 1st and 2nd codon positions	GTR+I+Γ
2	*COI* 2nd codon position	F81+Γ
3	*COI* and *COII* 3rd codon positions	GTR+Γ
4	*AK* 1st and 2nd codon positions	JC+I+Γ
5	*AK* 3rd codon position	SYM+I+Γ
6	*WG* 1st codon position	GTR+I+Γ
7	*WG* 2nd and 3rd codon positions	K80
8	*28S*	GTR+I+Γ
9	*ITS2*	HKY+Γ

Bayesian consensus trees showed three clades (Figs. 2–4) that we name informally as species Groups. These are the Ovatus Group (posterior probability = 1.0 in all analyses) which contains the type of the genus *A. ovatus*, the Morsei Group (posterior probability = 1.0 for concatenated and mtDNA analyses and 0.64 for nDNA analysis) named for *A. morsei* (Caudell, 1907), and the Diminutiva Group (posterior probability = 1.0 for concatenated and nDNA analyses and 0.99 for mt DNA analysis) named for *A. diminutiva* (Rentz & Birchim, 1968).

Comparison between nDNA (Fig. 2) and mtDNA (Fig. 3) topologies showed mitonuclear discordance. In each case this discordance was due to mtDNA capture between clades. Transfer of mtDNA was unidirectional among small *Aglaothorax* and always consisted of Diminutiva Group haplotypes found within the Morsei Group (Fig. 3). The concatenated analysis (Fig. 4) showed generally low support at internodes, found the Diminutiva Group at the crown of a grade of Morsei Group taxa, and split several taxa among multiple clades or paraphyletic grades.

Morphology

Genus *Aglaothorax* Caudell, 1907

Tropizaspis—Scudder, 1899: 83 (*Nomen nudum*).
Aglaothorax—Caudell, 1907: 290.
Neduba (*Aglaothorax*)—Rentz & Birchim, 1968: 59 (A change in status to subgenus rank).
Aglaothorax—Rentz & Colless, 1990 (Genus rank restored).

Type species. *Tropizaspis ovata* (Scudder, 1899)

Generic characters. The following description of the genus is based on topotypic *A. ovatus* (specimens ♂JAC000003080 and ♀JAC000003104) with variation from topotypic series. Female morphology is indicated where different from that of the male.

Head. Head well seated in pronotum. Labrum subtransverse ventrally, broadly rounded laterally, tapering to narrow base dorsally, with or without low median ridge, subcylindrical connection with clypeus bears a central depression. Clypeus appears as two stacked inverted rectangles as anteclypeus transitions to postclypeus dorsally along a rectangular stepwise lateral margin, clypeus sulcate along frontal plane, with or without a short dorsoventral groove on anteclypeus. Frons with ventral margin indented or emarginate, surface weakly convex, extends between antennal sockets as a narrow dorsal triangular or knob-like projection, median ocellus indicated as a small white oval on dorsal projection below frontal fastigium. Gena ovoid, slightly convex, with dorsoventral long axis. Vertex rectangular to trapezoidal dorsally, median and lateral carinae not raised, vaguely indicated as dark lines. Fastigium of vertex square to rectangular dorsally with median longitudinal linear or triangular groove, projects to anterior of scapes, in frontal view appears as two dorsal edges and one ventral edge radiating from a center point, widely

separated from fastigium of frons. Junction of vertex and occiput obsolete, occiput evenly convex. Eyes oval with axis trending anteroventrally. Antennae approximately 1.25 times body length, black with contrasting white annulations every few antennomeres and that do not often coincide with articulations.

Thorax. Male pronotum greatly expanded into a shield-like sclerite that completely covers the tegmina and the first two abdominal tergites, bounded by a thick cord around entire margin. Median carina runs entire length of pronotum but weakly developed as a faint line or shallow groove. Prozona as wide or wider than occiput at anterior, widened to posterior at a 30° angle, a lateral transverse groove crosses the prozona where it widens, the disk to the posterior with a posteromesally trending row of punctations and variably developed rugae, rounded at anterior onto lateral lobes. Metazona smooth and convex dorsally, separated from prozona by a curved groove that meets depressions at each anterolateral angle, thick lateral carinae transition to the lateral lobes at a right angle. Lateral lobes of pronotum longer than deep, trapezoidal below prozona, forming a right triangle below the metazona as they narrow to join the posterior carina at an acute angle. Female pronotum similar to male but less exaggerated, 1.0–2.8 times as long as wide. Auditory spiracle elongate oval, posterolateral facing, mostly hidden by lateral carina. Prosternum armed with spines, nipple-like knobs, transverse ridges, or unarmed. Mesosternal lobes subtriangular, metasternal lobes rounded.

Legs. Front coxa with stout anterolateral spine that projects distally to trochanter, other coxae unarmed. Dorsal surface of fore- and midfemur with a variable number of small spines (see Tables 2–4) and a single spine before genicular lobe on posterior margin, ventral cephalic and lateral surfaces strongly carinate. Foretibia rectangular in cross section, tympanum concealed by narrow curved slits equally developed on cephalic and posterior margins, with or without spine distal to tympanum, a single spine on apical caudal margin or both cephalic and caudal margins possess spines, and a variable number of spines on cephalic and caudal ventral carinae. Midtibia rectangular in cross section, a variable number of spines on dorsal margin and along cephalic and caudal ventral carinae (Tables 2–4). Hind femur short and robust, 1.2–1.6 times (female hind femora up to 2.5 times) longer than pronotum, not extending far beyond abdominal apex, with numerous small dorsal spines scattered along basal half, ventral surface with both margins strongly carinate, bearing a variable number of small spines (Tables 2–4). Hind tibia square in cross section, numerous spines on inner and outer dorsal carinae, apex with spines on both ventrolateral and ventromedial margins, apical spurs half or more the length of basitarsus, medial spur more well developed than lateral spur. Tarsal formula 4-4-4. All tarsomeres except pretarsus with ventrolateral expansions that bear inflated disc-like pads. Hind basitarsus with a pair of free plantulae.

Wings. Male tegmina brachypterous, ovoid, ambidextrous, with similarly developed stridulatory files on both tegmina, and either left or right tegmen situated dorsally with frequency 0.5. Wings absent. Female tegmina and wings absent.

Abdomen. Robust, tapered to posterior. T3 or T4 to T8 with a median carina in posterior half that may raise in prominence to form spines, especially on T4–T7. T1 posterior margin sometimes crenulate laterally.

Male terminalia. Supra-anal plate (= epiproct) rounded, tongue-like, heart-shaped, or quadrate, flat to dorsally convex. Cerci conical, as long or longer than T10. Paraprocts (= pseudocerci, infracercal plates) elongate, forcipate, cylindrical, triquetral, or dorsoventrally flattened in cross section, with mesoventral or mesal tooth situated subapically or apically. Male subgenital plate scoop-like, ventrolateral carinae converging to parallel, apex transverse to rounded and broad to narrow, with or without styli.

Female terminalia. Cerci reduced, tiny, scarcely 1/2 length of supra-anal plate. Ovipositor sword-like, gradually curved upward, 0.8–1.7 times as long as hind femur, with peg-like denticulations along caudal 1/3 on both dorsal and ventral margins. Subgenital plate with lateral edges extended into two caudally directed projections that range from digit-like and much longer than wide to triangular and barely as long as wide, ventral surface of plate flat to concave.

Etymology. *aglao* (*Gr.*) splendor, beauty, splendid, brilliant + *thorax* (*Gr.*) a breastplate, the thorax, presumably in reference to the greatly enlarged, shield-like, and in the type species, strikingly colored pronotum.

Diagnosis. The Nearctic Nedubini: *Aglaothorax*, *Neduba*, and *Phymonotus*, are immediately recognizable among the North American katydid fauna by having the male paraprocts modified into clasping organs rather than the cerci. Furthermore, the male tegmina are ambidextrous, with the left or right tegmen equally likely to lie uppermost, whereas in all other katydids the left tegmen overlies the right. Concerning habitus, *Aglaothorax* have wide, robust bodies rather than the cylindrical or fusiform bodies of *Phymonotus* and most *Neduba*. Green forms are absent in *Neduba* and *Phymonotus* while many individuals of the Ovatus Group of *Aglaothorax* have a green

body color with green pronotum markings. An enlarged dome-shaped pronotum separates male *Phymonotus* from *Aglaothorax* and *Neduba,* which have flat to slightly convex pronotal disks. Male *Aglaothorax*, like *Phymonotus*, have forcipate paraprocts with an apical internal tooth; *Neduba* have oblong paraprocts that do not possess a tooth. Female *Aglaothorax* have a subgenital plate with paired processes directed to the posterior; the subgenital plates of female *Neduba* and *Phymonotus* are at most notched along the posterior border.

Key to *Aglaothorax* species based on morphology, bioacoustics, and geography

The following key works best with series of specimens, and representatives of both sexes are required to navigate much of the key. Morphological diagnosis is based on constellations of characters. Single characters are rarely diagnostic because identical or similar character states may occur across several species. The morphological characters incorporated into the key are typical or average but may not cover the range of variation within species.

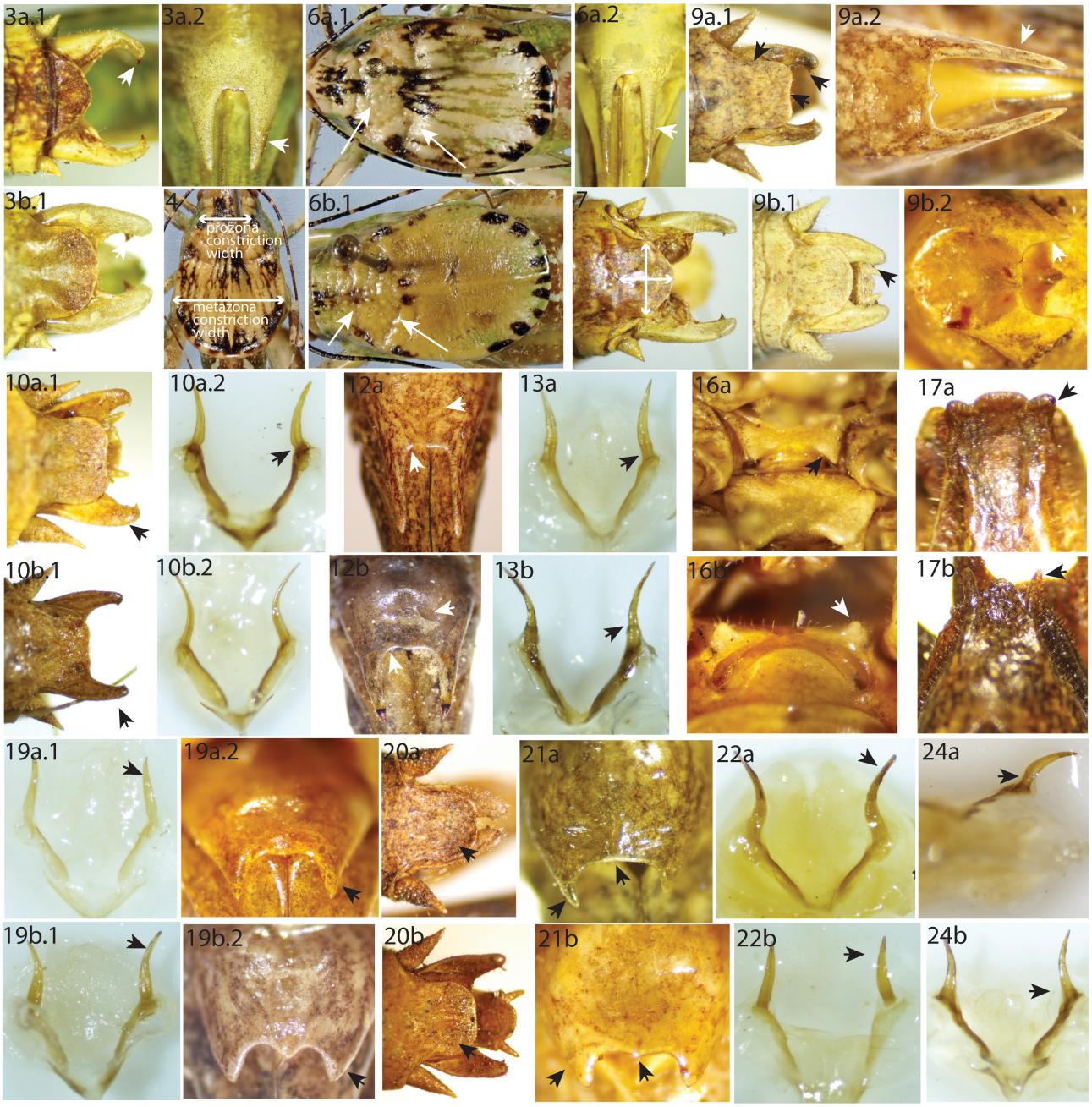


FIGURE 5. Diagnostic morphology of *Aglaothorax* used in species key.

1. Large body size, pronotum length >10 mm in males and >11 mm in females, female ovipositor length >16 mm. Green forms common (Plate 1; Ovatus Group). 2
- Small body size, male pronotum length <10 mm in males and females, female ovipositor length < 16 mm. Diverse color patterns but no green forms (Plates 2–3) 9
2. Body coloration wood brown. Abdomen without a central longitudinal red-brown stripe (Fig. 14, Plate 1). Male tegmina brown. Male prozona rugose, metazona with shallow oblique depressions and irregular fine rugae (Fig. 14). Male paraproct processes long, about 3 times as long as wide, dorsoventrally flattened, and with a subapical ventrally oriented tooth (as in Fig. 5-3b.1, Fig. 14). Female subgenital plate lateral processes of medium length, thick at base, tapering to a sharp point (Fig. 14, Plate 7). Inhabits high elevation woodlands of the San Gabriel and San Bernardino Mountains of Southern California (Fig. 6) . . . . . *gurneyi,* p. 36
- Body coloration variable but not wood brown. Abdomen with a central longitudinal red-brown stripe (Plate 1). Male tegmina ivory white. Male prozona variable, metazona smooth with only fine transverse grooves and punctate around apical 1/4 of periphery. Female subgenital plate variable 3
3. Male paraproct processes with mesally directed apical tooth (Fig. 5-3a.1). Female subgenital plate processes short, thick, tapering to a blunt point (Fig. 5-3a.2; female of *A. strobilion* unknown). Inhabits pinyon-juniper woodlands in mountain ranges of eastern Nevada 4
- Male paraproct tooth positioned subapically and ventrally (Fig. 5-3b.1). Female subgenital plate processes variable 5
4. Male paraproct processes long, thin, slender, about 3 times as long as wide (as in Fig. 5-3a.1, Fig. 10, Plate 4). Male pronotum constriction width narrow relative to metazona width (measured as in Fig. 5-4), ratio 2.24–2.47. Karyotype 2n♂=24 (Fig. 10). Mountain ranges of southeastern Nevada (Fig. 6) . . . . . *segnis,* p. 28
- Male paraproct processes slender but shorter than above, about 2 times as long as wide (Fig. 12, Plate 4). Male pronotum constriction width broad relative to metazona width, ratio 1.97–2.20. Typical Ovata Group karyotype of 2n♂=23. Mountain ranges of east central Nevada (Fig. 6) . . . . . *strobilion,* p. 32
5. Male pronotum distinctly rugose on prozona in addition to a posteromesally trending oblique groove or row of punctations on each side (as in Fig. 5-6a.1, 6b.1). Female subgenital plate processes long, slender, acuminate (as in Fig. 5-6a.2). 6
- Male prozona with few rugae in addition to the posteromesally trending groove or row of punctations on each side. Female subgenital plate variable 7
6. Male pronotum heavily and irregularly rugose on prozona (Figs. 5-6a.1, Fig. 8), metazona rises steeply above transverse sulcus. Pronotum with black coloration consisting of longitudinal streaks of varying intensity in center of disk in addition spots or bars around periphery of disk (Figs. 5-6a.1, Fig. 8). Male titillator arms stout, smoothly curved laterally (Fig. 8, Plate 10). Eastern slopes of Sierra Nevada, California, at moderate to high elevations (Fig. 6). . . . . *giganteus,* p. 23
- Male pronotum less rugose on prozona, rugae wart-like, transition to metazona at transverse sulcus not abrupt, both surfaces on similar planes (Fig. 5-6b.1). Pronotal disk rich yellow-green in life, black coloration reduced to a single central spot and irregular heavy black bars around periphery of disk. Male titillator arms long, slender, bowed laterally (Fig. 9, Plate 10). Distributed along the mountains bordering the Colorado Desert, California (Fig. 6) . . . . . *tinkhamorum,* p. 25
7. Male supra-anal plate wider than long (measured as in Fig. 5-7). Body ground color typically tan or light brown. Pronotum often with reduced coloration on center of disk, black markings commonly restricted to bars around the periphery of disk and a central pair of spots (Fig. 11, Plate 1). Female subgenital plate processes stout and of moderate length (as in Fig. 5-3a.2, Fig. 11, Plate 7). Mountains of southwestern Nevada (Fig. 6) . . . . . *armiger,* p. 30
- Male supra-anal plate as wide as long. Pronotum usually with more extensive coloration on disk. Female subgenital plate variable. Mountains of California. 8
8. Pronotum usually with wide white longitudinal stripes, and often fine brown streaks, on disk in addition to black streaks and central black spot (Fig. 7, Plate 1). Female subgenital plate lateral processes long, slender, acuminate (as in Fig. 5-6a.2, Fig. 7, Plate 7). Mountains surrounding and within California Mojave Desert (Fig. 6) . . . . . *ovatus,* p. 19
- Pronotum with heavy black longitudinal streaks on disk but without white and/or brown streaks (Fig. 13, Plate 1). Female subgenital plate lateral processes stout and of moderate length (as in Fig. 5-3a.2, Fig. 13, Plate 7). High elevation pinyon-juniper of White Mountains and Inyo Mountains of eastern California (Fig. 6) . . . . . *khioneos,* p. 34
9. Male supra-anal plate heart-shaped, expanded and bilobed caudally, or at least with caudal margin indented (Fig. 5-9a.1). Male paraproct processes with apical tooth. Female subgenital plate (except *A. constrictans*) processes long, digitiform (Fig. 5-9a.2; Diminutiva Group) 10
- Male supra-anal plate rounded and tongue-like (e.g. Fig. 5-9b.1) or square with rounded edges, dorsally flat to concave. Male paraproct processes with tooth position variable but commonly subapical (Fig. 5-9b.1). Female subgenital plate processes short triangular projections (Fig. 5-9b.2; Morsei Group) 15
10. Male paraproct processes short, blunt, as long as wide (Fig. 5-10a.1, Fig. 30, Plate 6). Male titillator arms short, barely curved, with distinct mesal notch at base (Fig. 5-10a.2, Fig. 30, Plate 13). Female subgenital plate processes short, triangular, barely longer than wide (as in Fig. 5-9b.2). South Coast Ranges of California (Fig. 27). . . . . *constrictans,* p. 73
- Male paraproct processes long, thin, cylindrical, much longer than wide (Fig. 5-10b.1). Male titillator arms long, curved, not notched (Fig. 5-10b.2) but may be slightly constricted at base. Female subgenital plate processes long, digitiform (as in Fig. 5-9a.2). 11
11. Male titillator arms long, thin, and strongly bowed laterally at 1/2 length (Fig. 5-10b.2, Fig. 31, Plate 13). Female subgenital plate lateral processes long, thin, sharply pointed (Fig. 5-9a.2, Fig. 31, Plate 9). Santa Monica Mountains of California (Fig. 27). . . . . *dactyla,* p. 76
- Male titillator arms shorter than above and smoothy curved. Female subgenital plate processes shorter, broader at base, tapering to a blunt apex (as in Fig. 5-12a, 5-12b). 12

12. Female subgenital plate lateral processes join caudal margin of plate at a right angle (Fig. 5-12a, Fig. 29, Plate 9). Ventral surface of plate flat anterior to caudal margin (Fig. 5-12a, Fig. 29, Plate 9). Karyotype unique among Diminutiva and Morsei Groups, 2n♂=23. Distributed in South Coast Ranges of California . . . . . *diminutiva,* p. 71
- Female subgenital plate lateral processes round onto caudal margin (Fig. 5-12b). Ventral surface of plate concave anterior to caudal margin (Fig. 5-12b). Typical small *Aglaothorax* karyotype 2n♂=24 13
13. Large body size for Diminutiva Group, male hind femur length >15 mm, pronotum length >9 mm. Male titillator arms slightly narrowed at base around entire circumference and barely curved (Fig. 5-13a, Fig. 33, Plate 13). Mountains of Ventura County, California . . . . . *oreibates,* p. 81
- Small body size, male hind femur length <14 mm, pronotum length <9 mm. Male titillator arms broad at base, tapered and smoothly curved (Fig. 5-13b) 14
14. Santa Ynez Mountains of Santa Barbara County, California (Fig. 27) . . . . . *poecilonotum,* p. 83
- Transverse Ranges of California including Tehachapi Mountains (Fig. 27) . . . . . *acrolophitus,* p. 78
15. Male paraproct process long, narrow, and cylindrical, more than 2 times longer than wide (as in Fig. 5-10b.1) 16
- Male paraproct process 2 times longer than wide or shorter (as in Fig. 5-9b.1, 5-10a.1) 18
16. Prosternal spines conical in both sexes (Fig. 5-16a). Male supra-anal plate concave, rounded or square with laterocaudal corners rounded (Fig. 27, Plate 8). Karyotype 2n♂=22. Distributed in Baja California, México (Fig. 15) . . . . . *sphenosternum,* p. 67
- Prosternal spines long, thin, spinelike in both sexes (Fig. 5-16b). Male supra-anal plate flat. Karyotype 2n♂=24 17
17. Male subgenital plate with thick, conical styli (Fig 5-17a, Fig. 23). Male supra-anal plate rounded, tongue-like (as in Fig. 9b.1, Fig. 23, Plate 5). Male titillators of moderate length and distinctly bowed at 1/2 to 2/3 length from base (Fig. 23, Plate 12). Transverse Ranges and adjacent basins (Fig. 15) . . . . . *conistylus,* p. 57
- Male subgenital plate with typical thin, cylindrical, straight to slightly curved styli (Fig. 5-17b). Male supra-anal plate square with laterocaudal corners rounded (Fig. 24, Plate 5). Male titillator arms short, nearly straight, barely curved laterally in apical 1/3 (Fig. 24, Plate 12). Peninsular Ranges of California (Fig. 15) . . . . . *nesiazo,* p. 60
18. Male paraproct with mesal tooth apical (as in Fig. 5-9a.1) 19
- Male paraproct with mesal tooth subapical (as in Fig. 5-9b.1) 20
19. Male titillator arms short, nearly straight, barely curved laterally in apical 1/3 (Fig. 5-19a.1, Fig. 26, Plate 12). Male stridulatory file tooth density 25–27 teeth/mm. Karyotype 2n♂=20 (Fig. 26). Female subgenital plate processes longer than wide (Fig. 5-19a.2, Fig. 26, Plate 8). Baja California, México (Fig. 15) . . . . . *kelainops,* p. 64
- Male titillator arms smoothly curved (Fig. 5-19b.1, Fig. 25, Plate 12). Male stridulatory file tooth density 27–33 teeth/mm. Karyotype 2n♂=24 (Fig. 25). Female subgenital plate processes as long as wide (Fig. 5-19b.2, Fig. 25, Plate 8). Baja California, México (Fig. 15) . . . . . *bufonoides,* p. 62
20. Male supra-anal plate concave dorsally (as in Fig. 5-20a). Male song with rapidly produced pulse trains that are grouped into echemes (“chirps”) (Figs. 17, 19, Plate 14) 21
- Male supra-anal plate flat dorsally (as in Fig. 5-20b). Male song variable but usually (except *A. amathitis* (Fig. 20, Plate 14) with slowly produced pulse trains that are not generally organized into echemes (Figs. 16, 21–23) 22
21. Male paraproct processes short, thick, knob-like, as long as wide (Fig. 5-20a, Figs. 17–18, Plate 5). Female subgenital plate without projection or tooth between short, triangular lateral processes (Fig. 5-21a). Song with long echemes, the syllables of which occur too rapidly to be counted by a human listener (Fig. 17, Plate 14). Found in Santa Monica Mountains west of Malibu Creek, California (Fig. 15) . . . . . *costalis,* p. 43
- Male paraproct processes about 2 times as long as wide (Fig. 19, Plate 5). Female subgenital plate with a low to pronounced rounded to triangular projection between short, triangular lateral processes (as in Fig. 5-21b, Fig. 19, Plate 8). Song with short echemes that consist of 4 ± 2 pulse trains that may occur slow enough to be counted at ambient temperature (Fig. 19, Plate 14). Found in Santa Monica Mountains east of Malibu Creek, California (Fig. 15) . . . . . *longipennis*, p. 47
22. Subapical tooth on male paraproct process located far basal from apex 23
- Subapical tooth on male paraproct process located close to apex 24
23. Male titillator arms of moderate length, evenly curved (Fig. 5-22a, Fig. 21, Plate 12). Found on northern chain of California Channel Islands (Fig. 15) . . . . . *islandica,* p. 52
- Male titillator arms short, nearly straight, barely curved laterally (Fig. 5-22b, Fig. 22, Plate 12). Found on mainland, at moderate to high elevations in the San Bernardino Mountains and San Jacinto Mountains of California (Fig. 15) . . . . . *hulodomus,* p. 55
24. Male titillator arms constricted at base (Fig. 5-24a, Fig. 16, Plate 11). Calling song with pulse trains produced slowly in irregular echemes (Fig. 16, Plate 14). San Gabriel Mountains, California (Fig. 15) . . . . . *morsei,* p. 39
- Male titillator arms not constricted at base (Fig. 5-24b, Fig. 20, Plate 11). Calling song with rapidly produced echemes (Fig. 20, Plate 14). Distributed on relict sand dunes and coastal bluffs of Los Angeles Basin and Palos Verdes Peninsula, California (Fig. 15) . . . . . *amathitis,* p. 50

Systematic Treatment

Ovatus Group

Members of the Ovatus Group are robust shield-backed katydids, the species being larger in body size on average than those of the other two *Aglaothorax* species Groups. This is the only species Group that contains individuals with green body coloration (Figs. 7–14, Plate 1). The male pronotum is greatly enlarged with thick margins and,

except for *A. gurneyi* with brown tegmina, the tegmina are ivory or white. The prosternal spines are reduced to ridges, are wedge-shaped, or are developed as nipple-like processes. Chaetotaxy (Table 2) is more variable within species (and sometimes also within individuals) than between species. The male supra-anal plate is semicircular, as wide as long to wider than long, the surface flat to concave (Figs. 7–14, Plate 4). The male subgenital plate has parallel to converging lateral carinae and a transverse, rounded, or bilobed posterior margin (Figs. 7–14). The male paraprocts are thick, cylindrical to triangular, and typically (except in *A. segnis* and *A. strobilion*, Figs. 10, 12) with a heavy subapical internal tooth that is mesoventrally or ventrally directed. The titillators are heavy, evenly curved and tapered with sharp tips (Plate 10). The female subgenital plate possesses long digitiform paired lateroposterior processes (Plate 7). The female ovipositor is shorter than the hind femur except in *A. ovatus*, in which it frequently exceeds hind femur length.

The Ovatus Group is distributed in fragmented populations throughout the Mojave and Great Basin Deserts, and also in the western Colorado Desert of Southern California (Fig. 6). Abundance at a given population varies greatly from year to year, with numerous individuals active on climatically favorable years and few to none on poor years. Ovatus Group males produce a loud, frequently repeated song that consists of brief echemes (Fig. 14). Males engage in alternating choruses.

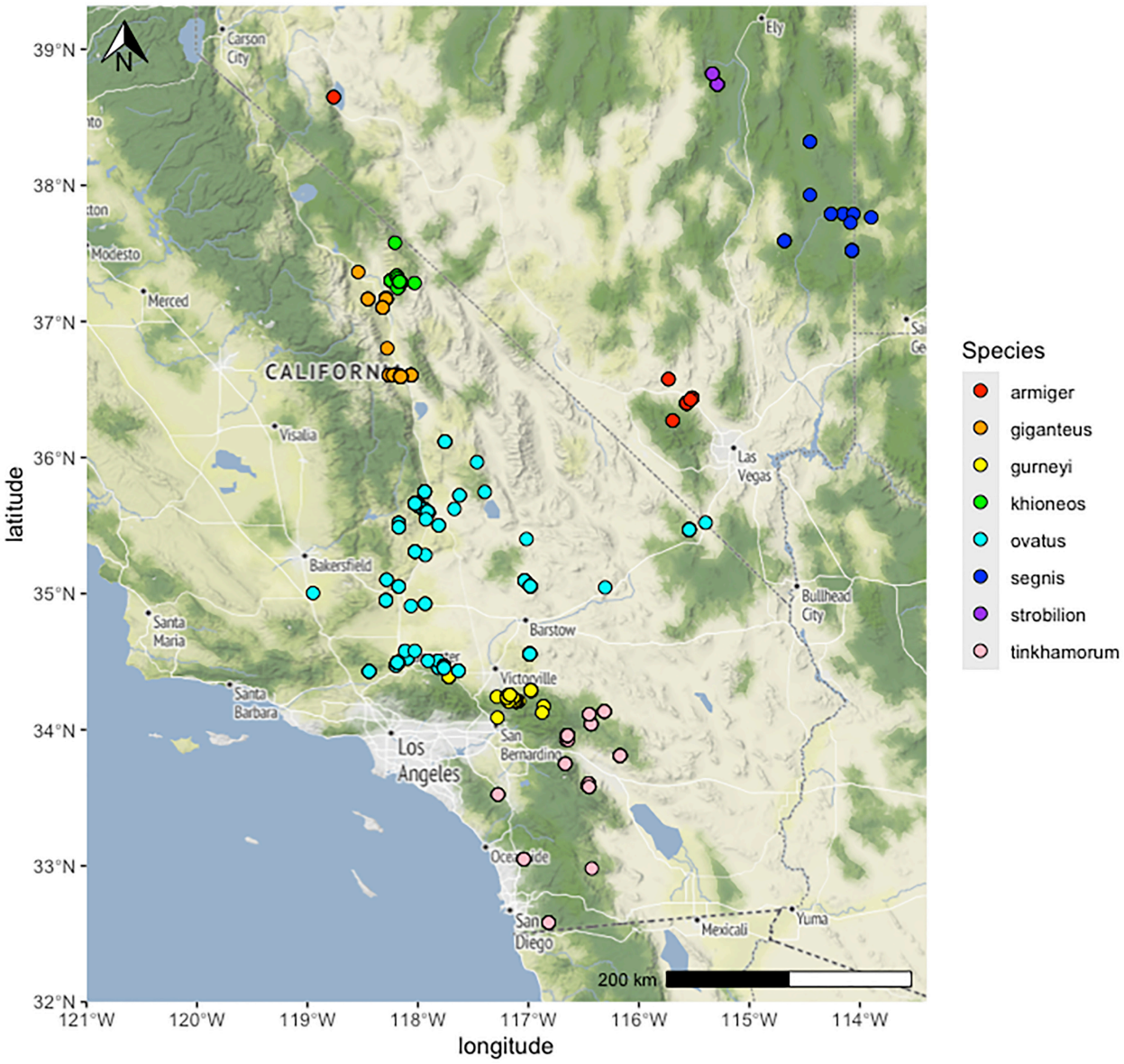


FIGURE 6. Distribution of Ovatus Group species.

TABLE 2. Comparative chaetotaxy of the Ovatus Group.

species	n	forefemur dorsal surface	foretibia auditory foramen	foretibia ventro-anterior margin	foretibia ventro-posterior margin	midfemur dorsal surface	midtibia dorso-anterior margin	midtibia dorso-posterior margin	midtibia ventro-anterior margin	midtibia ventro-posterior margin
ovatus	21	1–6	0–2	6–7	6–7	2–8	2–5	2–7	6–7	5–7
♀	9	0–5	0–2	5–5	6	0–8	1–3	1–5	5–7	6–7
giganteus	4	2–4	0	6	6	3–5	0–2	1–3	5–7	6–7
♀	4	3–6	0–1	6	6	3–8	1–3	1–3	6–7	6–7
tinkhamorum	12	1–6	0–1	6–7	6–7	1–7	2–4	2–4	5–7	5–7
♀	2	1	0–1	6	6	3	3–4	3–4	7	7
segnis	5	1–3	1	6	6	2–4	1–3	2–5	6–7	5–7
♀	2	0–2	1	5–6	6	2–4	2–3	3	6–7	6
armiger	5	0–3	0–1	6	5–6	0–4	1–4	1–4	6–7	6–7
♀	5	1–3	0–1	6	6	1–4	2–4	1–5	7	6–7
strobilion	5	0–1	0–1	6–7	6	1–4	2–4	1–4	7–8	6–8
♀	0	-	-	-	-	-	-	-	-	-
khioneos	3	1–3	0	6	6	0–2	2–3	2–3	7–8	7–8
♀	3	1–2	0–1	6	6	1–5	2–3	1–3	7–8	7
gurneyi	6	0–3	0	6	6	2–5	2–5	1–3	6–7	6–7
♀	8	1–5	0–1	6	6	2–5	2–3	2–4	7	6–7

Aglaothorax ovatus (Scudder, 1899)

Tropizaspis ovata—Scudder, 1899: 84.
Aglaothorax ovatus—Caudell, 1907: 291 (A revision in status).
Aglaothorax ovatus—Tinkham, 1944: 289. (Incorrect synonymy).
Neduba (*Aglaothorax*) *ovata*—Rentz & Birchim, 1968: 69 (A revision in status).
Neduba (*Aglaothorax*) *ovata longicauda*—Rentz & Birchim, 1968: 71 **New junior subjective synonym.**
Fig. 6 (distribution), Fig. 7 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 4 (male terminalia), Plate 7 (female subgenital plate), Plate 10 (male titillators), Plate 14 (male calling song).

Common name. Ovate Shieldback.

History of recognition. Described in *Tropizaspis* from a single male California specimen without a specific locality (Scudder 1899). After *Tropizaspis* fell as a *nomen nudum*, *ovatus* was designated as the type species of *Aglaothorax* (Caudell 1907), initially using the feminine gender. Confused with both *A. gurneyi* and *A. segnis* (Tinkham 1944). Transferred to *Neduba* (*Aglaothorax*) with *armiger* (Rehn & Hebard 1920) and *segnis* (Rehn & Hebard 1920) relegated to subspecies and the description of three new subspecies: *gigantea*, *longicauda*, and *tinkhamorum* (Rentz & Birchim 1968). Transferred back to *Aglaothorax* (Rentz & Colless 1990) where this species is currently classified (Cigliano *et al.* 2025). We raise *armiger, giganteus*, *segnis*, and *tinkhamorum* to species status based on morphological, phylogenetic, and cytogenetic evidence. Intergrades were reported between *ovatus* and *longicauda* (Rentz & Birchim 1968), and after examining large series from many populations, we conclude that more variation exists within than between *longicauda* and *ovatus* and synonymize the former name.

Type material. The holotype male is in the Academy of Natural Sciences of Philadelphia (ANSP). Images of the type are available at OSFO (Cigliano *et al.* 2025). The type locality of *ovatus* was narrowed to northern Los Angeles County (Rentz & Birchim 1968) where the fringes of the Mojave Desert meet the north slope of the San Gabriel Mountains. We specify the vicinity of Llano, Los Angeles County, California, USA as the type locality.

PARATYPES EXAMINED: (n=6) *longicauda* **USA, CA, Kern Co.**, E side of Sierra Nevada below Walker Pass, 35.662453, -118.026740, 1372 m, 28-V-1954, no collector, CAS, 1♀; Walker Pass, 35.662453, -118.026740, 22-VIII-1938, ER Tinkham, CAS, 5♂.

TOPOTYPES EXAMINED: (n=50) *ovatus* **USA, CA, Los Angeles Co.**, 2 miles S of State Highway 138 on County Road 4, 34.47615, -117.81777, 1280 m, 9-VI-1989, DB Weissman, DC Lightfoot, CAS, 3♂; 4.5 miles west of Desert Springs on Highway 138, 35.521625, -115.396298, 1-VI-1957, RX Schick, LACM, 1♂; Bob's Gap, 4 miles north of County Road N4 on Bob's Gap Road, 34.4550, -117.8139, 1300 m, 18-VI-2006, JA Cole, LACM, 2♂; County road N4 near Llano, 34.505828, -117.817841, 1280 m, 6-VIII-1988, DB Weissman & DC Lightfoot, CAS, 1♂; Largo Vista Road (county Road N4) at Fort Tejon Road, 34.46916, -117.76633, 1179 m, 14-VI-2017, JA Cole, LACM, 6♂; same data except JAC, 1♀; Largo Vista Road (county Road N4), 1 mile south of Fort Tejon Road, 34.4530, -117.7649, 1277 m, 22-VI-2008, JA Cole, LACM, 3♂; *longicauda* **USA, CA, Kern Co.**, 1.3 miles E of Walker Pass on State Highway 178, 35.662450, -118.003532, 1460 m, 5-VIII-1988, DB Weissman, DC Lightfoot, CAS, 2♂; Freeman Canyon, 1.5 miles southeast of Walker Pass on SR178, 35.6509, -118.0055, 1470 m, 10-VII-2003, JA Cole, JF Eguizabal, LACM, 3♂, 1♀; same data except JAC, 1♂; Freeman Canyon, 2 miles west of Summit on SR178, 35.6514, -118.0048, 1454 m, 13-14-VII-2005, JA Cole, LACM, 6♂; same data except 24-VI-2008, AMNH, 1♂; same data except JAC 1♂, 1♀; same data except LACM, 1♂, 1 pair in copula; Freeman Canyon, 3.3 miles northwest of SR14 on SR178, 35.62278, -117.95278, 1213 m, 31-V-2023, JA Cole, C Wong, LACM, 1♂; same data except JAC, 1♂, 1♀; Freeman Canyon, SR178 3 miles west of SR14, 35.62019, -117.9502, 1086 m, 28-V-2017, JA Cole, JAC, 2♂; same data except LACM, 3♂; Jawbone Butterbredt Area of Critical Environmental Concern, SR178 at SR14, 35.60239, -117.91468, 1011 m, 28-V-2017, JA Cole; LACM, 4♂; same data except JAC, 2♂; Walker Pass, 35.662453, -118.026740, 1060 m, 18-VIII-1982, DB Weissman, CAS, 2♂.

Measurements. (mm, ♂n=21, ♀n=9) Hind femur ♂17.39–20.96, ♀19.49–23.55, pronotum total length ♂11.60–14.61, ♀12.17–15.70, prozona length ♂5.41–6.70, ♀5.73–7.45, metazona dorsal length ♂6.19–8.10, ♀6.41–8.30, pronotum constriction width ♂3.37–4.60, ♀4.00–4.82, metazona dorsal width ♂7.64–9.83, ♀8.60–10.28, head width ♂5.27–6.79, ♀6.05–7.80, ovipositor length ♀17.88–28.84.

Distribution. Distributed widely but locally across the Mojave Desert of California from the desert floor (624 m, JA Cole, LACM) to high elevations (1470 m, JA Cole & JF Eguizabal, LACM).

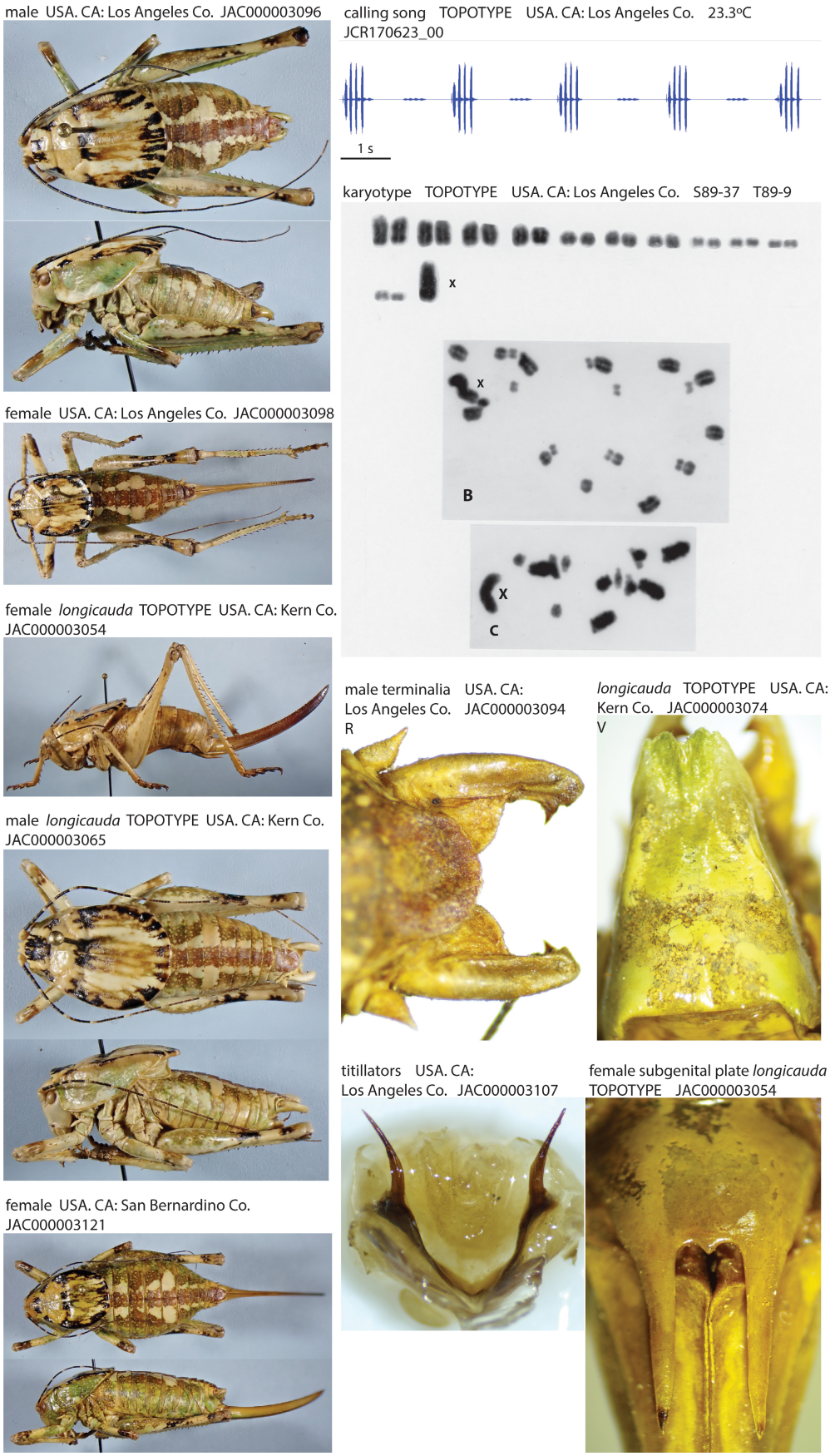


FIGURE 7. *A. ovatus* male and female habitus, calling song, male and female terminalia, and karyotype. Idiogram top panel A shows 2n♂=23 karyotype; B. Mitotic plate showing all 23 chromosomes; C. Metaphase I. On all 3 photos, single X chromosome is marked.

Habitat. Creosote desert, pinyon-juniper, and Joshua tree woodlands. On California juniper (*Juniperus californica* Carriere), Mormon Tea (*Ephedra* spp.), Creosote Bush (*Larrea tridentata* (DC.) Coville), Cholla (*Opuntia* spp.), and Joshua Tree (*Yucca brevifolia*). Generally found in low bushes but may be arboreal in Joshua trees and junipers. When disturbed at night, *A. ovatus* retreat into thorny vegetation or towards the base of yucca leaves.

Seasonal occurrence. Adults active from spring (9-V-1941, EC VanDyke, CAS) into fall (13-X-1995, G Pratt, CAS). Nymphs from April (15-IV-1957, DM Horton, LACM). Adult activity commences earlier in the season at low elevations.

Stridulatory file. (n=21) length 4.00–5.70 mm, 68–107 teeth, tooth density 18.5±1.9 (14.4–21.4) teeth/mm.

Song. (n=86) Loud, incessant song with frequently produced echemes ("chirps"). The calling song was onomatopoeically described as "zic-zic-zic, zic-zic-zic-zic" (Tinkham 1944) which corresponds to one 3 and one 4 pulse train echeme, respectively. Pulse trains 80±20 ms in length repeat at a rate of 9.16±0.96 s^{-1}. Mean peak frequency is 14.13±3.02 kHz, with ultrasonic peak frequencies as high as 23.75 kHz revealed in recordings with high frequency equipment. Variable length echemes group on average 6±11 pulse trains. Males tend to begin a bout of singing with isolated pulse trains and add pulse trains to echemes as singing continues. In rare circumstances males may produce large numbers of pulse trains in an echeme, such as after separating from a female post-mating. The maximum pulse train number that we have observed in an echeme is 106. Echemes are repeated frequently, being separated by 1–5 s (mean 1.87±0.79 s) silent intervals. Males may produce irregular bouts of song at dusk, with onset of calling in one instance timed exactly at sundown. Wary males cease singing some distance from an observer and are sensitive to white light. Males are alternating chorusers. When in proximity, males produce only 1–2 pulse trains that may constitute an aggressive interaction. Males may stridulate loudly when handled.

Karyotype. (n=9) 2n♂=23(22t+Xt), topotype T89-9 (S89-37).

Recognition. Morphology, coloration, geography. Body ground coloration most often green but also may be tan or light brown. The abdominal dorsum has a longitudinal reddish stripe and the tegmina are white, unlike *A. gurneyi* in which the body coloration is always wood brown, the abdomen lacks a dorsal reddish stripe, and the tegmina are brown. The pronotum has broad longitudinal white stripes and fine brown stripes on the disk, lacking in all other Ovatus Group species which have at most fine black streaks on the disk; *A. armiger* and *A. tinkhamorum* have the center of the pronotal disk largely unmarked. The *A. ovatus* male paraproct process has a subapical, ventrally directed heavy tooth in contrast with the apical tooth and slender processes of *A. segnis* and *A. strobilion*. The prozona is not heavily rugose like that of *A. giganteus*. The *A. ovatus* ovipositor is typically longer than the hind femur; all other Ovatus Group species have the ovipositor shorter than the hind femur. The distribution of this species encompasses the Mojave Desert ecosystem.

Notes. This is the iconic Shield-backed Katydid featured in field guides (e.g. Capinera *et al.* 2004) as an exemplary orthopteran of the Mojave Desert. Isolation at higher elevations around the periphery of the desert as pinyon-juniper habitats retreated due to warming climate was advanced as a biogeographical hypothesis (Rentz & Birchim 1968). This hypothesis is partially supported by phylogeographic structure (Figs. 2–4) that may reflect geographic isolation. Expanded sampling shows that *A. ovatus* is not limited to the fringes of the Mojave Desert, but occupies a wide range of elevations from 600 to 1500 m. Although the habitat of this katydid occurs over a wide geographic expanse, populations of *A. ovatus* are scattered, which may be the result of localized extinction, the hottest parts of the desert no longer being habitable by the lineage, coupled with low dispersal ability.

Subspecies *longicauda* applied to populations from the Scodie Mountains at the extreme southeastern corner of the Sierra Nevada at Walker Pass, Kern County, California, where to the east pinyon-juniper habitats descend through Joshua Tree woodland down to creosote desert. The subspecific epithet described the long ovipositors in females of this population, which approach 30 mm in length while ovipositors of *A. ovatus* range from 18–23 mm in length. Ovipositors are longer than the hind femur in both *longicauda* and *A. ovatus*, but scaling by hind femur length as a proxy for body size diminishes the apparent extremes: *longicauda* ovipositors are 15-20% longer than the hind femur, while *A. ovatus* ovipositors are 1-10% longer. Extreme ovipositor length in *longicauda* thus correlates with massive female body size. Morphological intermediates were reported between southern Sierra Nevada and nominate Mojave Desert *A. ovatus* (Rentz & Birchim 1968), and *longicauda* exemplars were scattered among the phylogeographic structure of the Ovatus Group populations (Figs. 2–4). We therefore abandon *longicauda* as a subspecific category.

We describe a mating sequence in a Los Angeles County population that adds to what is known of mating in this species (Rentz & Birchim 1968). During pair formation and while the female was orienting, the male

emitted brief pulse trains, often in pairs, that were of qualitatively low amplitude (not measured). The female then mounted the male, whereupon the male paraprocts grasped the base of the female subgenital plate and held on throughout copulation. During copulation the male titillator arms periodically scraped against the female ovipositor. Spermatophore transfer took approximately 2 min. When pairs separated, the males sometimes made a long series of loud pulse trains.

Material examined. (n=149) **All USA, CA, Inyo Co.**, Argus Mountains, NE of Ridgecrest, 35.622456, -117.670897, 1790 m, 7-16-IX-1995, GF Pratt, CAS, 1♂; Argus Range, Birchum Spring, 35.966502, -117.466261, 13-X-1995, G Pratt, CAS, 1♀; Argus, 35.747177, -117.395335, 18-VII-1973, K Beany, CAS, 1♂; China Lake NAWS, Haiwee Spring, 36.116988, -117.756274, 6-VI-2003, G Pratt, C Pierce, CAS, 2♂; China Lake NAWS, Lower Haiwee Spring, 36.116988, -117.756274, 18-V-1996, G Pratt, J Emmel, CAS, 1♂; China Lake NAWS, Mtn. Springs Cyn., 35.722282, -117.624163, 17-VII-1998, G Pratt, M van Tilborg, CAS, 1♂; China Lake NWC, Birchum Spring, 35.722282, -117.624163, 5-VIII-1995, G Pratt, C Pierce, CAS, 1♂; **Kern Co**., 10 miles S of Inyokern, 35.501852, -117.812567, 7-VI-1962, GH Nelson and family, CAS, 2♀; 3 miles W of junction Hwys 178 and 14 on Hwy 178, 35.61919, -117.94957, 1158 m, 9-VI-1983, DB Weissman, CAS, 5♂; 3.7 mi. E Sopp Rd & Powerline Rd., 16-VI-1998, G Pratt, E van Baal, CAS, 2♂; 32 miles N of Mojave, 35.516665, -118.173965, 1006 m, 9-VI-1983, DB Weissman, CAS, 5♂, 1♀; 5 miles W of junction Hwys 178 and 14 on Hwy 178, 35.63757, -117.97683, 1341 m, 9-VI-1983, DB Weissman, CAS, 6♂, 1♀; about 0.5 miles S of junction Hwys 14 and 178 on Hwy 14, 35.59455, -117.90621, 945 m, 9-VI-1983, DB Weissman, CAS, 4♂; about 10 miles NW of Inyokern, Short Canyon, 35.749397, -117.938780, 1158 m, 9-VI-1983, DB Weissman, CAS, 7♂; Edwards AFB, East Rosamond Hills, 34.909421, -118.063683, 2-V-1996, G Pratt, B Deyhers, CAS, 1♂; Jawbone Canyon, 35.308294, -118.025905, 789 m, 8-VII-1973, E Rau, LACM, 2♂, 1♀; jct. Backus Road and Tehachapi Willow Springs Road, 34.95072, -118.29014, 725 m, 28-V-2009, DB Weissman, DC Lightfoot, CAS, 3♂; Mojave Desert, Randsburg, 35.2833, -117.9333, 27-V-1073, AJ Gaudin, CSUN, 1♀; Red Rock Canyon Park, on plateau N of park off Highway 14, 30 mi. N Mojave, 35.487653, -118.173965, 28-VI-1976, PH Sullivan, CAS, 1♂, 1♀; Sierra Nevada, Jawbone Canyon, 35.308294, -118.025905, 23-V-2017, MM Dickson, CSUN 1♂; SR14, 4.5 miles south of SR178, 35.54594, -117.92847, 933 m, 28-V-2009, DB Weissman, DC Lightfoot, CAS, 1♂; Tehachapi Pass, 35.10219, -118.28369, 13-V-1953, LACM, 2♂; Wheeler Ridge, 35.004413, -118.949546, 294 m, 13-V-1953, LACM, 1♂; **Los Angeles Co.**, Los Angeles, 1-VII, Coquillett, USNM, 1♂; same data except VII, Coquillett, USNM, 1♂; Acton Canyon, Sierra Hwy., 0.5 mi. E Crown Valley Rd., 34.473883, -188.199520 915 m, 20-VI-2003, JN Hogue, JA Cole, CSUN, 3♂; Edwards AFB, 165th St, 34.926088, -117.935068, 7-V-1997, G Pratt, C Pierce, CAS, 2♂; Mint Canyon, 34.429162, -118.442305, 15-V-1962, S Nakagawa, CSUN, 3♂; same data except V-1962, Frolich, CSUN, 1♀; Mojave, -35.052470, -118.173964, 840 m, 15-IV-1957, DM Horton, LACM, 1♂; Old Nadeau Road at Pearblossom Highway, 5 miles south of Palmdale, 34.5236, -118.0956, 903 m, 13-VI-2003, JA Cole, LACM, 2♂; Palmdale, 34.579434, -118.116461, 9-V-1941, EC VanDyke, CAS, 1♂; Palmdale, 5 miles east, 34.579403, -118.028361, 29-IV-1956, F Sala, LACM, 1♀; Sierra Highway, 0.6 miles west of Crown Valley Road, Acton, 34.4936, -118.1834, 929 m, 13-VI-2003, JA Cole, J Hogue, LACM, 1♂; same data except 17-VI-2003, JA Cole, J Hogue, LACM, 3♂; same data except JAC, 1♂; same data except 18-19-VI-2008, JA Cole, LACM, 4♂; same data except 20-VI-2003, JA Cole, J Hogue, AMNH, 1♂, 1♀; same data except JAC, 1♂; same data except LACM, 1♀; same data except 23-VI-2005, JA Cole, LACM, 5♂; same data except 21-VI-2018, JA Cole, JAC, 1♂; same data except 25-V-2017, JA Cole, LACM, 5♂, 1♀; same data except JAC, 2♂, 1♀; Sierra Highway, 0.6 miles west of Crown Valley Road, Acton, 34.49393, -118.18736, 870 m, 29-VI-2003, DB Weissman, CAS, 13♂, 1♀; **San Bernardino Co.**, China Lake NAWS, Eagle Crags, Mesquite Spring, 35.401136, -117.017850, 9-VI-1995, G Pratt, C Pierce, CAS, 1♂; Coolgardie Road, 3.3 miles northwest of Copper City Road, 33.09538, -117.03453, 1095 m, 15-VI-2019, JA Cole, LACM, 3♂; same data except JAC, 1♂; Copper City Road, 4.7 miles north of Irwin Road, Barstow, 35.05157, -116.98058, 1131 m, 15-VI-2019, JA Cole, JAC, 1♂; Copper City Road, 5 miles north of Irwin Road, Barstow, 35.05585, -116.98421, 1160 m, 15-VI-2019, JA Cole, LACM, 4♂; same data except JAC, 1♂; Desert Springs, 34.4333, -117.6333, 11-V-1955, no collector, CAS, 1♀; Desert Springs, 34.4333, -117.6333, 1219 m, 25-VI-1956, ER Tinkham, CAS, 3♂; Granite Mountains wash, 2 miles southwest of SR247 off Spinel Street, 34.5574, -116.9882, 1004 m, 1-2-V-2013, JA Cole, LACM, 11♂; same data except JAC, 1♀; Mojave River, 35.045321, -116.305388, 1-VII-1937, R Miller, CAS, 1♀; Mountain Pass, 35.470260, -115.544998, 1400 m, 4-VIII-1991, DB Weissman, DC Lightfoot, CAS, 6♂, 1♀.

Aglaothorax giganteus (Rentz & Birchim, 1968) stat. rev.

Neduba (*Aglaothorax*) *ovata gigantea*—Rentz & Birchim, 1968: 77.
Aglaothorax segnis—Tinkham, 1944: 291 (Incorrect synonymy).
Aglaothorax giganteus **stat. rev.** (Revised to species status with corrected gender).
Fig. 6 (distribution), Fig. 8 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 4 (male terminalia), Plate 7 (female subgenital plate), Plate 10 (male titillators), Plate 14 (male calling song).

Common name. Gigantic Shieldback.

History of recognition. Described as a subspecies of *Neduba* (*Aglaothorax*) *ovata* (Rentz & Birchim 1968). Confused with *A. segnis* (Tinkham 1944). Returned to *Aglaothorax* (Rentz & Colles 1990) where this species remains as a subspecies of *A. ovatus* (Cigliano *et al.* 2025). We elevate *A. giganteus* to species rank based on morphology, geography, and phylogeny.

Type material. The holotype male in ANSP is from 8 miles west of Lone Pine on the eastern slope of the Sierra Nevada, Inyo County, California, USA. Images of the holotype and allotype are available at OSFO (Cigliano *et al.* 2025). PARATYPES EXAMINED: (n=39) **USA, CA, Inyo Co.**, 11 mi. W Lone Pine, 36.605879, -118.261588, 19-VII-1961, DC Rentz, LACM, 1♂; same data except, 6-VII-1961, DC Rentz, LACM, 1♀; Big Pine Canyon, 37.164931, -118.289546, 16-VIII-1938, ER Tinkham, CAS, 24♂; Big Pine Canyon, Big Pine, 37.164931, -118.289546, 4-VIIII-1931, ER Tinkham, CAS, 4♂; Big Pine Cyn, 9 mi W Big Pine, 37.164818, -118.453317, 25-VIII-1957, ER Tinkham, CAS, 2♂, 1♀; Lone Pine Canyon, 36.60611, -118.06194, 20-VIII-1938, ER Tinkham, CAS, 5♂; Lone Pine, 36.606044, -118.062865, 28-VII-1940, LC Kiutert, CAS, 1♂. TOPOTYPES EXAMINED (n=34): **USA, CA, Inyo Co**., 11 mi. W Lone Pine, 36.605879, -118.261588, no date, ER Tinkham, CAS, 2♂; 6.8 M W Big Pine on road to Sage Flat Camp, 37.164931, -118.289623, 2042 m, 28-VIII-1996, DB Weissman, BI Weissman, DCF Rentz, CAS, 2♂; 7 miles W Lone Pine on road to Whitney Portal, 36.605957, -118.207391, 1785 m, 5-VIII-1978, DB Weissman, CAS, 1♂; 7-8 miles W of Lone Pine on Whitney Portal, 36.605957, -118.207391, 1785 m, 18-VIII-1982, DB Weissman, CAS, 2♂, 1♀; 9 mi. W Lone Pine, 36.605934, -118.225457, 8-VII-1961, JK Drew, CAS, 1♂, 1♀; Whitney Portal Road, 4.8 miles west of Lone Pine, 36.59500, -118.15194, 1558 m, 10-VII-2019, JA Cole, J Bailey, JAC, 2♂; Whitney Portal Road, 6 miles west of Lone Pine, 36.5949, -118.1563, 1611 m, 8-9-VII-2008, JA Cole, AMNH, 2♂; same data except JAC, 4♂; same data except LACM, 8♂; Whitney Portal Road, 6 miles west of Lone Pine, 36.59511, -118.16033, 1636 m, 1-VII-2017, JA Cole, LACM, 4♂; same data except JAC 3♂, 1♀.

Measurements. (mm, ♂n=4, ♀n=2) Hind femur ♂18.65–20.45, ♀20.53–22.75, pronotum total length ♂13.95–15.10, ♀14.95–16.23, prozona length ♂6.08–6.90, ♀7.14–8.09, metazona dorsal length ♂7.60–8.64, ♀7.76–8.69, pronotum constriction width ♂4.30–4.70, ♀3.80–5.40, metazona dorsal width ♂9.10–9.40, ♀9.65–10.91, head width ♂6.05–6.20, ♀6.48–7.64, ovipositor length ♀20.88–23.30.

Distribution. Eastern Sierra Nevada at moderate to high elevations.

Habitat. Desert scrub and pinyon-juniper woodland. Taken from Big Sagebrush (*Artemisia tridentata* Nutt.), Crucifixion Thorn (*Castela emoryi*), Singleleaf Pinyon (*Pinus monophylla* Torr. & Frém.), and Stansbury Cliffrose (*Purshia stansburiana* (Torr.) Henrickson). Inhabits elevations between 1500 and 2000 m.

Seasonal occurrence. Summer (1-VII-2017, JA Cole, LACM) through fall (9-X-1995, DB Weissman & VF Lee, CAS).

Stridulatory file. (n=4) length 5.00–5.55 mm, 83–98 teeth, tooth density 17.7±0.9 (16.6–18.7) teeth/mm.

Song. (n=15). Loud song of frequently repeated echemes as in *A. ovatus*. Pulse trains 60±20 ms in length are repeated at a rate of 9.52±0.88 s^{-1}. Mean peak frequency is 12.26±3.41 kHz, with high frequency recordings finding peak frequency energy as high as 19.46 kHz. Echemes group 2–6 (mean 3±1) pulse trains with 0.79–3.02 (mean 1.88±0.64) s silent intervals between echemes. At McMurray Meadows, Inyo County, California on 11-VII-2003, a 100 m transect was made along a chorus. Four males were found, each in large *Purshia* bushes, spaced from their nearest neighbors by 25 to 50 m. Singing males were not common and, at this date early in the season, may have been among the first males to mature at this high elevation site.

Karyotype. (n=3) 2n♂=23 (22t+Xt), topotype T82-148 (S82-71).

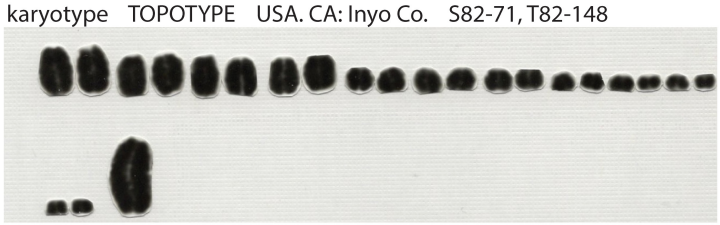
male TOPOTYPE USA. CA: Inyo Co.
JAC00000115



calling song TOPOTYPE USA. CA: Inyo Co. 25.0ºC JCR08LO-03



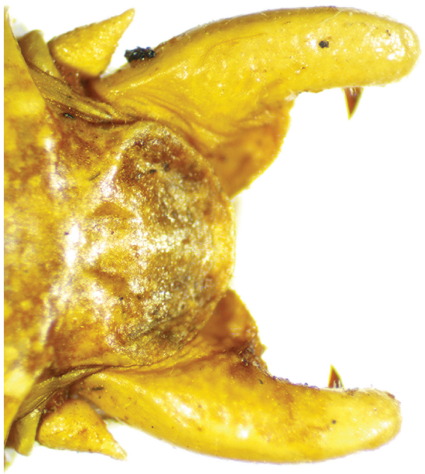
karyotype TOPOTYPE USA. CA: Inyo Co. S82-71, T82-148

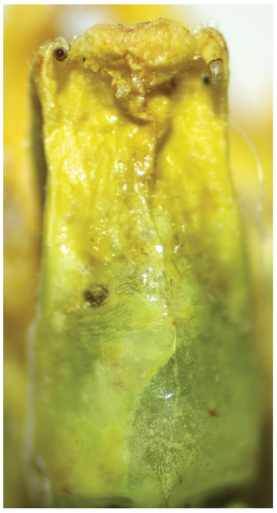


female TOPOTYPE USA. CA: Inyo Co.
JAC000003031



male terminalia TOPOTYPE USA. CA: Inyo Co.
JAC000003035 S82-71
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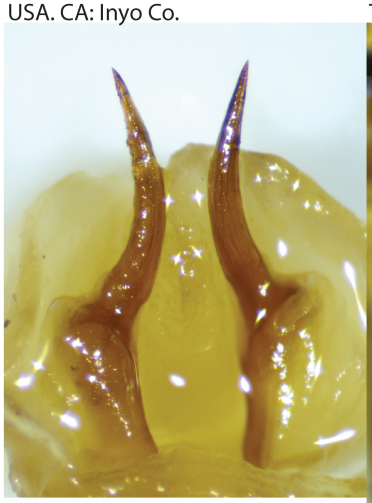




male USA. CA: Inyo Co. JAC000003046



titillator PARATYPE
USA. CA: Inyo Co.



female subgenital plate
TOPOTYPE JAC000003031



FIGURE 8. *A. giganteus* male and female habitus, calling song, male and female terminalia, and karyotype.

Recognition. Large body size, pronotum 14–15 mm long in male, a size range beginning at the maximum size of male *A. ovatus*. Red-brown middorsal abdominal stripe and white tegmina, unlike the unstriped abdomen, wood-brown body, and brown tegmina of *A. gurneyi*. Male paraproct process with a heavy, subapical, ventrally directed tooth, unlike the apical mesally directed tooth of *A. segnis* and *A. strobilion*. Pronotum heavily and irregularly rugose on prozona; the only other Ovatus Group species that approaches this condition is *A. tinkhamorum*, but in that species the prozona appears warty rather than wrinkled. *A. giganteus* males have an abrupt, strong elevation of the metazona after the transverse sulcus unlike all other Ovatus Group species. Pronotum with abundant longitudinal black streaks on disk; no broad white longitudinal stripes as in *A. ovatus*, and not with reduced black streaking on disk as in *A. armiger* and *A. tinkhamorum*. Female body size overlaps with *A. ovatus*, but in that species the ovipositor tends to be longer than the hind femur.

Notes. The concatenated phylogenetic consensus (Fig. 4) found a monophyletic *A. giganteus* but paraphyletic relationships were observed with nDNA (Fig. 2) and mtDNA (Fig. 3) gene trees. The original description (Rentz & Birchim 1968) expounds upon this species. Among the discussion, a courtship-copulation sequence was described, and variation between years was hypothesized to be dependent upon variable climate in their arid habitat. We noticed variation in abundance over years as well: the katydids were abundant during collecting events in 2003, 2008, and 2017, all wetter than average years for California that accompanied El Niño Southern Oscillation (ENSO) events, the 2017 event being a particularly strong one. During those years katydids could be found generally throughout the habitat on all types of vegetation. An increase in the number of eggs broken from diapause and increased survivorship due to an abundance of vegetation for food and water are non-mutually exclusive hypotheses for the population booms.

Material examined. (n=11) **All USA, CA, Inyo Co.**, 4.3 miles W of Independence, off Onion Valley Road, 36.802685, -118.277974, 1770 m, 9-X-1995, DB Weissman, VF Lee, CAS, 1♂; Buttermilk Brea, 8 miles west of Bishop, 37.363451, -118.541063, 1981 m, 3-VII-1973, KE Stager, LACM, 1♀; McMurray Meadows Road, 3.0 miles south of Glacier Lodge Road, 6 miles southwest of Big Pine, 37.1023, -118.3196, 13-VII-2003, JA Cole, JF Eguizabal, LACM, 6♂; same data except JAC, 2♂; same data except 4-VIII-2004, JA Cole, LACM, 1♂.

Aglaothorax tinkhamorum (Rentz & Birchim, 1968) stat. rev.

Neduba (*Aglaothorax*) *ovata tinkhamorum*—Rentz & Birchim, 1968: 81.
Aglaothorax segnis—Tinkham, 1944: 291 (Incorrect synonymy).
Aglaothorax tinkhamorum **stat. rev.** (Revised to species status).
Fig. 6 (distribution), Fig. 9 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 4 (male terminalia), Plate 7 (female subgenital plate), Plate 10 (male titillators), Plate 14 (male calling song).

Common name. Tinkham's Shieldback.

History of recognition. Described as a subspecies of *Neduba* (*Aglaothorax*) *ovata* (Rentz & Birchim 1968). Returned to *Aglaothorax* (Rentz & Colless 1990) where this species remains as a subspecies of *A. ovatus* (Cigliano *et al.* 2025). We elevate *A. tinkhamorum* to species rank based on morphology, geography, and phylogeny.

Type material. The holotype male in ANSP is from Pinyon Flats along state highway 74 at 4000 feet in the Santa Rosa Mountains, Riverside County, California, USA. Images of the holotype and allotype are available at OSFO (Cigliano *et al.* 2025). PARATYPES EXAMINED: (n=6) **USA, CA, Riverside Co.**, Santa Rosa Mtns, Pinyon Flats, 33.524192, -117.276148, 1219 m, 13-IX-1957, ER Tinkham, CAS, 3♂; **San Bernardino Co.**, Little San Bernardino Mountains, 1 mi. W of Yucca Valley, 34.114173, -116.449759, 999 m, 30-VI-1953, ER Tinkham, CAS, 3♂.

TOPOTYPES EXAMINED: (n=28) **USA, CA, Riverside Co.**, Cactus Spring Trailhead, 0.4 mi. S of SR74 on Pinyon Flats Sta. Rd., 33.5804, -116.4507, 1200 m, 28-29-VI-2004, JA Cole, JF Eguizabal, LACM, 1♂; Pinyon Flat Campground, 14 miles southwest of Palm Desert on SR74, 33.5856, -116.4570, 1219 m, 27-28-VI-2005, JA Cole, AMNH, 1♂; same data except LACM, 5♂; same data except 28-29-VI-2003, JA Cole, AMNH, 1♂; same data except LACM, 4♂; same data except 3-4-VII-2008, JA Cole, LACM, 7♂; Pinyon Flat, San Jacinto Mountains, 33.7500, -116.6667, 27-V-1939, ER Tinkham, CAS, 1♀ nymph; same data except 29-VI-1975, ER Tinkham, CAS, 2♂; Pinyon Flats, intersection of Pinyon Drive and Hwy 74, 33.603360, -116.455847, 1158 m, 26-VIII-1982, DB Weissman, CAS, 5♂; Ribbonwood Equestrian Campground, Santa Rosa Mountains, 33.58000, -116.45167, 1234 m, 26-VIII-2020, JA Cole, J Bailey, LACM, 1♂.

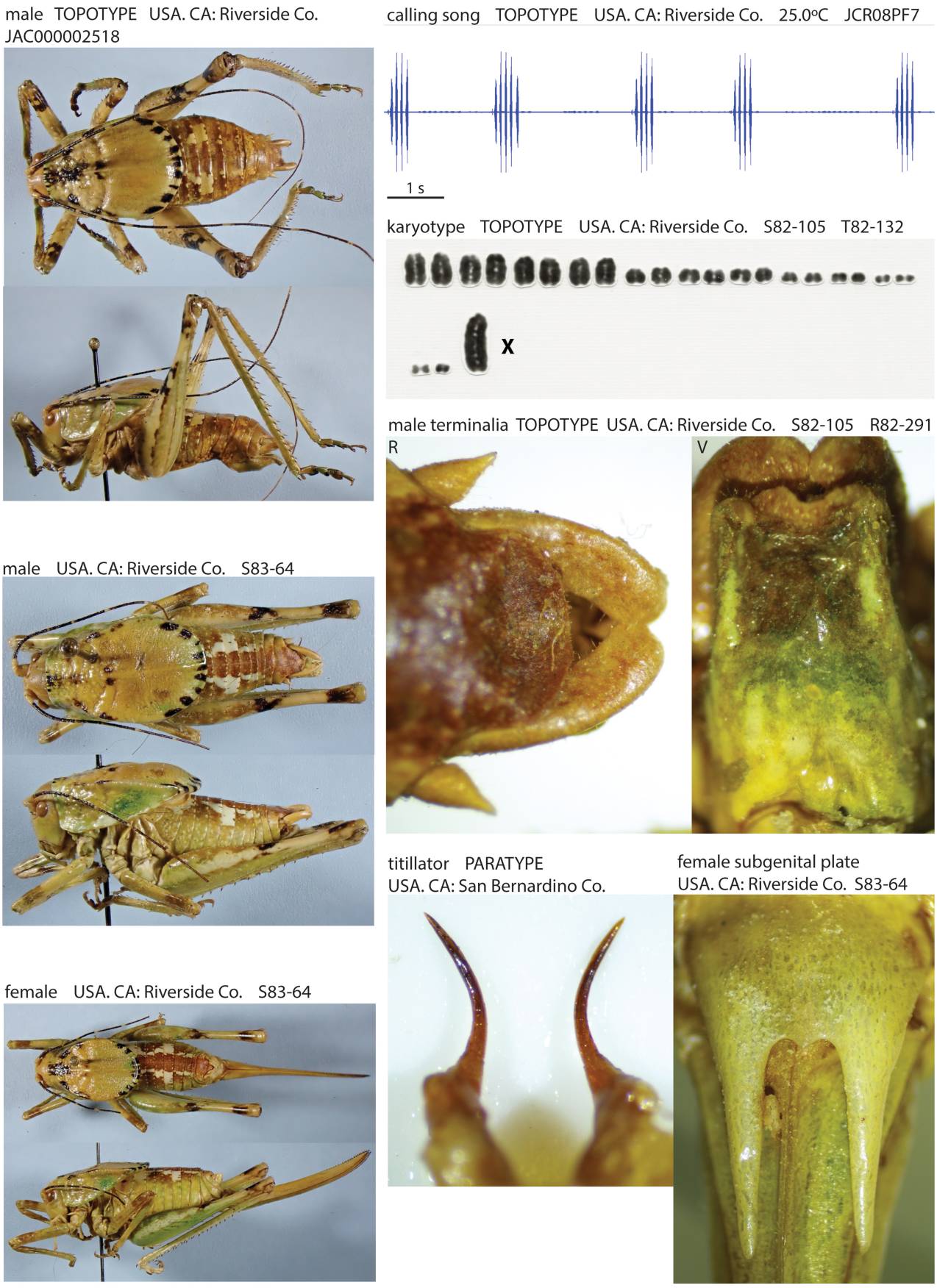


FIGURE 9. *A. tinkhamorum* male and female habitus, calling song, male and female terminalia, and karyotype. Idiogram shows karyotype 2n♂=23. Marked X chromosome is largest in complement.

Measurements. (mm, ♂n=12, ♀n=2) Hind femur ♂16.00–20.59, ♀20.85–21.46, pronotum total length ♂11.75–15.08, ♀12.95–13.43, prozona length ♂5.10–6.21, ♀6.26–6.79, metazona dorsal length ♂6.65–8.99, ♀6.16–7.17, pronotum constriction width ♂3.65–4.90, ♀3.80–4.44, metazona dorsal width ♂7.76–9.85, ♀8.79–9.15, head width ♂4.95–6.19, ♀6.30–6.83, ovipositor length ♀20.15–21.35.

Distribution. Southern California mountain ranges bordering the Colorado Desert including the Santa Rosa and Little San Bernardino Mountains.

Habitat. Pinyon-juniper and yucca woodland. Type series taken from Parry Pinyon (*Pinus quadrifolia* Par. ex Sudlow) and Joshua Tree. Also recorded from *Ceanothus* sp.

Seasonal occurrence. Late spring (29-V-1963, EL Sleeper, CAS) through summer and into fall (21-IX-1962, RC Stephens, CAS). Nymphs through late spring (27-V-1939, ER Tinkham, CAS).

Stridulatory file. (n=12) length 3.90–6.30 mm, 89–113 teeth, tooth density 20.3±1.8 (17.8–23.0) teeth/mm.

Song. (n=36) A loud calling song that consists of echemes ("chirps") as in other Ovatus Group species. Males may call with single pulse trains before sunset. Pulse trains 70±20 ms in length are repeated at a rate of 9.08±1.23 s^{-1}. Mean peak frequency is 13.83±4.79 kHz; recordings with ultrasonic equipment found significant sound energy in the ultrasonic, with peak frequencies as high as 26.19 kHz. Echemes group 3±1 (range 1–6) pulse trains. Echemes are separated by silent intervals that last 1–5 (mean 2.48±0.91) s. At the type locality on 28–29 June 2004, JAC observed alternating choruses of seven nearest neighbor males, each situated in its own juniper tree, on a cool 16.6ºC summer night. Males perched between 1.85–2.10 m above the ground. The average spacing between males was 15.8 m, with the closest pair situated 0.6 m apart. Two of the seven junipers harbored two males each, but only one male in each case was acoustically active. This suggests that males may employ satellite behavior (reviewed in Greenfield 2002) to intercept females that are phonotaxing to calling males.

Karyotype. (n=7) 2n♂=23 (22t+Xt), topotype T82-132 (S82-105).

Recognition. Morphology, geography. The abdomen has a longitudinal red-brown stripe and the tegmina are white, unlike the wood-brown abdomen and tegmina of *A. gurneyi*. The male paraproct processes have a subapical ventrally directed tooth, unlike the apical tooth found in *A. segnis* and *A. strobilion*. Body ground color in life usually a rich green against which contrasts a yellow pronotal disk. The pronotal disk has a pair of central black spots and lacks black longitudinal streaking and never has any broad white longitudinal stripes as in *A. ovatus*. *A. armiger* has reduced black streaking on the pronotal disk, but the male supra-anal plate is longer than wide in that species but as long as wide in *A. tinkhamorum*. Geographically, *A. tinkhamorum* occurs where the Peninsular Ranges meet the Colorado Desert in California.

Notes. This species replaces *A. ovatus* to the south along the fringes of the Colorado Desert. At the type locality *A. hulodomus* is sympatric where chaparral vegetation is interspersed with pinyon-juniper. Genetics (Figs. 2–4) found this species more closely related to the eastern Mojave species *A. armiger*, *A. segnis*, and *A. strobilion* than to the western Mojave *A. ovatus*.

Material examined. (n=65) **All USA, CA, Riverside Co.**, 1 mi. W Whitewater Canyon, 33.92655, -116.65886, IV-1972, ER Tinkham, CAS, 1♀; Berdoo Canyon, 33.810156, -116.170507, 1-VII-1975, ER Tinkham, CAS, 3♂, 2♀; Cactus Spring Trailhead, 0.4 mi. S of SR74 on Pinyon Flats Sta. Rd., 33.5804, -116.4507, 1200 m, 28-29-VI-2004, JA Cole, JF Eguizabal, LACM, 5♂; mouth of Whitewater Canyon, 33.92424, -116.64175, 21-VI-1973, ER Tinkham, CAS, 1♀; LACM, 1♂; Upper Berdoo Canyon, Little San Bernardino Mtns, 33.810156, -116.170507, 1-VII-1975, ER Tinkham, CAS, 1♂; Whitewater Canyon, 33.9579, -116.6463, 396 m, 20-VI-1974, ER Tinkham, CAS, 3♂, 1♀; same data except 4-VI-1975, ER Tinkham, CAS, 2♂; same data except 7-VI-1983, DB Weissman, CAS, 11♂, 1♀; same data except late IV-early V, ER Tinkham, CAS, 1♂; same data except no date, ER Tinkham, CAS, 8♂; same data except 431 m, 27-VI-2005, JA Cole, LACM, 2♂; same data except 21-IV-1973, VV Omotov, LACM, 1♂; Whitewater Canyon, NW of Palm Springs, 33.9579, -116.6463, 396 m, 24-IV-1982, DB Weissman, CAS, 1♂; **San Bernardino Co.,** 5 mi S Yucca Valley, 34.041633, -116.432235, VII-1971, ER Tinkham, CAS, 3♂, 1♀; Joshua Tree NM, L Covington Flat, 34.134728, -116.313066, 21-IX-1962, RC Stephens, CAS, 1♀; same data except 30-VII-1960, J Geest, CAS, 1♂; Joshua Tree NM, Long Cyn Cholla Br., 34.134728, -116.313066, 29-V-1963, EL Sleeper, CAS, 1♂; Joshua Tree NM, Pleasant Valley Quail Guzzler, 34.134728, -116.313066, 10-VI-1966, EL Sleeper, SL Jenkins, CAS, 1♂; Joshua Tree NM, U Covington Flat, 34.134728, -116.313066, 22-VII-1960, EL Sleeper, CAS, 1♂; same data except 8-VII-1960, EL Sleeper, CAS, 1♂; Little San Bernardino Mountains, 1 mi. W of Yucca Valley, 34.114173, -116.449759, 999 m, 30-VI-1953, ER Tinkham, CAS, 1♂; **San Diego Co.,** County Road S22 SW of Borrego Springs, 33.048669, -117.041941, 370-1040 m, 3-VI-1989, DB Weissman, DC Lightfoot,

CAS, 2♂; Culp Cyn, 5 mi. W Borrego Springs, 33.048669, -117.041941, 28-VI-1975, ER Tinkham, CAS, 2♂; Mason Valley, 32.980881, -116.426682, 23-V-1943, JH Comstock, LACM, 1♀; San Ysidro Mountains, 32.5833, -116.8167, no date, ER Tinkham, CAS, 3♂; same data except 3-VI-1975, ER Tinkham, CAS, 2♂.

Aglaothorax segnis Rehn & Hebard, 1920 comb. restored

Aglaothorax segnis—Rehn & Hebard, 1920: 225.
Aglaothorax segnis—Tinkham, 1944: 291 (Incorrect synonymy).
Neduba (*Aglaothorax*) *ovata segnis*—Rentz & Birchim, 1968: 85 (A change in status).
Aglaothorax segnis **comb. restored** (Restored to species status as proposed by Rehn & Hebard, 1920).
Fig. 6 (distribution), Fig. 10 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 4 (male terminalia), Plate 7 (female subgenital plate), Plate 10 (male titillators), Plate 14 (male calling song).

Common name. Sluggish Shieldback.

History of recognition. Described in *Aglaothorax* (Rehn & Hebard 1920). Name erroneously applied to eastern Sierra Nevada populations that belong to both *A. giganteus* and *A. ovatus* (Tinkham 1944). Transferred to *Neduba* (*Aglaothorax*) and relegated to a subspecies of *ovatus* (Rentz & Birchim 1968). Returned to *Aglaothorax* (Rentz & Colless 1990) where this species remains as a subspecies of *A. ovatus* (Cigliano *et al.* 2025). Based on phylogenetic and cytogenetic evidence, we elevate *A. segnis* to species rank, reinstating the taxonomic status of this species as originally described.

Type material. The holotype male housed at ANSP is from Crestline, Lincoln County, Nevada, taken from Joshua tree at 6000 feet elevation. Images of the type are available at OSFO (Cigliano *et al.* 2025). TOPOTYPES EXAMINED: (n=10) **USA, NV, Lincoln Co.**, 13 miles E Panaca on State Highway 319, 37.790280, -114.150913, 1950 m, 11-VIII-1988, DB Weissman, DC Lightfoot, CAS, 1♂, 1♀; 16 miles E Panaca Summit, 37.764601, -113.897074, 11-VIII-1988, DB Weissman, DC Lightfoot, CAS, 1♂; 18 miles E Panaca on State Highway 319, 37.790059, -114.059173, 1720 m, 11-VIII-1988, DB Weissman, DC Lightfoot, CAS, 1♂; 7 miles E of Panaca, 37.790450, -114.260999, 1829 m, 20-VIII-1982, DB Weissman, CAS, 2♂; Beaver Dam State Park, 37.521362, -114.072202, 12-IX-1973, RC Bechtel, GM Nishida, NDAC, 4♂.

Measurements. (mm, ♂n=5, ♀n=2) Hind femur ♂16.65–17.35, ♀19.40–20.74, pronotum total length ♂11.15–13.99, ♀13.34–14.35, prozona length ♂4.56–5.66, ♀5.62–6.15, metazona dorsal length ♂6.59–8.44, ♀7.72–8.20, pronotum constriction width ♂2.97–3.90, ♀3.69–5.00, metazona dorsal width ♂7.35–8.75, ♀8.50–9.25, head width ♂5.06–5.62, ♀6.05–6.67, ovipositor length ♀19.41–20.41.

Distribution. Mountain ranges of southeastern Nevada at high elevation. The type locality is in the Cedar Range. Other populations are known from the Clover Mountains and Bristol Range.

Habitat. Pinyon-juniper woodland. Taken from high branches of Utah Juniper (*Juniperus osteosperma* (Torr.) Little).

Seasonal occurrence. Limited records suggest mid- to late summer adult activity (4-VIII-2005, JA Cole, LACM) that extends into Fall (12-IX-1973, RC Bechtel & GM Nishida, CAS).

Stridulatory file. (n=5) length 4.85–5.10 mm, 102–117 teeth, tooth density 21.7±1.1 (20.6–23.4) teeth/mm.

Song. (n=18) Brief echemes ("chirps") similar to *A. armiger*. Pulse trains 50±10 ms in length are repeated at a rate of 10.1±1.52 s^{-1}. Mean peak frequency is 14.13±2.77 kHz; high frequency recordings show song energy at the ultrasonic boundary at 20.25 kHz. Echemes group 3±1 pulse trains with 0.71–3.56 (mean 1.53±0.75) s of silence between echemes.

Karyotype. (n=6) 2n♂=24 (22t+XtYt), topotype T88-43 (S88-93).

Recognition. Morphology, geography, and karyotype. *A. segnis* is separated from all Ovatus Group species except *A. strobilion* and most *A. gurneyi* by the apical, mesally directed tooth on the male paraproct process; rarely, the cercus terminates in a double tooth, with one of the two teeth positioned apically. All other Ovatus Group species have a subapical ventrally directed tooth. The male paraproct in *A. segnis* is about three times as long as wide, as opposed to thick and about twice as long as wide in other Ovatus Group species. The *A. segnis* male supra-anal plate is wider than long and reflexed caudally, a condition like that of *A. armiger* and *A. strobilion* but unlike *A. giganteus*, *A. khioneos*, *A. ovatu*s, and *A tinkhamorum*, which have supra-anal plates that are as long as wide. *A. segnis* and *A. strobilion* have abundant longitudinal black streaks on the pronotal disk, unlike the disk of *A. armiger* which typically has reduced black marking. The *A. segnis* pronotum is broader than that of *A. strobilion*, with a concomitant increase

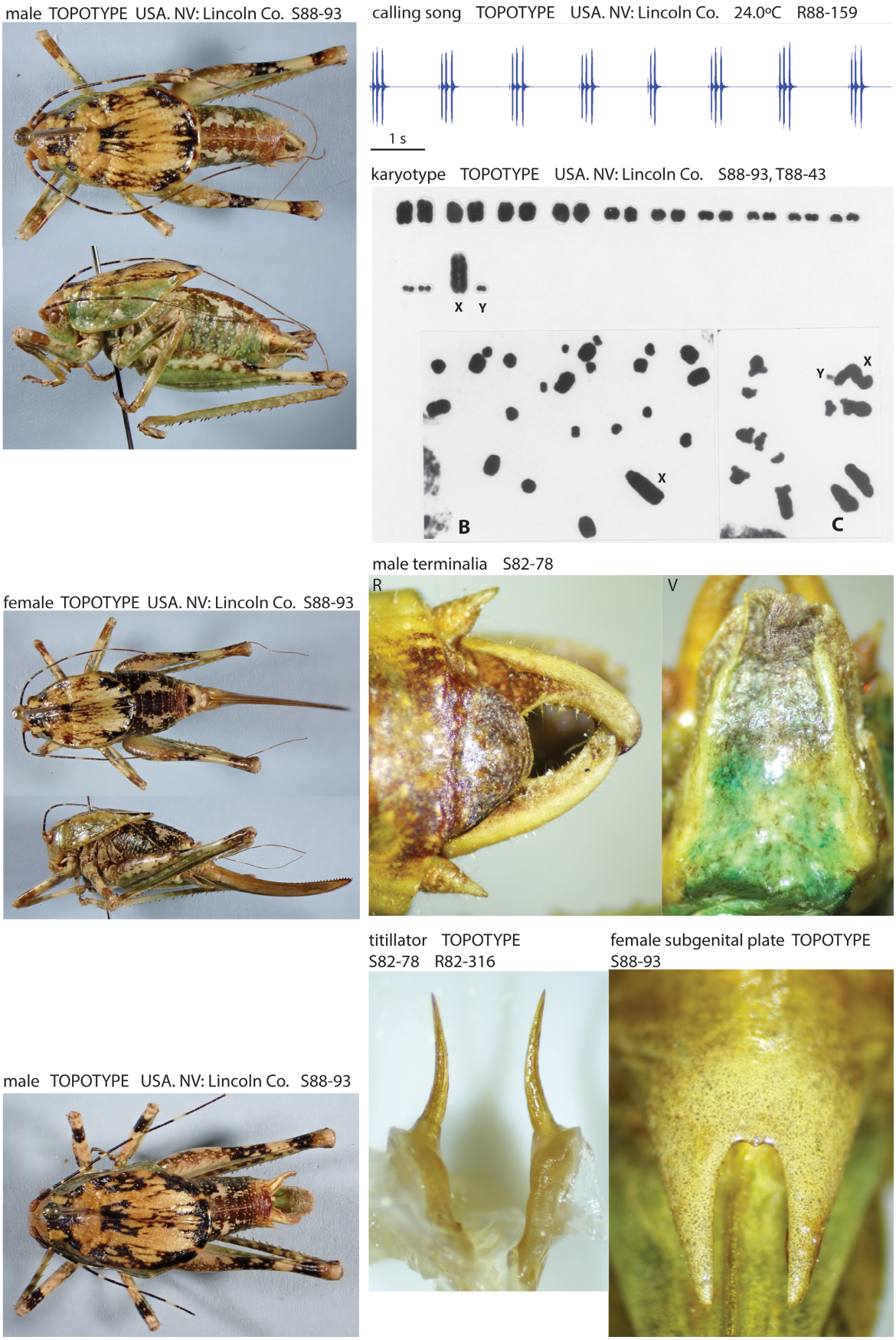


FIGURE 10. *A. segnis* male and female habitus, calling song, male and female terminalia, and karyotype. Idiogram top panel shows karyotype 2n♂=24; B. Plate showing all 24 chromosomes; C. Metaphase I, showing 11 autosomal pairs and associated XY pair.

in the ratio of the pronotal constriction width to metazona width in the former versus the latter (*A. segnis* 2.24–2.47 vs. *A. strobilion* 1.97–2.20). Female *A. segnis* have the shortest subgenital plate lateral processes of any Ovatus Group species (although females of *A. strobilion* are unknown). Geographically, *A. segnis* occupies mountain ranges in the northeasternmost extent of the Mojave Desert where that desert interdigitates with the Great Basin Desert. The 2n♂=24 karyotype is shared only with *A. gurneyi*; all other Ovatus Group species have 2n♂=23, including *A. strobilion*, which superficially resembles this species.

Notes. This species inhabits remote areas and is thus seldom encountered. Individuals perch high in large trees and are thus difficult to collect when found. The 2n♂=24 karyotype is shared with another sky island endemic Ovatus Group species, *A. gurneyi* of the California Transverse Ranges.

Material examined. (n=7) **All USA, NV, Lincoln Co.**, 27 mi. N Pioche on Hwy. 93, 38.32116, -114.452214, 1981 m, 20-VIII-1982, DB Weissman, CAS, 2♂; Hwy. 319, 1.9 miles west of Utah State Line, 37.72564, -114.0844, 1804 m, 19-VIII-2009, DB Weissman, DC Lightfoot, CAS, 1♂; Oak Spring Summit Picnic Area, along US93, 9.3 mi. E of Caliente, 37.5923, -114.6828, 1901 m, 4-VIII-2005, JA Cole, LACM, 1♂; same data except JAC, 2♂; Pioche, 37.929685, -114.452214, 1848 m, 20-VIII-1958, RC Bechtel, NDAC, 1♀.

Aglaothorax armiger Rehn & Hebard, 1920 comb. restored

Aglaothorax armiger—Rehn & Hebard, 1920: 229.
Aglaothorax armiger—Tinkham, 1944: 292.
Neduba (*Aglaothorax*) *ovata armiger*—Rentz & Birchim 1968: 83 (A change in status).
Aglaothorax armiger **comb. restored** (Restored to species status as proposed by Rehn & Hebard, 1920).
Fig. 6 (distribution), Fig. 11 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 4 (male terminalia), Plate 7 (female subgenital plate), Plate 10 (male titillators), Plate 14 (male calling song).

Common name. Armored Shieldback.

History of recognition. Described in *Aglaothorax* (Rehn & Hebard 1920). Correctly identified and associated with type material by Tinkham (1944). Transferred to *Neduba* (*Aglaothorax*) and relegated to a subspecies of *N. (A.) ovata* (Rentz & Birchim 1968). Transferred back to *Aglaothorax* (Rentz & Colless 1990) where this species is currently classified as an *A. ovatus* subspecies (Cigliano *et al.* 2025). We elevate *A. armiger* to species rank based on phylogenetic and morphological evidence, reinstating the taxonomic status of this species as originally described.

Type material. The holotype male deposited in ANSP is from Lee Canyon, Spring Mountains, Clark County, Nevada, taken from Joshua tree at 6000 feet elevation. Images of the holotype and allotype are available at OSFO (Cigliano *et al.* 2025). TOPOTYPES EXAMINED: (n=29) **USA, NV, Clark Co.**, Charleston Peak, 36.272185, -115.695019, 15-VIII-1931, ER Tinkham, CAS, 1♂; same data except 20-X-1939, ER Tinkham, CAS, 2♂; Lee Canyon Road between mileposts 6 and 9, 36.399963, -115.567516, 15-VIII-1998, DB Weissman, DC Lightfoot, CAS, 1♂; Lee Canyon Road, 36.399963, -115.567516, 1100-2200 m, 21-VII-1990, DB Weissman, DC Lightfoot, CAS, 3♂, 3♀; Lee Canyon Road, 4 miles southwest of US95, 36.43806, -115.51806, 1320 m, 8-VI-2023, JA Cole, AMNH, 1♂, 1♀; same data except LACM 2♂, 2♀; same data except JAC, 2♂, 2♀; Lee Canyon Road, 5.2 miles southwest of US95, 36.42624, -115.53464, 1426 m, 15-VI-2018, JA Cole, LACM, 1♂; Lee Canyon, 36.399963, -115.567516, 1830 m, 2-VIII-1991, DB Weissman, DC Lightfoot, CAS, 1♂; Lee Canyon, 36.399963, -115.567516, 6300-7500’ m, 30-VIII-1986, DB Weissman, DI Weissman, DCF Rentz, CAS, 5♂, 2♀.

Measurements. (mm, ♂n=5 , ♀n=5) Hind femur ♂16.20–17.80, ♀19.10–20.37, pronotum total length ♂11.07–12.80, ♀12.79–14.80, prozona length ♂4.51–5.80, ♀6.18–6.61, metazona dorsal length ♂6.56–7.00, ♀6.61–8.19, pronotum constriction width ♂3.40–3.90, ♀4.15–4.93, metazona dorsal width ♂7.24–8.05, ♀8.15–9.75, head width ♂5.22–6.00, ♀6.40–6.68, ovipositor length ♀17.65–20.47.

Distribution. Eastern Mojave Desert in Nevada. The type locality is along the eastern slope of the Charleston Mountains, Clark County.

Habitat. Joshua Tree and pinyon-juniper woodlands. The description states that occurrence at the type locality was restricted to Joshua tree woodland, where they were found 4–8 feet above the ground, and found most often at 5–6 feet hiding in the dry leaves at the base of green leaves (Rehn & Hebard 1920). Topotype specimens were later taken from juniper and mixed conifer woodlands (Tinkham 1944). We found them on Joshua Trees and yucca at night, sometimes 4 m above the ground.

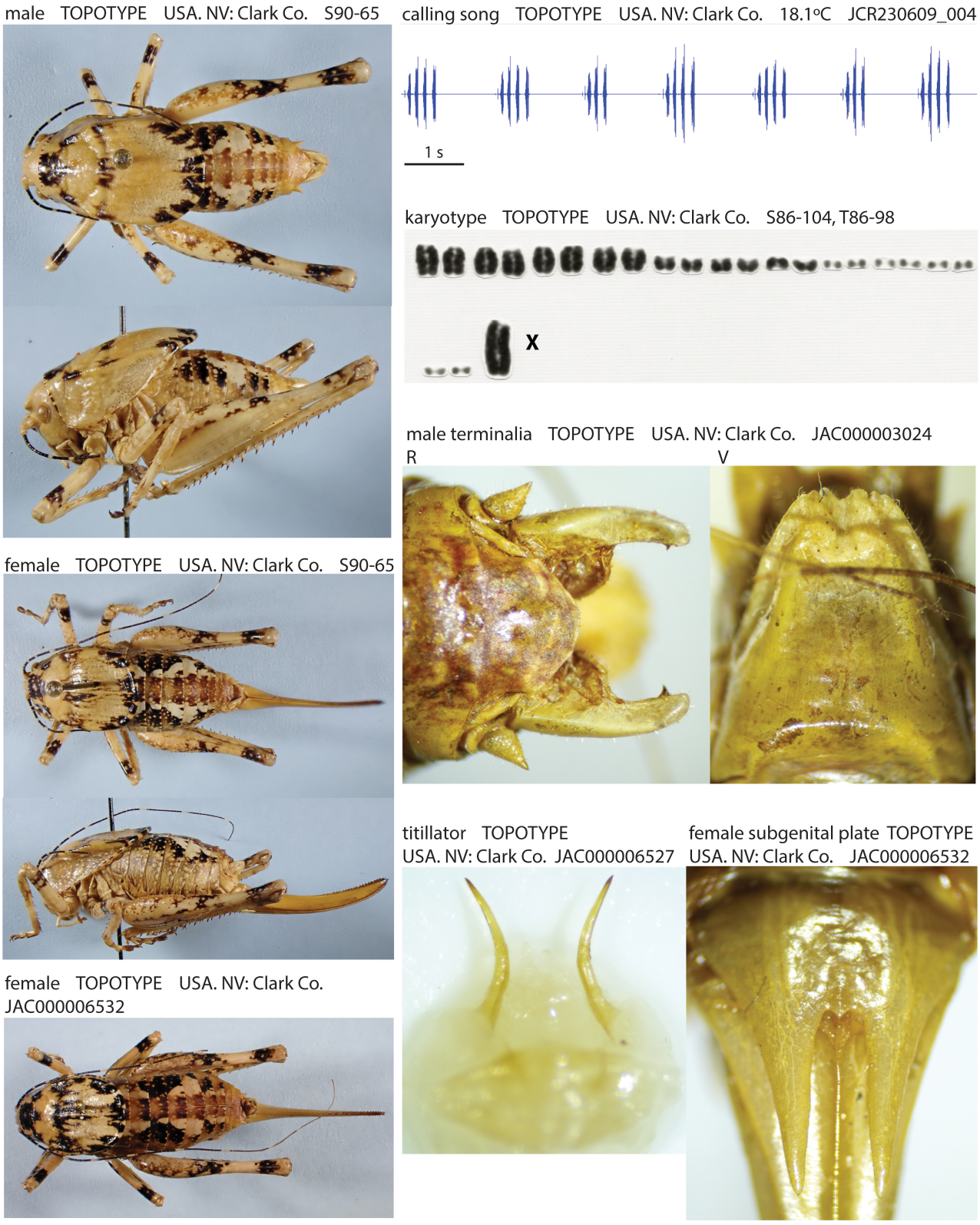


FIGURE 11. *A. armiger* male and female habitus, calling song, male and female terminalia, and karyotype. Idiogram shows karyotype 2n♂=23. Marked X chromosome is largest in complement.

Seasonal occurrence. Summer (8-VI-2023, JA Cole, LACM) through Fall (20-X-1939, ER Tinkham, CAS), maturing earlier at lower elevations. Nymphs alongside adults in late spring (8-VI-2023, JA Cole, LACM), with one female observed eclosing that night.

Stridulatory file. (n=5) length 3.90–4.80 mm, 94–106 teeth, tooth density 23.1±1.4 (20.8–24.1) teeth/mm.

Song. (n=7) Sporadic song that consists of single pulse trains or brief echemes. Pulse trains 50 ms in length are repeated at a rate of 10.26±0.97 s^{-1}. Mean peak frequency is 11.58±0.83 kHz. Males may produce pulse trains alone or group them into echemes containing 1–4 (mean 3±1) pulse trains. Isolated pulse trains are more likely to occur at the onset of singing or after a male is disturbed. Silent intervals between echemes last 1–6 (mean 2.16±1.70) s. The original description mentions intermittent sound production during an afternoon (Rehn & Hebard 1920).

Karyotype. (n=5) 2n♂=23(22t+Xt), S86-104, T86-98, topotype.

Recognition. Morphology, coloration, geography. Ground color is generally tan or yellow, unlike the rich green that is common in other Ovatus Group species or the wood-brown coloration of *A. gurneyi*. The abdominal dorsum has a reddish stripe and the tegmina are white, unlike the wood-brown unstriped abdomen and brown tegmina of *A. gurneyi*. The male supra-anal plate of *A. armiger* is wider than long in contrast to *A. giganteus*, *A. khioneos*, *A. ovatus*, and *A. tinkhamorum*, which have supra-anal plates that are as long as wide. From 16 to 18 mm long, the hind femora appear shorter than those of *A. giganteus*, *A. ovatus*, and *A. tinkhamorum*. The male paraproct process is about twice as long as wide, cylindrical, and with a subapical ventrally directed heavy triangular tooth, unlike the apical tooth on the slenderer processes of *A. segnis* and *A. strobilion*. Black markings are generally reduced on the pronotal disk to a central pair of black spots and perhaps limited black streaking, a coloration otherwise approached only by *A. tinkhamorum*.

Notes. The type locality of *A. armiger*, Lee Canyon, is a sky island in the eastern Mojave Desert that is known for its endemism, and as a biodiversity hotspot for Orthoptera in particular (Rentz 1972). *A. armiger* populations are distributed to the east of Mount Charleston in the rain shadow. White Mountains, California populations classified as this species (Rentz & Birchim 1968) are here described as new (see *A. khioneos* species account below).

Material examined. (n=4) **All USA, NV, Clark Co.**, Willow Creek, 36.576070, -115.732522, 1820 m, 16-VI-1985, JB Knight, NDAC, 2♂; **Mineral Co.**, Cottonwood Creek, 38.648524, -118.762961, 2286 m, 9-VIII-1990, RC Bechtel, JB Knight, SD Cichowlaz, NDAC, 2♂.

Aglaothorax strobilion Cole, Weissman, and Lightfoot, sp. nov.

Fig. 6 (distribution), Fig. 12 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 4 (male terminalia), Plate 7 (female subgenital plate), Plate 10 (male titillators), Plate 14 (male calling song)

Common name. Currant Shieldback.

History of recognition. Noted as intergrades between *armiger* and *segnis* with small body size (Rentz & Birchim 1968). We describe this population as a new species based on cytogenetic, morphological, and phylogenetic evidence, and also the remote, isolated geography.

Type material. HOLOTYPE MALE: **USA, NV, Nye Co.**, Currant Summit, 38.82081, -115.33528, 1950 m, 19-VIII-2009, DB Weissman, DC Lightfoot, CAS S09-140, R09-211, D36, T09-7, SING0371, deposited at CAS, Entomology type #20383. PARATYPES (n=8) **USA, NV, Nye Co.**, 9.9 M E Currant on Hwy. 6, 38.742013, -115.290742, 2042 m, 29-VIII-1986, DB Weissman, BI Weissman, DCF Rentz, CAS, 6♂; same data as holotype, CAS, 2♂.

Measurements. (mm, ♂n=5) Hind femur ♂14.86–17.58, pronotum total length ♂9.85–11.73, prozona length ♂4.26–5.13, metazona dorsal length ♂5.59–6.60, pronotum constriction width ♂3.37–3.75, metazona dorsal width ♂6.80–7.62, head width ♂5.06–5.62.

Distribution. Limited records are from the Currant Mountain Wilderness in the White Pine Range, Humboldt-Toiyabe National Forest, Nevada.

Habitat. Pinyon-juniper woodland at high elevations, from 1950–2050 m. Sings from high in junipers.

Seasonal occurrence. Limited records suggest late summer adult activity (19-VIII-2009, DB Weissman & DC Lightfoot, CAS to 29-VIII-1986, DB Weissman, BI Weissman, DCF Rentz, CAS). Adult activity late in the season corresponds with high elevation habitat.

Stridulatory file. (n=5) length 3.90–4.15 mm, 85–107 teeth, tooth density 24.5±2.3 (20.7–26.6) teeth/mm.

Song. (n=2) Pulse trains 50±10 ms in length are repeated at a rate of 9.65±0.57 s^{-1}. Mean peak frequency is 11.45±1.71 kHz. Echemes group 2–4 (mean 3±1) pulse trains with 0.93–1.77 (mean 1.35±0.60) s of silence between echemes.

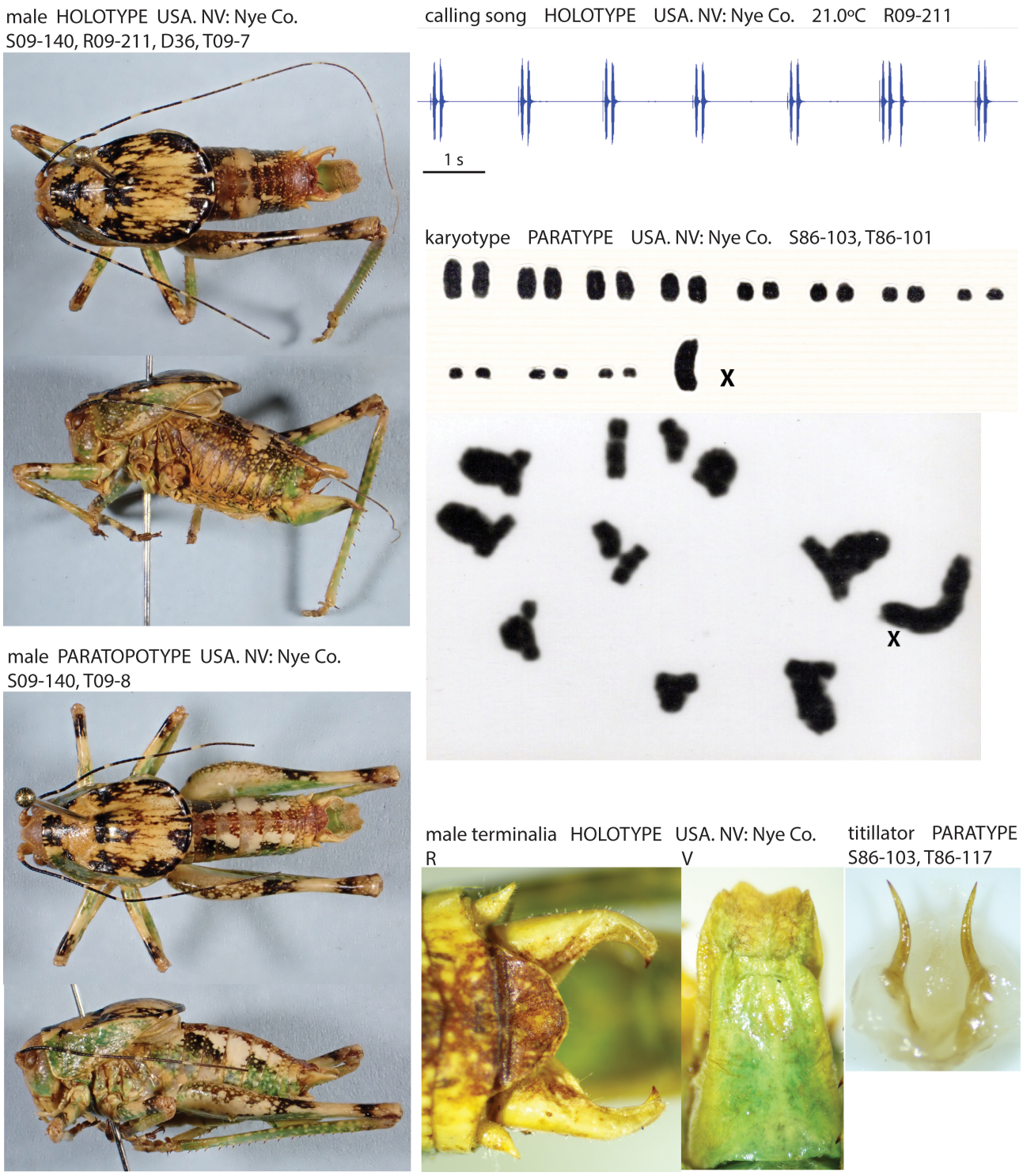


FIGURE 12. *A. strobilion* male habitus, calling song, terminalia, and karyotype.

Karyotype. (n=5) 2n♂=23 (22t+Xt), S86-103, T86-101, paratype.

Recognition. Morphology, karyotype. Small body size for Ovatus Group, pronotum length 10–12 mm. Similar in habitus to *A. segnis* but smaller. Like *A. segnis* and unlike all other Ovata Group species, including *A. armiger*, paraproct process with apical, mesally directed tooth. Paraproct processes shorter in *A. strobilion,* about 2 times as long as wide, than *A. segnis* in which those processes are about 3 times as long as wide. Pronotal disk with abundant black longitudinal streaks unlike *A. armiger*, which has reduced black streaking on pronotal disk. Karyotype 2n♂=23, typical for Ovatus Group but unlike 2n♂=24 *A. segn*is. Female unknown.

Etymology. Gr. *strobilion* a small pinecone. Refers to the small body size and pinyon-juniper habitat preference.

Notes. This population highlights the need for additional fieldwork in the mountains of the Nevada Basin and Range province, where endemics may yet be found on remote mountain island habitats. The impetus to delve further into this population came from its classification as an intergrade (Rentz & Birchim 1968). Karyotyping showed that this population (Fig. 12) did not have the same chromosome complement as *A. segnis* (Fig. 10). The concatenated phylogenetic hypothesis found this population more closely related to *A. armiger* (Fig. 4), with which it shares the typical 2n♂=23 karyotype, than with the karyotypically divergent *A. segnis*. The type locality of *A. strobilion* is separated from that of *A. segnis* by about 150 km and from that of *A. armiger* by approximately 280 km (Fig. 6). A distinct constellation of characters, together with its geographic isolation, prompted specific distinction.

Material examined. See Type Material above.

Aglaothorax khioneos Cole, Weissman, and Lightfoot, sp. nov.

Fig. 6 (distribution), Fig. 13 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 4 (male terminalia), Plate 7 (female subgenital plate), Plate 10 (male titillators), Plate 14 (male calling song)

Common name. White Mountains Shieldback.

History of recognition. Previously treated as a population of *N.* (*A.*) *armiger* (Rentz & Birchim 1968). We describe this population as new based on morphological and phylogenetic evidence.

Type material. HOLOTYPE MALE: **USA, CA, Inyo Co.**, Cedar Flat Group Camps, Inyo National Forest, jct. SR168 and White Mountain Road, 37.28385, -118.15546, 2276 m, 17-VII-2023, JA Cole, C Wong, DNA814, SING1435, JCR230817_003, deposited at CAS, Entomology type #20384. PARATYPES: (n=27) **USA, CA, Inyo Co.,** same data as holotype, LACM, 6♂; SR168 and White Mountain Road, 37.28200, -118.02999, 2224 m, 23-VIII-2019, JA Cole, J Bailey, SA Downing, LACM, 1♂; Westgard Pass, 10 miles east of Big Pine on SR168, 37.2491, -118.1753, 1968 m, 15-VIII-2002, JA Cole, LACM, 1♂; Westgard Pass, 9.5 miles east of Big Pine on SR168, 37.2458, -118.1853, 1887 m, 13-VII-2003, JA Cole, JF Eguizabal, LACM, 1♂; White Mountain Road, 1.2 miles NW of SR168, 37.29290, -118.16749, 2283 m, 11-IX-2016, JA Cole, J Bailey, LACM, 3♂, 1♀; same data except 17-IX-2017, JA Cole, K Halsey, JAC, 1♂; 4-5 miles W of Westgard Pass, 37.300172, -118.245132, 1968 m, 19-VIII-1982, DB Weissman, CAS, 5♂, 1♀; Grandview Campground, 19 miles northeast of Big Pine off SR168 and White Mountain Road, 37.3332, -118.1923, 2610 m, 2-3-VIII-2005, JA Cole, LACM, 2♂; same data except 5-VIII-2004, JA Cole, LACM, 2♂; Pinyon Picnic Area, 4 miles north of SR168 on White Mountain Road, 37.3143, -118.1811, 2353 m, 2-VIII-2005, JA Cole, AMNH, 1♂; same data except LACM, 1♂; **Mono Co.,** White Mountains, 37.578355, -118.207943, 14-VIII-1985, DM Martinelli, CAS, 1♀.

Measurements. (mm, ♂n=3, ♀n=3) Hind femur ♂17.51–17.96, ♀18.70–20.72, pronotum total length ♂12.01–12.64, ♀11.68–12.84, prozona length ♂5.21–5.53, ♀5.86–6.08, metazona dorsal length ♂6.62–7.22, ♀5.82–6.85, pronotum constriction width ♂3.69–4.20, ♀4.05–4.35, metazona dorsal width ♂7.86–8.10, ♀8.25–9.15, head width ♂5.34–5.54, ♀6.14–6.36, ovipositor length ♀17.15–18.35.

Distribution. White Mountains of California at high elevations above 1900 m.

Habitat. Pinyon-juniper woodland, arboreal on Utah Juniper (*Juniperus osteosperma*) and Pinyon Pine. Most males called from higher than 3 m in Pinyon Pines and junipers.

On favorable years populations occur in washes down to 1880 m elevation.

Seasonal occurrence. Summer (13-VII-2003, JA Cole, JF Eguizabal, LACM) into Fall (17-IX-2017, JA Cole, K Halsey, LACM). Late onset of adult activity due to high elevation occurrence.

Stridulatory file. (n=3) length 4.50–4.70 mm, 88–102 teeth, tooth density 20.6±1.4 (19.6–22.2) teeth/mm.

Song. (n=27). Pulse trains 40±10 ms in length repeat at a rate of 9.6±1.0 s^{-1}. Mean peak frequency is 13.98±2.30 kHz, with peak frequencies as high as 17.54 kHz in high frequency recordings. Echemes contain 2–5 pulse trains, with 1–3 (mean 1.65±0.60) s silent intervals between echemes.

Karyotype. (n=3) 2n♂=23 (22t+Xt), S82-75, T82-149, 150, 163.

male HOLOTYPE USA. CA: Inyo Co. JAC000006537



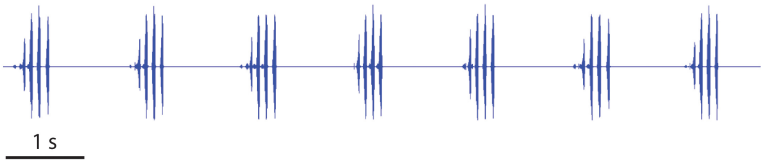
female PARATOPOTYPE USA. CA: Inyo Co. JAC000006543



male PARATOPOTYPE USA. CA: Inyo Co. JAC000006540



calling song PARATYPE USA. CA: Inyo Co. 25.0ºC JAC05GV2-06



karyotype PARATYPE USA. CA: Inyo Co. S82-75, T82-150

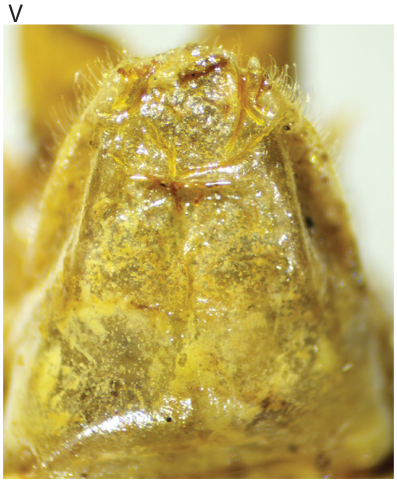


male terminalia PARATOPOTYPE USA. CA: Inyo Co. JAC000003020

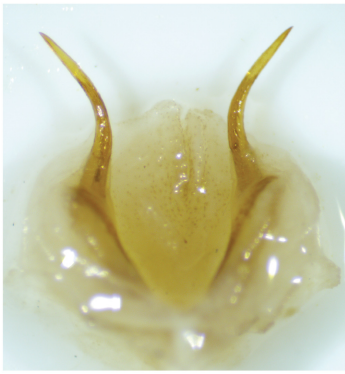
R



V



titillator PARATYPE JAC000003019



female subgenital plate PARATOPOTYPE JAC000003022

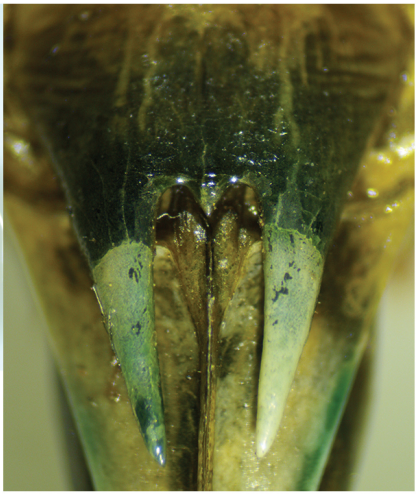


FIGURE 13. *A. khioneos* male and female habitus, calling song, male and female terminalia, and karyotype.

Recognition. Morphology, karyotype. Body usually green (may be tan at lower elevations), abdomen with longitudinal dorsal red stripe; body is wood brown without a dorsal abdominal stripe in *A. gurneyi* and usually tan in *A. armiger*. Black streaks present on the center of the pronotal disk, which are commonly limited to the periphery of the disk in *A. armiger.* Pronotum without white stripes as in *A. ovatus*. Male paraproct process with subapical ventrally directed tooth, unlike the apical, mesally directed tooth of *A. segnis* and *A. strobilion*. Male pronotum is not heavily rugose as in *A. giganteus* and *A. tinkhamorum*.

Etymology. Gr. *khioneos* snowy white. Descriptive of the White Mountains type locality.

Notes. Gene trees found conflicting relationships of this lineage: nDNA (Fig. 2) found *A. khioneos* related to *A. ovatus* and *A. giganteus*, while mtDNA (Fig. 3) found relationship with the eastern Mojave *A. armiger*, *A. segnis*, *A. strobilion*, and Colorado Desert *A. tinkhamorum*. The White Mountains are geographically situated between the Spring Mountains of Nevada and the Sierra Nevada of California, suggesting a hypothesis of gene flow when Ovatus Group populations were panmictic.

Material examined. See Type Material above.

Aglaothorax gurneyi (Rentz & Birchim, 1968)

Aglaothorax ovatus—Tinkham, 1944: 289 (Incorrect synonymy).
Neduba (*Aglaothorax*) *gurneyi*—Rentz & Birchim, 1968: 65.
Fig. 6 (distribution), Fig. 14 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 4 (male terminalia), Plate 7 (female subgenital plate), Plate 10 (male titillators), Plate 14 (male calling song).

Common name. Gurney's Shieldback.

History of recognition. Confused with *A. ovatus* (Tinkham 1944) before description. Described in *Neduba* (*Aglaothorax*) (Rentz & Birchim 1968). Returned to *Aglaothorax* (Rentz & Colless 1990) where it is currently classified (Cigliano *et al.* 2025). See Cigliano *et al.* (2025) for complete synonymy.

Type material. The holotype male deposited in ANSP is from Lake Arrowhead in the San Bernardino Mountains, San Bernardino County, California. Images of the type are available at OSFO (Cigliano *et al.* 2025). PARATYPES EXAMINED: (n=5), **USA, CA, San Bernardino Co.,** Barton Flats, 34.172509, -116.863083, 1937 m, 21-VIII-1936, no collector, CAS, 1♀; Lake Arrowhead, 34.248340, -117.189208, 22-VIII-1958, P. Paige, CAS, 1♂; same data except IX-1958, P Palge, CAS, 1♂; same data except VII-1958, no collector, CAS, 1♂; San Bernardino Mountains, 4 mi. W of Running Springs, 34.207766, -117.179377, 2195 m, 12-X-1952, ER Tinkham, CAS, 1♂; TOPOTYPES EXAMINED: (n=11) **USA, CA, San Bernardino Co.,** San Bernardino Mountains, 0.8 mi. E of Lake Arrowhead City on Hwy 173, 34.248339, -117.175167, 1520 m, 20-VII-1992, DB Weissman, CAS, 2♂, 2♀; SR173 near Old Mill Road, Cedar Glen, 34.2562, -117.1683, 1900 m, 12-VII-2002, JA Cole, AMNH, 1♂, 1♀; same data except LACM, 2♂, 3♀.

Measurements. (mm, ♂n=6, ♀n=8) Hind femur ♂18.04–19.80, ♀19.84–22.60, pronotum total length ♂12.15–13.40, ♀11.35–13.10, prozona length ♂4.77–5.48, ♀5.25–7.54, metazona dorsal length ♂6.82–8.18, ♀5.05–7.50, pronotum constriction width ♂3.35–3.75, ♀2.94–4.77, metazona dorsal width ♂8.05–9.20, ♀7.21–8.80, head width ♂5.40–5.90, ♀5.25–6.74, ovipositor length ♀16.75–19.45.

Distribution. San Bernardino and San Gabriel Mountains of the Transverse Ranges of Southern California.

Habitat. Coniferous forest understory. Taken from *Ceanothus* spp., Whorl-leaf Penstemon (*Keckiella* sp.), peavines (*Lathyrus* sp.), *Pinus* spp., and California Black Oak (*Quercus kelloggii* Newberry). Hides in leaf litter at the base of vegetation during the day. Several males (S89-56) collected singing at night from piles of brown twigs on the ground. Males also heard in the canopy.

Seasonal occurrence. Summer (7-VII-2004, JA Cole, LACM) through Fall (12-X-1952, ER Tinkham, CAS), adults presumably active until first freezing weather. Nymphs present into summer (1-VII, no collector, CAS).

Stridulatory file. (n=6) length 4.75–5.30 mm, 93–105 teeth, tooth density 19.3±0.8 (18.2–20.2) teeth/mm.

Song. (n=28) Frequently repeated single pulse trains or echemes that consist of no more than two pulse trains. Pulse trains last 70±20 s and repeat at a rate of 8.20±0.94 s^{-1}. Mean peak frequency is 12.41±3.08 kHz, with high frequency recordings showing peak frequencies as high as 18.93 kHz. The silent interval between echemes lasts 0.41–0.94 (mean 0.70±0.11) s.

Karyotype. (n=5) 2n♂=24 (22t+XtYt), T89-38 (S89-56).



FIGURE 14. *A. gurneyi* male and female habitus, calling song, male and female terminalia, and karyotype. Idiogram shows karyotype 2n♂=24. Sex chromosomes X and Y are marked.

Recognition. Morphology, song, geography, habitat, karyotype. Body color wood-brown instead of the green, yellow, or tan of other Ovatus Group species, and without a reddish middorsal abdominal stripe. Tegmina brown instead of white as in other Ovatus Group species. Calling song with maximum of 2 pulse trains/echeme. Geography and habitat unique among Ovatus Group species: high elevation coniferous woodland in San Gabriel and San Bernardino Mountains as opposed to desert shrubland, pinyon-juniper, or Joshua tree woodland. Karyotype 2n♂=24 shared only with *A. segnis* among the Ovatus Group species.

Notes. This species is sister to all other members of the Ovatus Group (Figs. 2–4; Cole 2016) suggesting that this is a relict lineage that has been isolated in the sky islands of the San Bernardino and San Gabriel Mountains for some time. Populations are sympatric with *A. hulodomus* in the San Bernardino Mountains where chaparral meets mixed woodland. This is the only Ovatus Group species that inhabits mesic mixed woodlands. Males call from a variety of heights, most commonly on the forest floor but also in low bushes and high in conifers and oaks. Singing males may be difficult to approach surrounded by dry oak and pine leaf litter, the disturbance of which renders the singer silent for many minutes.

Material examined. (n=51) **Los Angeles Co.**, Mescal Picnic Area, Angeles National Forest, 5 miles northwest of Wrightwood on County Road N4 (Big Pines Highway), 34.3901, -117.7206, 1868 m, 16-VII-2002, JA Cole, 1♂, 1♀ JAC; same data except 7-VII-2004, 2♂, LACM; same data except 8-IX-2008, 4♂, LACM; same data except 1♂ JAC; **San Bernardino Co.**, 0.7 mi. W of Skyforest on Hwy. 18, 34.235284, -117.191491, 1707 m, 17-VIII-1982, DB Weissman, CAS, 2♂; Arrowbear Lake, 34.21106, -117.08507, 1867 m, 19-20-VII-2013, JA Cole, JF Eguizabal, 1♂ song record; Barton Flats, 34.172509, -116.863083, 1937 m, 1-VII-1936, no collector, CAS, 1♀; Camp O-ongo, near Running Springs, 34.207786, -117.109205, 25-30-VIII-1968, CL Hogue, LACM, 2♂; same data except 28-31-VIII-1967, CL Hogue, LACM, 2♂; same data except 16-22-VIII-1980, CL & JN Hogue, LACM, 1♂, 1♀; same data except 24-25-VIII-1981, CL & JN Hogue, LACM, 1♂; same data except 1-IX-1970, CL Hogue, LACM, 1♂; same data except 21-27-VIII-1982, JN Hogue, CSUN, 1♂; same data except 23-VIII-1979, JN Hogue, CSUN, 1♂; same data except 25-VIII-1975, JN Hogue, CSUN, 2♂, 1♀; same data except 27-VIII-1975, JN Hogue, CSUN, 1♂; same data except 29-VIII-1973, JN Hogue, CSUN, 1♂; Crestline, 34.241951, -117.285599, 1439 m, 2-IX-1933, W Brandler, LACM, 1♀; Hanna Flat Campground, San Bernardino National Forest, 34.28778, -116.97556, 2152 m, 10-11-VIII-2022, JA Cole, C Wong, LACM, 1♂; same data except JAC, 2♂; same data except 10-VIII-2023, JA Cole, C Wong, JAC, 1♂; Hanna Flat, San Bernardino National Forest, 34.28945, -116.97948, 4-IX-1953, A Menke, LACM, 1♂; Running Springs, 34.21518, -117.12670 1913 m, 19-20-VII-2013, JA Cole, JF Ramirez, LACM, 5♂, 2♀, 1 pair in copula; San Bernardino Mountains, 2.5 mi. NW of Running Springs on Hwy. 18, 34.233429, -117.140217, 1829 m, 17-VIII-1982, DB Weissman, CAS, 5♂; San Bernardino Mountains, State Highway 18, 0.7 mi. W & E of Skyforest, 34.235284, -117.191491, 1750 m, 26-VII-1989, DB & DW Weissman, CAS, 5♂; San Bernardino, 34.088624, -117.280598, 9-VIII-1978, ER Tinkham, CAS, 1♂; Tiron, San Bernardino Mountains, 34.125566, -116.876415, 1829 m, 1-XI-1982, ER Tinkham, CAS, 1♂;

ERRONEOUS LABELS: (n=2) **USA, CA, San Bernardino Co.**, Blythe, 33.610302, -114.596346, 81 m, 1-VIII-1933, LJ Muchmore, LACM, 1♂, 1♀.

Morsei Group

The Morsei Group is one of two Groups of small *Aglaothorax* species, the other being the Diminutiva Group. Body coloration may be highly variable within species (Figs. 16–26, Plate 2) but all species lack the green body coloration found in the Ovatus Group (Plate 1). The prosternal spines are usually long and divergent but may be conical (*A. sphenosternum* and rarely *A. bufonoides* and *A. kelainops*) or reduced and nipple-like. Chaetotaxy is more variable within species (and sometimes within individuals) than between (Table 3). The male supra-anal plate is rounded, square, or heart-shaped with the dorsal surface flat to concave. The male subgenital plate has a narrow to wide apex that is transverse to rounded to pyramidal. Most males have a subapical internal tooth on the paraproct, but the tooth is apically situated in *A. bufonoides*, *A. conistylus*, *A. kelainops*, most *A. nesiazo*, and *A. sphenosternum*. The titillators are always short, often barely curved, and may have a notch at the base. The female subgenital plate always has short, triangular lateroposterior processes. The ovipositor is saber-like, regularly upcurved with the apical 1/4 bearing knob-like serrations and is always shorter than the hind femur, from about 1/2 to 3/4 its length.

Relationships within the Group were poorly resolved with nDNA (Fig. 2) but were clearer with mtDNA (Fig.

3), producing a modicum of consensus in the concatenated analysis (Fig. 4). Frequent capture of Diminutiva Group mtDNA was found by this Group (Fig. 3).

This species Group contains the extremes of calling song variation in the genus, from pulse trains produced slowly at approximately 5 s^{-1} to rapidly at 15 s^{-1}. This entire range of variation may be observed across the Transverse Ranges of Southern California, with the fast rate extreme found in the western Santa Monica Mountains and a regular clinal decrease in rate to the east (Cole 2010; Rentz & Weissman 1981). Echemes may contain a regular or irregular count of pulse trains.

Aglaothorax morsei (Caudell, 1907)

Neduba morsei—Caudell, 1907: 301.
Neduba (Aglaothorax) morsei—Rentz & Birchim, 1968: 61 (A change in status).
Fig. 15 (distribution), Fig. 16 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 5 (male terminalia), Plate 8 (female subgenital plate), Plate 11 (male titillators), Plate 14 (male calling song).

Common name. Morse's Shieldback

History of recognition. Described in *Neduba* (Caudell 1907). Transferred to *Neduba* (*Aglaothorax*) (Rentz & Birchim 1968). Five subspecies were described from the California Channel Islands and adjacent mainland: *A. m. costalis*, *curtatus*, *islandica*, *santacruzae*, and *tectinota* (Rentz & Weissman 1981). All *morsei* subspecies were reassigned to *Aglaothorax* (Rentz & Colless 1990) where this species remains classified (Cigliano *et al.* 2025). *A. morsei* was separated from *A. diminutiva* by the subapical condition of the mesal tooth on the male paraproct (Rentz & Weissman 1981). Our results show that the position of this tooth is largely but not completely consistent between the Morsei Group and Diminutiva Group clades. Phylogenetically, the subspecies mentioned above are not conspecific with *A. morsei*, and they are variously elevated to full species or synonymized under *A. costalis* in this work (see *A. costalis* species account below, p. 43). Yet other populations represent new species described herein. We consider a record from Flagstaff, Coconino County, Arizona (Rentz & Birchim 1968) as erroneous because during our extensive years of collecting in Arizona, we have never encountered this easily recognized song.

Type material. The holotype male in ANSP is from Mount Wilson, Los Angeles County, California (Caudell 1907). Drawings of the damaged holotype were published in Rentz & Weissman (1981). TOPOTYPES EXAMINED: (n=3) **USA, CA, Los Angeles Co.**, Eaton Canyon Park, 34.180561, -118.095903, 29-VI-1964, PH Sullivan, CAS, 1♂; Eaton Canyon Wash, Pasadena, 34.16224, -118.08500, 16-VII-1964, RH Crandall, CAS, 1♂; Henninger Flats Road, 34.192505, -118.087569, 1067 m, 15-VIII-1982, DB Weissman, CAS, 1♂.

Measurements. (mm, ♂n=7 , ♀n=6) Hind femur ♂14.15–16.90, ♀16.84–18.04, pronotum total length ♂7.65–10.25, ♀7.62–8.84, prozona length ♂3.50–4.10, ♀0.18–4.34, metazona dorsal length ♂4.11–6.45, ♀3.66–7.83, pronotum constriction width ♂2.55-3.55, ♀2.93–3.30, metazona dorsal width ♂5.60–7.17, ♀5.65–6.17, head width ♂3.65–4.40, ♀4.50–5.63, ovipositor length ♀11.89–13.72.

Distribution. South slope of the San Gabriel Mountains of Southern California.

Habitat. Coastal sage scrub, oak woodland, and riparian habitats. Taken from Pacific Madrone (*Arbutus menziesii* Pursh), Monkeyflower (*Diplacus* spp.), Whorl-leaved Penstemon (*Keckiella* sp.), Laurel Sumac (*Malosma laurina* (Nutt.) Nutt. ex Abrams), *Phacelia* spp., Wild Currants (*Ribes* spp.), Elderberry (*Sambucus* sp.), Poison Oak (*Toxicodendron diversilobum* (Torr. & A. Gray) Greene), and Canyon Sunflower (*Venegasia carpesioides* DC.).

Seasonal occurrence. Adult activity from late spring (6-VI-2007, JA Cole, LACM) through winter (9-XII-2003, JN Hogue, CSUN). Nymphs in spring (12-IV-2017, JA Cole & K Halsey, LACM) through early summer (14-VI-2007, JA Cole & JF Eguizabal, LACM).

Stridulatory file. (n=7) length 3.10–4.20 mm, 89–109 teeth, tooth density 27.2±1.3 (25.8–28.9) teeth/mm.

Song. (n=35) Typical song structure for small *Aglaothorax* that sounds slow to the human ear with countable pulse trains. Pulse trains of 50±10 ms duration are delivered at a rate of 5.43±1.18 s^{-1}. Mean peak frequency is 17.16±3.15 kHz, and borders on the ultrasonic at 20.10 kHz in recordings with high frequency equipment. Pulse trains are grouped into irregular length echemes that consist of 4–24 (mean 12±5) pulse trains. The echeme repetition rate is 3–8 min^{-1}. At topotype locality S82-58 above Eaton Canyon, males were calling frequently even at 0500 h on 15-VIII-1982, and only stopped at daybreak.

Karyotype. (n=2) 2n♂=24 (22t+XtYt), topotype T82-115 (S82-58).

TABLE 3. Comparative chaetotaxy of the Morsei Group.

species	n	fore-femur dorsal surface	foretibia auditory foramen	foretibia ventro-anterior margin	foretibia ventro-posterior margin	midfemur dorsal surface	midtibia dorso-anterior margin	midtibia dorso-posterior margin	midtibia ventro-anterior margin	midtibia ventro-posterior margin
morsei	7	1–4	1	6	6	2-3	1–3	2–3	6–8	6–8
♀	6	3–4	1	6–7	6	2–4	2–3	2–3	7	6–7
costalis	17	1–5	0–1	6	5–6	2–5	1–3	1–4	6–9	5–7
♀	14	1–6	0–1	6	5–7	2–5	2–3	2–3	7–8	6–7
longipennis	14	1–5	0–1	5–6	6	1-3	2–3	2–3	6–7	6–7
♀	6	0–5	0–1	6	5–6	0–3	1–3	2–3	6–7	5–7
amathitis	12	1–4	0–1	6	6	1–6	1–3	2–3	5–7	6–7
♀	11	1–5	0–1	6	6	3–5	2–3	3	7	6–7
islandica	8	1–4	0	6	6	1–3	1–3	1–3	7	6–7
♀	8	2–4	0–1	6	5–6	2–3	1–3	1–3	7–8	6–7
hulodomus	9	1–4	1	6	6	0–4	2–3	1–3	6–8	5–6
♀	6	2–4	1	5–6	6	2–3	1–3	3–4	7	6–7
conistylus	7	2–5	1	6–7	6–7	2–3	2–4	3	6–7	6–7
♀	3	4–5	1	6	6	2–4	2–4	3–5	7	6–7
nesiazo	9	1–4	1	6–7	5–6	0–3	1–3	1–3	6–7	5–7
♀	7	2–3	1	5–6	6	1–2	2–3	2–3	6–7	6–7
bufonoides	10	1–3	0–1	6	6	1–3	2–3	1–4	6–7	6–7
♀	5	3–4	0–1	6	6	2–3	1–4	2–3	7	6–7
kelainops	11	2–4	1	6–7	6	1–3	2–3	3	6–7	6–7
♀	6	2–4	1	5–6	5–6	0–3	2–3	2–3	6–8	6–7
sphenosternum	7	2-4	1	6–7	6	2–4	3–5	2–4	6–7	6–7
♀	1	4	1	6	6	3	3	3	7	6

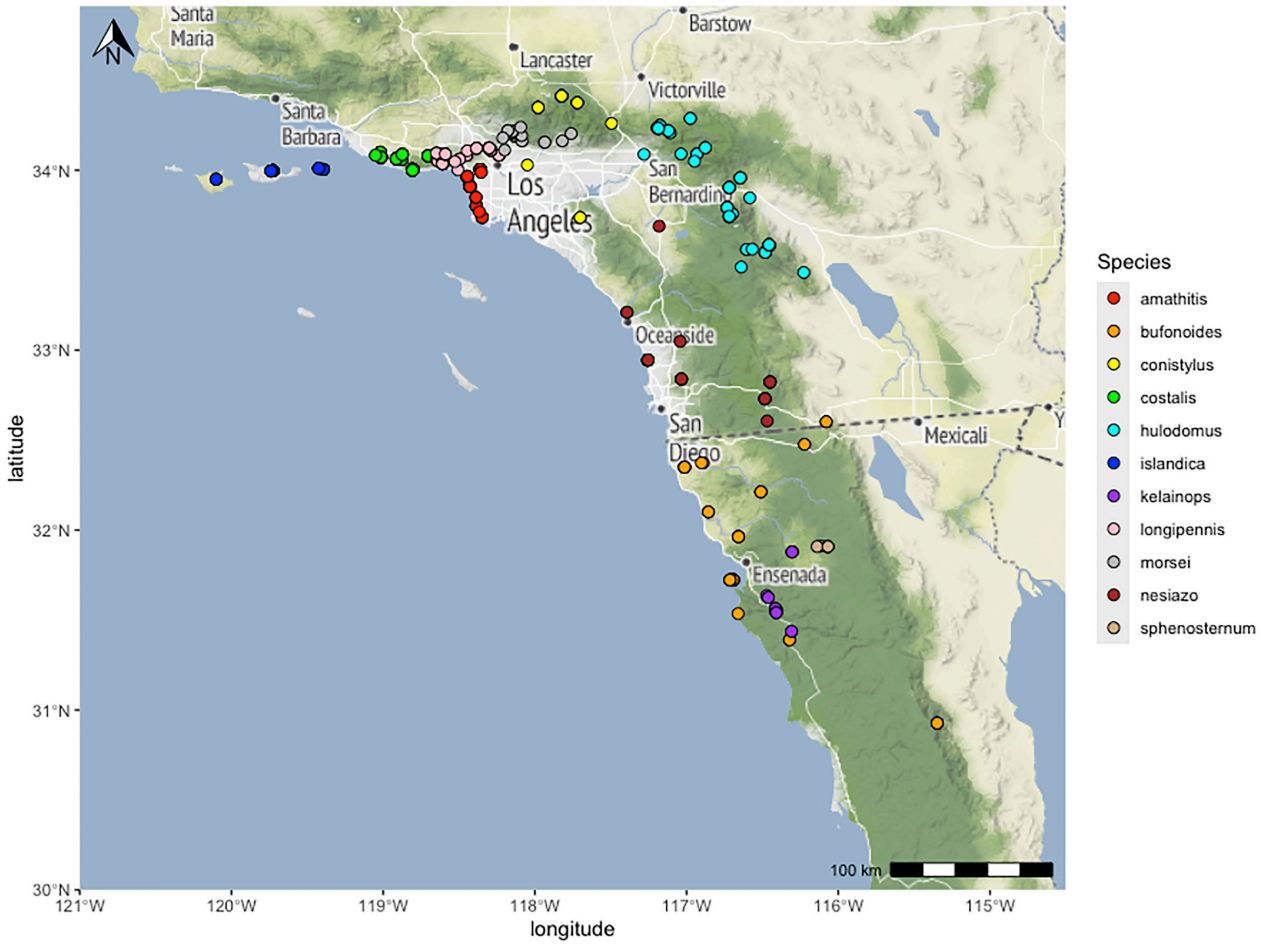


FIGURE 15. Distribution of Morsei Group species.

Recognition. Morphology, geography. The mesal tooth on the male paraproct process is positioned before the apex and the subgenital plate is flat and rounded or square with rounded edges, unlike Diminutiva Group species which have the mesal tooth apical and the supra-anal plate heart-shaped or indented on the caudal margin. The length of the paraproct process is short, as long as wide to about two times as long as wide, eliminating *A. nesiazo* from consideration as well as *A. conistylus*, which also has thick, cone-shaped styli on the male subgenital plate. *A. costalis* has short paraproct process about as long as wide, but the supra-anal plate is concave dorsally. The tooth is positioned closer to the apex of the paraproct process in *A. morsei* than in *A. hulodomus*. The male titillator arms are short, curved, have a mesal notch at the base; no other Morsei Group species has notched titillator arms, and the titillator arms of *A. hulodomus* and *A. nesiazo* are nearly straight. Most Diminutiva Group species have long, bowed titillator arms, although notably among this Group *A. constrictans* has short titillators that are notched at the base. The female subgenital plate lateral processes are triangular and usually as long as wide, never digitiform as in co-distributed Diminutiva Group species.

Notes. This species is common in the understory of riparian areas, mixed woodland, and on thickly vegetated hillsides. *A. morsei* may be sympatric with *A. acrolophitus* of the Diminutiva Group but the two are separated by habitat: mesic and xerophytic, respectively. The western boundary of the range of *A. morsei* corresponds with a recognized Transverse Range biogeographic break (Chatzimanolis & Caterino 2007), and is replaced by *A. longipennis* to the west of that break. To the east *A. morsei* is replaced by *A. conistylus* in xeric mountain habitats of the eastern San Gabriel Mountains and the surrounding lowlands, and by *A. hulodomus* in the San Bernardino Mountains. Wayward mtDNA (Fig. 3) may reflect gene flow between the aforementioned lineages.

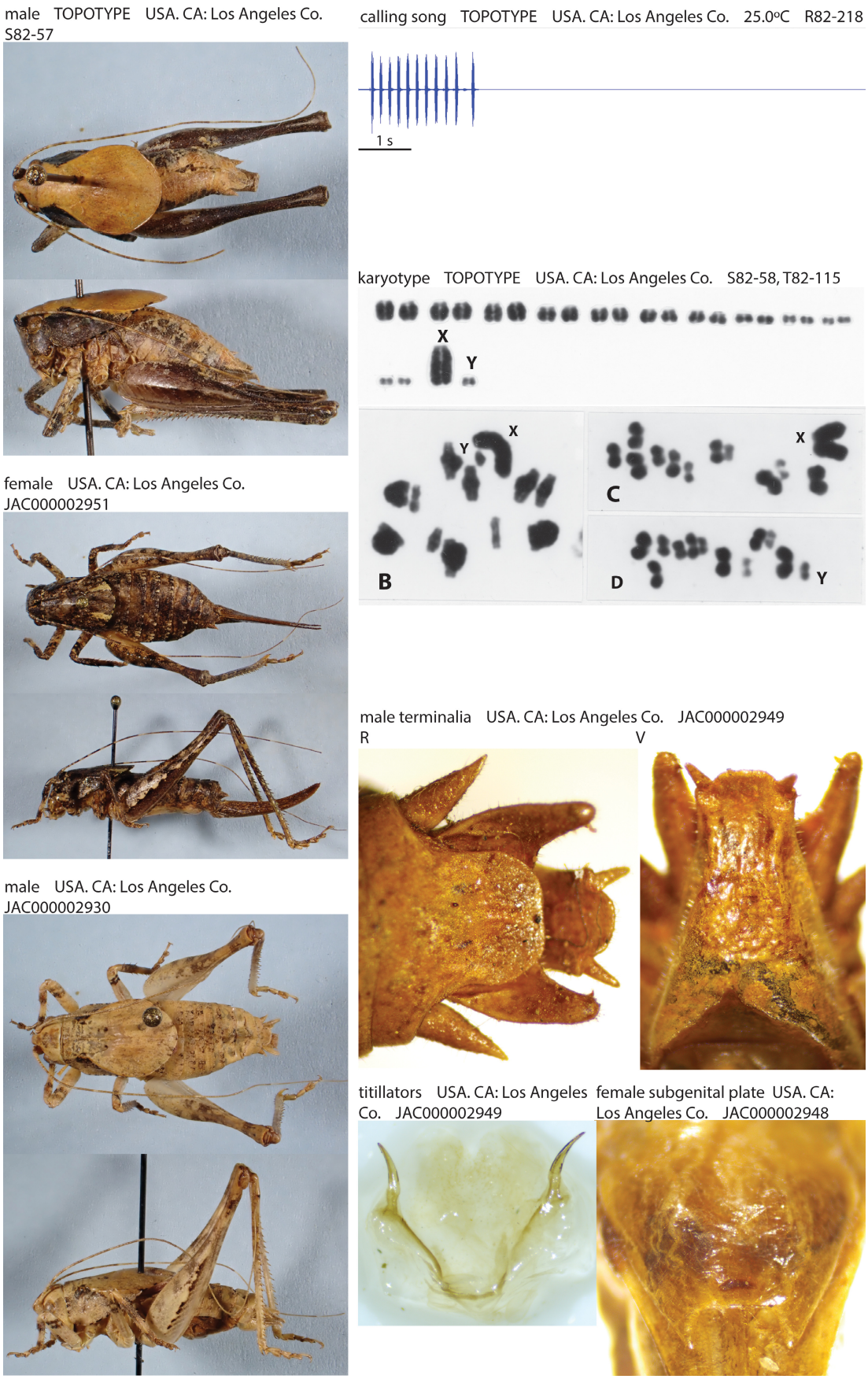


FIGURE 16. *A. morsei* male and female habitus, calling song, male and female terminalia, and karyotype. Idiogram top panel shows karyotype 2n♂=24; B. Metaphase I plate showing associated X and Y chromosomes, which ensures proper segregation to opposite poles; C and D showing metaphase II cells with X chromosome in C and Y chromosome in D.

A variety of color patterns may be observed in a single locality, helping individuals blend in with the visually complex backgrounds of the leaf litter and understory vegetation. As with *Neduba* (Cole *et al.* 2021), a hypothesis of the color pattern diversity is apostatic selection, during which visual predators reduce the numbers of the most common color morph until that morph becomes rare, whereupon predators switch to a new common morph while the original target increases in frequency (Bond & Kamil 1998, 2002). Apostatic patterns may have simple genetic mechanisms and may evolve rapidly and repeatedly, leading to color pattern convergence (Nosil *et al.* 2018; Villoutreix *et al.* 2023).

Material examined. (n=55) **All USA, CA, Los Angeles Co.**, Fish Canyon Trailhead, Duarte, 34.15554, -117.93524, 236 m, 17-VI-2015, JA Cole, GE Bell, Y Tiemsanjai, S Tipyatabiankarn, LACM, 2♀; Los Angeles Co., Altadena, 34.189728, -118.131182, 1080 m, 10-VIII-1981, RH Crandall, LACM, 1♀; same data except 11-VI-1989, RH Crandall, LACM, 1♂; same data except, 6-VI-1990, RH Crandall, LACM, 1♂; Arroyo Seco along Gabrielino Recreation Trail, Angeles National Forest, end of Windsor Boulevard, Altadena, 34.2065, -118.1670, 355 m, 24-VI-2007, JA Cole, JF Eguizabal, AMNH, 1♂, 1♀; same data except LACM, 3♂, 1♀; same data except 3-IX-2021, JA Cole, JF Eguizabal, LACM, 1♂; same data except 7-VI-2007, JA Cole, JM Hogue, MFJ Storc, LACM, 2♂, 4♀; same data except JAC, 1♀; Big Dalton Canyon, San Dimas Experimental Forest, 1-2 miles North of Glendora on Big Dalton Road, 34.1627, -117.8196, 483 m, 17-IV-2017, JA Cole, K Halsey, LACM, 1♂; Chaney Trail Drive, Altadena, near jct. Loma Alta Drive, 34.20696, -118.14840, 546 m, 17-18-VI-2015, JA Cole, GE Bell, Y Tiemsanjai, S Tipyatabiankarn, JAC, 1♂; Millard Canyon Campground, Angeles National Forest, end of Chaney Trail Rd., 34.2162, -118.1484, 546 m, 1-VIII-1954, RH Crandall, LACM, 2♂; same data except 13-14-VI-2007, JA Cole, JF Eguizabal, LACM, 7♂, 5♀; same data except JAC, 1♀; same data except 29-30-V-2008, JA Cole, AMNH, 1♂, 1♀; same data except LACM, 5♀; same data except JAC, 1♀; same data except 6-VI-2007, JA Cole, LACM, 3♀; same data except 8-VI-2007, JA Cole, LACM, 1♂; same data except JAC, 1♂; Pasadena, above Arroyo Seco near Devil's Gate Dam, 34.22059, -118.17836, 320 m, 9-XII-2003, JN Hogue, CSUN, 2♂; Tanbark Flat, 34.20389, -117.76061, 18-VII-1956, A Menke Jr, LACM, 1♀; QUESTIONABLE PLACEMENT: (n=3) **USA, CA, Los Angeles Co**., Eaton Saddle Trailhead, Angeles National Forest, 34.23928, -118.09336, 1549 m, 13-IX-2023, JA Cole, C Wong, LACM, 1♂; Highland Park, 34.111953, -118.198962, 183 m, 10-VIII-1975, no collector, CAS, 1♀; San Rafael Hills, 34.179728, -118.210629, 7-X-1956, CL Hogue, LACM, 1♀.

Aglaothorax costalis (Rentz & Weissman, 1981) stat. rev.

Neduba (*Aglaothorax*) *morsei costalis*—Rentz & Weissman, 1981: 99.
Aglaothorax costalis **stat. rev.** (Revised to species level).
Neduba (*Aglaothorax*) *morsei curtatus*—Rentz & Weissman, 1981: 100 **New junior subjective synonym.**
Neduba (*Aglaothorax*) *morsei tectinota*—Rentz & Weissman, 1981: 104 **New junior subjective synonym.**
Fig. 15 (distribution), Figs. 17–18 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 5 (male terminalia), Plate 8 (female subgenital plate), Plate 11 (male titillators), Plate 14 (male calling song).

Common name. Coastal Shieldback

History of recognition. Described as a subspecies of *Neduba* (*Aglaothorax*) *morsei* (Rentz & Weissman 1981). All *morsei* subspecies were returned to *Aglaothorax* (Rentz & Colless 1990) where this species remains classified (Cigliano *et al.* 2025). We elevate this taxon to species rank based on morphological and bioacoustical evidence. Furthermore, we synonymize the two other Santa Monica Mountains subspecies: *A. m. curtatus* and *A. m. tectinota*, under *A. costalis*. With large series now available, the morphological and bioacoustical characters used to separate these subspecies vary more within populations than between taxa. *A. m. curtatus* was named for a short echeme consisting of few pulse trains, but the number of pulse trains per echeme is variable and *A. costalis* songs show clinal song variation from east to west across the Santa Monica Mountains (Cole 2010).

Type material. The holotype male in CAS is from Point Mugu State Park, Ventura County, California (Rentz & Weissman 1981). Images of the type are available at OSFO (Cigliano *et al.* 2025). PARATYPES EXAMINED: (n=17) *costalis* **USA, CA, Ventura Co.**, Point Mugu State Park, 34.100007, -119.017600 4 m, 13-VIII-1973, DB Weissman, CAS, 2♂, 2♀; same data except 20-VIII-1974, DB Weissman, CAS, 1♂; same data except 21-VIII-1974, DB Weissman, CAS, 1♂, 1♀; *tectinota* **USA, CA, Los Angeles Co.,** Point Dume, corner Birdview and Cliffside Dr., 34.000278, -118.806667, 60 m, 13-VIII-1973, DB Weissman, CAS, 1♂, 1♀; same data except 18-VIII-1974, DB

Weissman, CAS, 6♂, 1♀; *curtatus* USA, CA, Los Angeles Co., SR23S & Mulholland Hwy., 34.0873, -118.8742, 548 m, 13-VII-1972, DB Weissman, CAS, 1♂; TOPOTYPES EXAMINED: (n=128) *costalis* **USA, CA, Ventura Co.**, Point Mugu State Park, 34.100007, -119.017600 4 m, 21-VIII-1974, DB Weissman, CAS, 1♂; Point Mugu State Park, Sycamore Canyon, 34.0728, -119.0145, 4 m, 11-VI-2007, JA Cole, JF Eguizabal, LACM, 1♂; same data except JAC, 1♂; same data except 14-15-VI-2007, JA Cole, JF Eguizabal, LACM 1♀; same data except LACM, 10♂, 1♀; same data except 16-17-VI-2008, JA Cole, LACM, 5♀; same data except JAC, 3♀; same data except 19-VI-2007, JA Cole, JF Eguizabal, LACM, 8♀; same data except 2-3-VI-2008, JA Cole, LACM, 4♀; same data except 28-V-2007, JA Cole, LACM, 1♂; same data except JAC, 1♂; same data except 4-VI-2007, JA Cole, JN Hogue, LACM, 1♂, 3♀; same data except 5-6-VI-2006, JA Cole, LACM, 1♀; same data except 6-7-VII-2006, JA Cole, AMNH, 1♂; same data except 6-VII-2006, JA Cole, LACM, 3♂; same data except 9-10-VI-2008, JA Cole, LACM, 4♀; same data except JAC, 2♂; same data except 9-VI-2005, JA Cole, LACM, 2♂; same data except 9-VI-2005, JA Cole, JA Eguizabal, LACM, 1♂; Point Mugu State Park, visitor parking lot, 34.083332, -119.050003, 4 m, 5-VII-1982, DB Weissman, CAS, 2♂; *curtatus* **USA, CA, Los Angeles Co.,** jct. SR23S & Mulholland Highway, 34.0873, -118.8742, 464 m, 1-VII-2008, JA Cole, LACM, 7♂; same data except, 17-VI-2008, JA Cole, LACM, 2♂, 2♀; same data except JAC, 2♂, 2♀; same data except 14-VIII-1982, DB Weissman, CAS, 1♀; *tectinota* **USA, CA, Los Angeles Co.,** Point Dume Headlands State Park, Birdview and Cliffside Drive, 34.0046, -118.8055, 44 m, 1-VI-2006, JA Cole, JF Eguizabal, LACM, 2♂; same data except 1-VII-2008, JA Cole, LACM, 1♀; same data except JAC,1♀; same data except 10-22-VI-2005, JA Cole, JF Eguizabal, LACM, 1♂; same data except 10-VI-2005, JA Cole, JF Eguizabal, LACM, 5♂, 1♀; same data except JAC, 1♂; same data except 12-13-X-2006, JA Cole, LACM, 10♂; same data except 12-VI-2006, JA Cole, JAC, 1 pair in copula; same data except 12-VI-2006, JA Cole, JF Eguizabal, LACM, 5♀; same data except 16-VI-2006, JA Cole, GL Miller, LACM, 5♀; same data except 22-VI-2005, JA Cole, LACM, 2♂; same data except 22-VI-2005, JA Cole, JF Eguizabal, LACM, 1♂; same data except JAC, 1♂; same data except 26-V-2008, JA Cole, SC DeVaney, LACM, ♀; same data except JA Cole, JF Eguizabal, AMNH, 1♂; same data except LACM, 11♂, 2♀; same data except JAC, 1♂, 1♀; same data except 6-VI-2006, JA Cole, JAC, 1♀; same data except 6-VI-2006, JA Cole, JF Eguizabal, LACM, 1♀; same data except 1-VI-2006, JA Cole, JF Eguizabal, LACM, 1♂; Point Dume, area E of intersection Cliffside and Birdview Drives, 34.000278, -118.806667, 60 m, 5-VII-1982, DB Weissman, CAS, 2♂.

Measurements. (mm, ♂n=14, ♀n=14) Hind femur ♂12.91–15.66, ♀14.60–17.04, pronotum total length ♂7.80–9.52, ♀6.55–8.20, prozona length ♂2.90–5.23, ♀3.54–5.05, metazona dorsal length ♂4.15–5.07, ♀2.60–4.05, pronotum constriction width ♂2.45–3.25, ♀2.54–3.31, metazona dorsal width ♂5.70–7.15, ♀5.35–6.37, head width ♂3.35–4.12, ♀3.88-4.34, ovipositor length ♀10.60–12.89.

Distribution. Santa Monica Mountains of Southern California west of Malibu Creek.

Habitat. Coastal sage scrub, inland chaparral, and riparian habitats. Taken from Monkeyflower, Laurel Sumac (*Malosma laurina*), and Elderberry (*Sambucus* spp.). Nymphs commonly fed on Elderberry flowers and leaves at night.

Seasonal occurrence. Adult activity from late spring (2-VI-2005, JA Cole, LACM) through fall (15-X-2006, JA Cole, LACM). Nymphs from spring (28-V-2007, JA Cole, LACM) through early summer (19-VI-2007, JA Cole, LACM).

Stridulatory file. (n=15) length 2.50–3.70 mm, 78–117 teeth, tooth density 29.3±3.0 (24.6–34.8) teeth/mm.

Song. (n=170) The *A. costalis* song is a high frequency "shuffling" sound caused by echemes ("chirps") that consist of pulse trains that are produced too rapidly to count by ear. Pulse trains of 60±30 ms repeat at a rapid rate of 14.77±1.66 s^{-1}. Mean peak frequency is 17.50±3.67 kHz with significant sound energy in the ultrasonic, where peak frequencies as high as 29.40 kHz were detected with ultrasonic equipment. Echemes are rather consistent in length within a population and contain 10±4 pulse trains (range 3–23) that are repeated at a variable rate of 1–23 (mean 13±4) min^{-1}. Echeme length decreases and pulse train rate increases across a cline from west to east (Cole 2010). Males engage in synchronous choruses.

Karyotype. (n=3) 2n♂=24 (22t+XtYt), topotype T82-21 (S82-33).

Recognition. Morphology, geography, song. The male supra-anal plate is rounded, tongue-like, and dorsally concave, unlike the plates of the Diminutiva Group that have an indentation on the apical margin. The male paraproct has a subapical internal tooth as opposed to the apical tooth of Diminutiva Group species including syntopic *A. dactyla*. The paraproct processes are knob-like, about as long as wide unlike all other Morsei Group species except for *A. morsei*, which have a flat supra-anal plate. The male titillator arms are short and curved, in contrast to the long, distinctly bowed arms of most Diminutiva Group species. Among Morsei Group species with short titillator arms, the lack of a basal notch or constriction eliminates *A. morsei* from consideration, and distinct curvature eliminates *A. hulodomus* and *A. nesiazo*, both of which have nearly straight titillator arms. The female subgenital plate has a

straight apical margin without any projection or tooth as in other Morsei Group species. The short triangular lateral processes of the female subgenital plate are about as long as wide, never long and digitiform as in sympatric *A. dactyla* or other members of the Diminutiva Group. Echemes of *A. costalis* are long with rapidly produced syllables that cannot be counted by a human listener. Echemes of *A. longipennis* distributed to the east are short with the syllables produced more slowly, often slow enough to count at cool ambient temperatures. *A. amathitis* have long echemes of many syllables but produce echemes slow enough to count at ambient temperature.

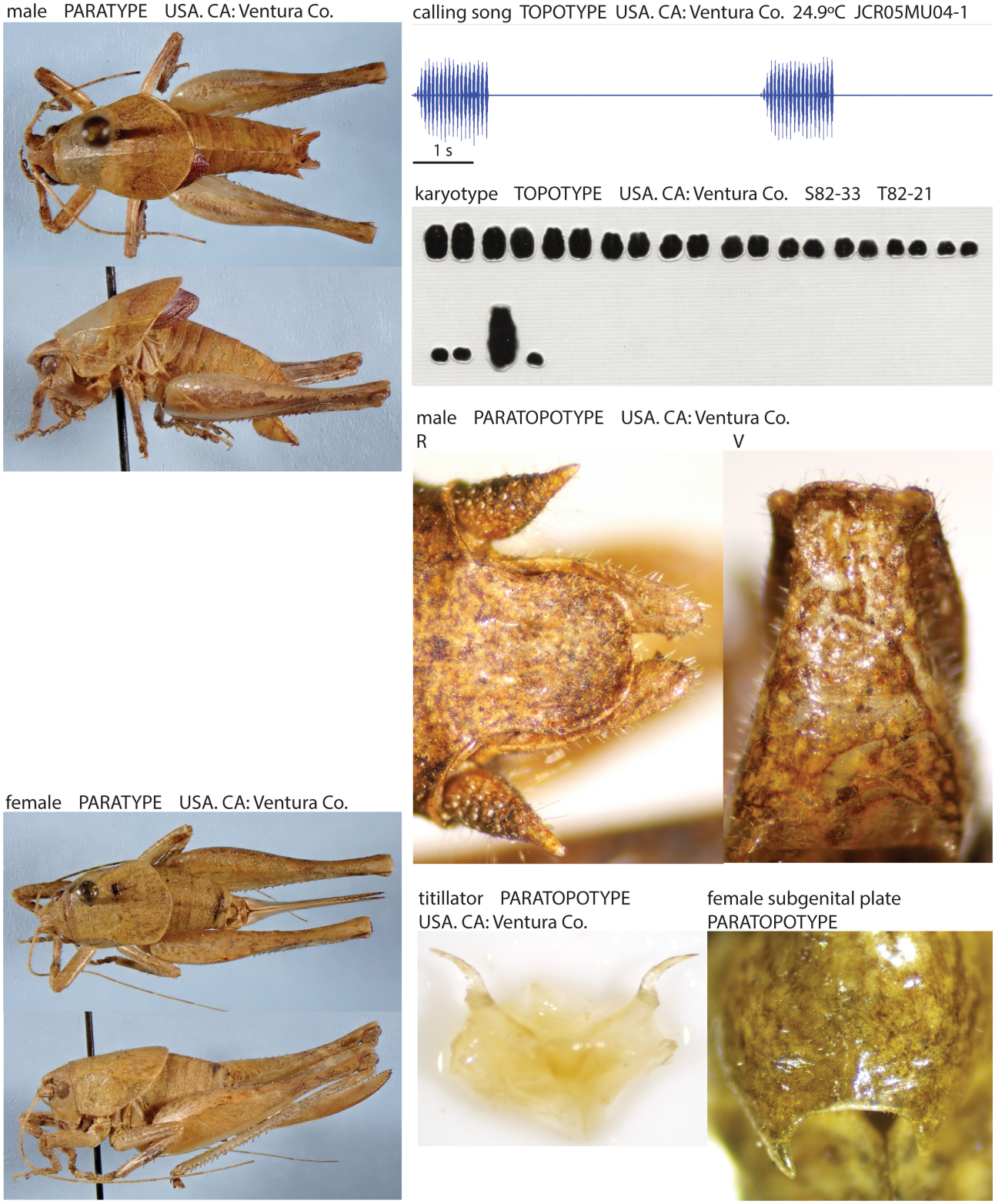


FIGURE 17. *A. costalis* male and female habitus, calling song, male and female terminalia, and karyotype. Idiogram shows karyotype 2n♂=24.

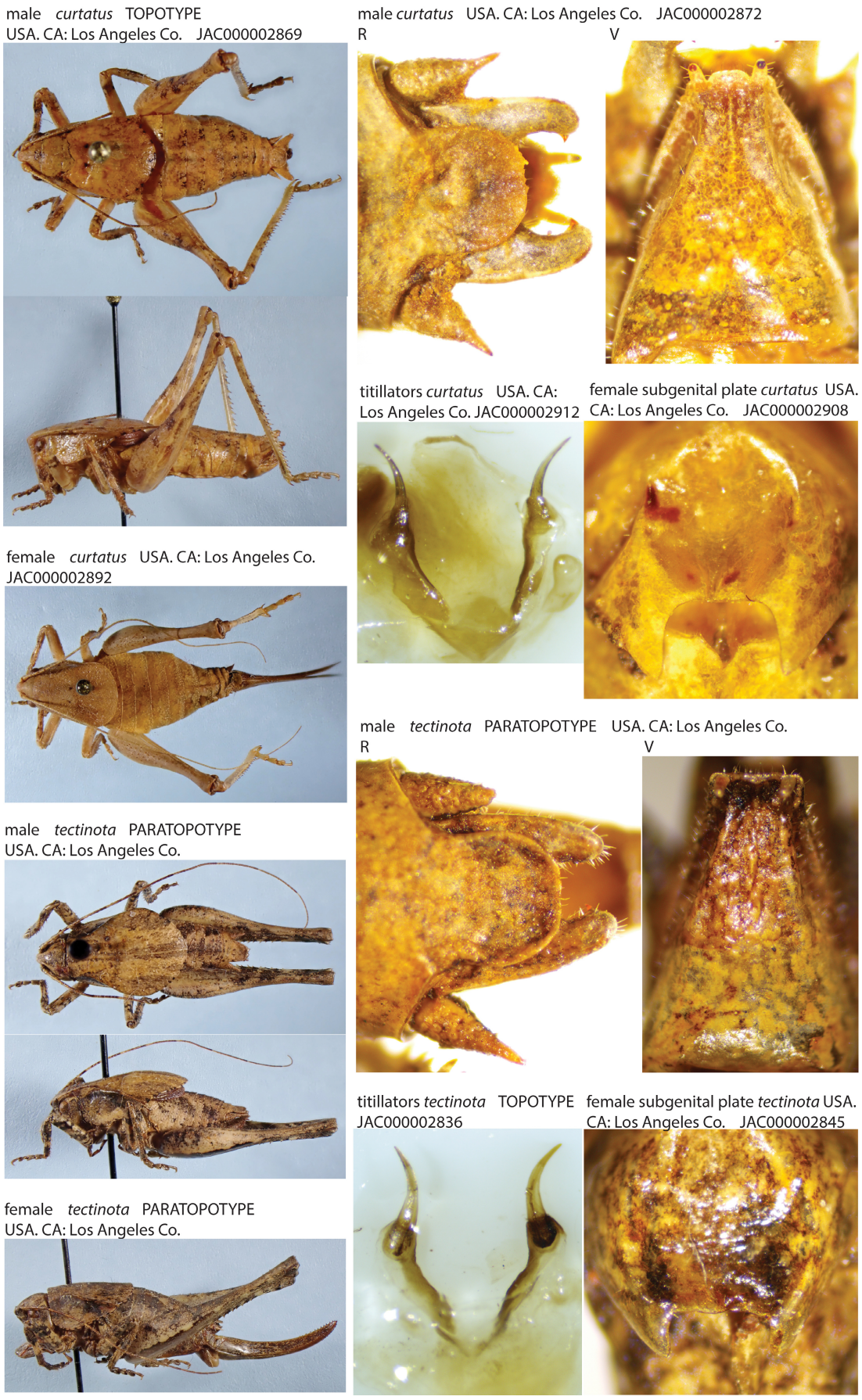


FIGURE 18. Variation in *A. costalis* including previously recognized subspecies synonymized in this work.

Notes. *A. costalis* is a common species across the western Santa Monica Mountains. Sympatry with *A. dactyla* furnishes a case of evolution in action, as the two species show partial partitioning by song, habitat, and phenology. Of the two species *A costalis* occurs in more mesic habitats than does *A. dactyla*. *A. costalis* has a later activity period in midsummer into early winter, while *A. dactyla* adult activity peaks in spring. During wet years populations of both species are syntopic to a greater degree while on drier years, *A. costalis* is limited to riparian areas and other mesic habitats while *A. dactyla* is found on the drier upland slopes. The fast *A. costalis* pulse train rate represents a song extreme for the genus that is located at the contact zone with *A. dactyla* at west end of the Santa Monica Mountains. The pulse train rate decreases to the east away from the contact zone along a cline (Cole 2010). Evolution of this extreme rate was driven by reinforcement due to a history of hybridization with sympatric *A. dactyla* (Cole 2016). Our phylogenetic hypotheses again found significant introgression of *A. dactyla* mtDNA (Fig. 3) into the *A. costalis* lineage that is consistent with hybridization. Both nDNA (Fig. 2) and mtDNA (Fig. 3) recovered this species as monophyletic from the closely related *A. amathitis* and *A. longipennis*.

At Point Dume State Park, Los Angeles County, California, 13 males were mapped along a 122 m transect. Males were clustered into three choruses with 4–5 males each that were separated by 17.8–20.4 m. Within choruses, males were separated by 1.2–14.9 m.

Material examined. (n=53) **All USA, CA, Los Angeles Co.**, Backbone Trail near Tapia Park, 5 miles north of SR1 on Malibu Canyon Road, 34.0799, -118.7037, 156 m, 11-X-2002, JA Cole, LACM, 2♂; same data except JAC, 1♂; same data except 11-XI-2001, JA Cole, LACM, 1♀; same data except 28-VII-2004, JA Cole, LACM, 2♂, 1♀; same data except 29-XII-2006, JA Cole, LACM, 2♂; Charmlee Wilderness Park, 3.8 miles north of SR1 on Encinal Canyon Road, 34.0608, -118.8771, 427 m, 2-VI-2005, JA Cole, LACM, 1♂; same data except 2,7-9-VI-2005, JA Cole, JF Eguizabal, LACM, 4♂; same data except 29-30-V-2,7-VI-2005, JA Cole, JF Eguizabal, LACM, 1♀; same data except 29-30-VI-2006, JA Cole, JF Eguizabal, LACM, 6♂, 3♀; JAC, 1♀; same data except 7-VI-2005, JA Cole, JF Eguizabal, AMNH, 1♀; same data except LACM, 2♂; Leo Carrillo State Park, Nicholas Flat, at end of Decker School Rd., 34.0638, -118.9128, 457 m, 11-X-2002, JA Cole, JAC, 1♂; same data except 13-XII-2005, JA Cole, LACM, 3♂, 1♀; same data except 18-VI-2007, JA Cole, LACM, 1♀; same data except 21-VII-2004, JA Cole, LACM, 2♂; same data except 30-V-2007, JA Cole, LACM, 4♂, 5♀; same data except 31-V-1997, JA Cole, LACM, 1♀; same data except 5-VI-2007, JA Cole, LACM, 1♂, 2♀; same data except JAC, 2♀; Malibu, corner of Malibu Canyon Rd and Pacific Coast Highway, 34.005008, -118.810089, 1-VII-1976, DB Weissman, CAS, 1♂; Solstice Canyon, Santa Monica Mountains, 34.001944, -118.5075, 65 m, 19-VI-2-VII-2009, BV Brown, JN Hogue, LACM, 1♂.

Aglaothorax longipennis (Rentz & Weissman, 1981)

Neduba (*Aglaothorax*) *longipennis*—Rentz & Weissman 1981: 96.

Fig. 15 (distribution), Fig. 19 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 5 (male terminalia), Plate 8 (female subgenital plate), Plate 11 (male titillators), Plate 14 (male calling song).

Common name. Santa Monica Mountains Shieldback

History of recognition. Described in *Neduba* (*Aglaothorax*) (Rentz & Weissman 1981). Returned to *Aglaothorax* (Rentz & Colles 1990) where this species remains classified (Cigliano *et al.* 2025).

Type material. The holotype male in CAS is from the entrance to Big Rock Canyon along Big Rock Drive, Malibu, Los Angeles County, California. Images of the type are available at OSFO (Cigliano *et al.* 2025). PARATYPES EXAMINED: (n=11) **USA, CA, Los Angeles Co.,** Malibu, Big Rock Canyon Near Piedra Chica Rd., 34.035842, -118.609528, 19-VI-1975, DB Weissman, CAS, 7♂, 4♀; TOPOTYPES EXAMINED: (n=8) **USA, CA, Los Angeles Co.,** Malibu, Big Rock Canyon Rd at Rockport Road, 34.035842, -118.609528, 27-VI-1976, DB Weissman, CAS, 1♂; Malibu, intersection of Big Rock and Inland Roads, 34.035842, -118.609528, 5-VII-1982, DB Weissman, CAS, 6♂; junction Big Rock Drive and SR1, 34.0377, -118.6088, 5 m, 16-17-VI-2008, JA Cole, LACM, 1♂.

Measurements. (mm, ♂n=14, ♀n=6) Hind femur ♂12.75–15.82, ♀14.73–17.45, pronotum total length ♂7.54–9.90, ♀6.57–8.45, prozona length ♂3.15–4.31, ♀3.58–4.65, metazona dorsal length ♂4.33–5.95, ♀2.83–4.33, pronotum constriction width ♂2.40–3.20, ♀2.84–3.62, metazona dorsal width ♂5.52–7.06, ♀5.05–6.51, head width ♂3.55–4.11, ♀4.10–4.54, ovipositor length ♀11.30–13.25.

Distribution. Santa Monica Mountains of Southern California east of Malibu Creek, Los Angeles County.

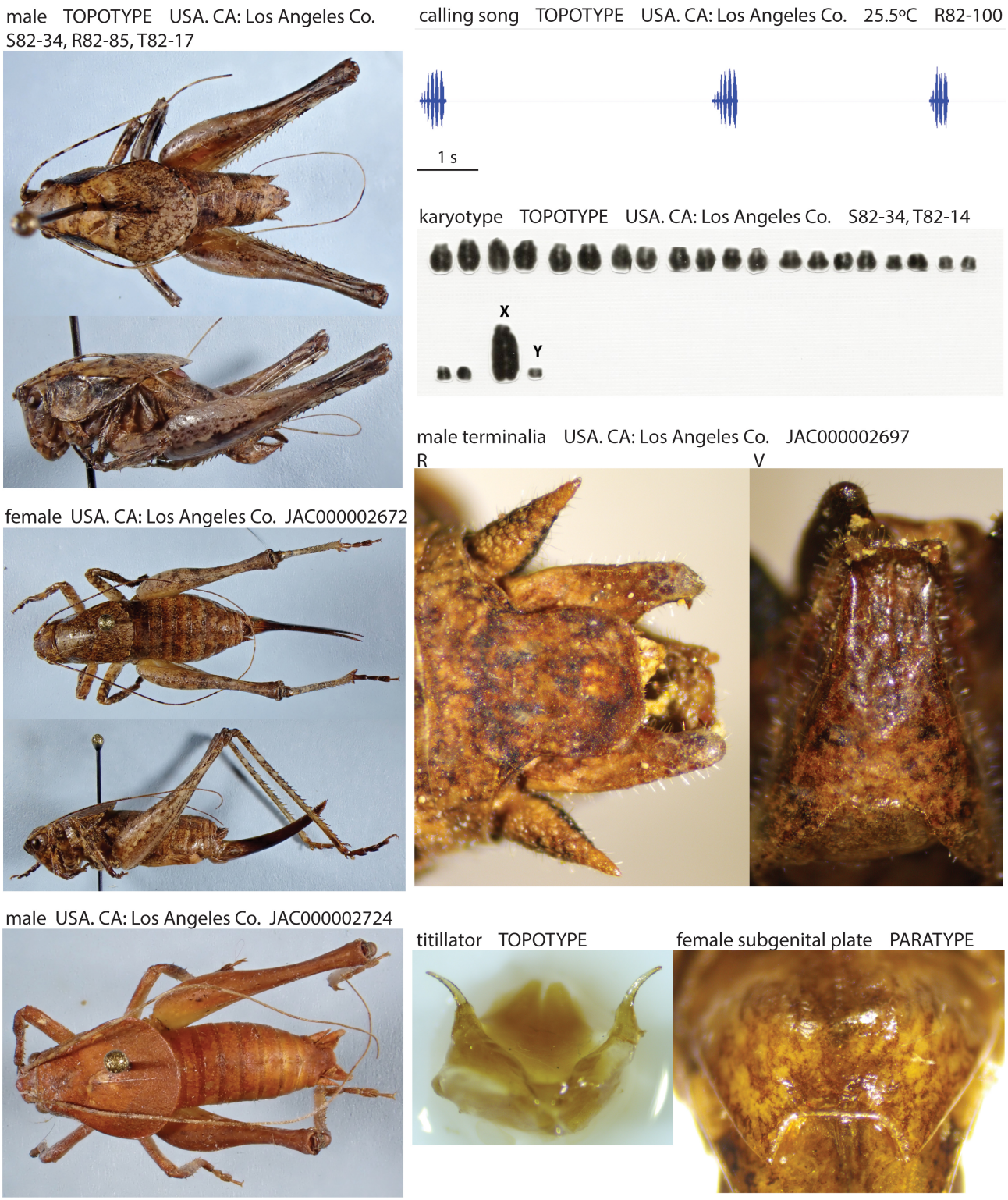


FIGURE 19. *A. longipennis* male and female habitus, calling song, male and female terminalia, and karyotype. Idiogram shows karyotype 2n♂=24.

Habitat. Coastal sage scrub, riparian, and canyons. Generally associated with north facing slopes and canyon bottoms, where they prefer dense tangles of vegetation. Taken from common Buckwheat (*Eriogonum fasciculatum* Benth.), Ornamental figs (*Ficus* sp.) Toyon (*Heteromeles arbutifolia* (Lind.) M. Roem), Laurel Sumac, ornamental pines (*Pinus* spp.), and Scrub Oak (*Quercus berberidifolia* Liebm.). Nymphs were common at night feeding on Canyon Sunflower flowers.

Seasonal occurrence. Adult activity from late spring (18-VI-2022, JA Cole & K Halsey, LACM) into winter (26-XII-2002, JA Cole & JF Eguizabal, LACM). Nymphs from spring (28-V-2008, JA Cole, LACM) through summer (26-VII-1969, BW Howard, LACM).

Stridulatory file. (n=6) length 3.10–3.90 mm, 80–100 teeth, tooth density 26.2±1.2 (24.6–27.8) teeth/mm.

Song. (n=95) A ventriloquistic and often brief song made late at night. Singing begins close to midnight, often around 2300 h, with acoustical activity increasing through the early morning hours, ceasing near dawn. Pulse trains are delivered at a rate slow enough to discern by ear at the cool nighttime temperatures of the habitat, but at 25ºC pulse trains occur too fast to count. Pulse trains last 70±40 ms and are produced at a rate of 13.04±1.83 s^{-1}. Mean peak frequency is 14.95±3.42 kHz, with peak frequencies shifting towards the ultrasonic boundary as high as 19.80 kHz using ultrasonic recording equipment. Male generally produce brief echemes with 4±2 pulse trains/echeme, but later in the evening echeme length increases to as many as 11 pulse trains/echeme. Echeme repetition is sporadic, especially earlier in the evening when two min may pass between echemes, but over the course of the night the echeme rate may be as high as 31 min^{-1}. Males overlap pulse trains in synchronous choruses.

Karyotype. (n=1) 2n♂=24 (22t+XtYt), topotype T82-14 (S82-34).

Recognition. Morphology, song, and geography. The rounded, tongue-like male supra-anal plate, short titillator arms and subapical tooth on the paraproct process place *A. longipennis* in the Morsei Group and separate it from sympatric *A. dactyla* and other members of the Diminutiva Group, which have caudally indented or heart-shaped supra-anal plates and an apical tooth on the paraproct. The cylindrical paraproct process is about twice as long as wide; two neighboring western Transverse Range Morsei Group species, *A. costalis* and many *A. morsei* have short paraproct processes that are knob-like and about as long as wide. The closely related *A. amathitis*, as well as some *A. morsei*, also have similar length paraproct processes, but in *A. longipennis* the supra-anal plate is concave while it is flat in the former two species. The male titillator arms are short and curved unlike the long, bowed titillator arms of most Diminutiva Group species, and lack a notch at the base characteristic of *A. morsei* and *A. constrictans*. The species was named for the protrusion of the male tegmina beyond the posterior edge of the pronotum (Rentz & Weissman 1981). This character is not diagnostic as it depends on the posture of a living male and in dried specimens depends upon preservation. Female *A. longipennis* have a subgenital plate with short lateral processes, unlike the long digitiform processes of sympatric *A. dactyla* and most other Diminutiva Group species. The apical margin of the *A. longipennis* female subgenital plate has a low rounded to triangular emargination unlike that of *A. costalis*, which have a straight apical margin. The song of *A. longipennis* is also diagnostic. Only two species approach the rapid pulse train rate of 11–15 s^{-1} in *A. longipennis*: *A. costalis* has a faster rate at about 13–17 s^{-1} while *A. amathitis* has a slower rate of 9–11 s^{-1}. Both *A. costalis* and *A. amathitis* have more pulse trains in their echemes: 6–14 in *A. costalis*, 4–16 in *A. amathitis* compared with only 2–6 in *A. longipennis*. The range of *A longipennis* is restricted to the Santa Monica Mountains east of Malibu Creek while *A. amathitis* is found on relict sand dunes in the Los Angeles Basin.

Notes. A petition was submitted to list *A. longipennis* as federally endangered (Nagano *et al.* 1994) under the assumption that its range may be restricted to the type locality at Big Rock Drive in Malibu, which has been developed since its description. The IUCN Red List categorizes it as Critically Endangered (Orthopteroid Specialist Group 1996). Our distributional records extend the range of this species throughout the eastern Santa Monica Mountains. Rather than being rare in the strict sense, *A. longipennis* is poorly known because of secretive habits. These katydids prefer dense tangles of vegetation and sing late at night, and then only sporadically. *A. longipennis* is common across much of its range and is protected by Regional, State, and National Park lands such as Griffith Park, Topanga State Park, and the Backbone Trail National Recreation Area. Much of the sample size in this study consisted of adults reared from nymphs that were found feeding on flowers at night. At Topanga State Park, a wide variety of color patterns occur that may be the result of apostatic selection as in *A. morsei* (see species account above, p. 39) and in many species of the related genus *Neduba* (Cole *et al.* 2021). Like *A. costalis*, the *A. longipennis* lineage has captured mtDNA from *A. dactyla* (Fig. 3), suggesting recent or historical hybridization. The two species are sympatric at the type locality of Big Rock Canyon, Malibu.

Material examined. (n=89) **All USA, CA, Los Angeles Co.**, Bel Air Area, 34.083342, -118.448691, 11-VII-1966, C Ishida, LACM, 1♀; same data except 12-VII-1966, C Ishida, LACM, 1♂; Beverly Glen, 34.107786, -118.445636, 20-VII-1960, JAR, LACM, 1♂; Elysian Park, Angel's Point, 34.08330, -118.23658, 205 m, 18-19-V-2022, JA Cole, K Halsey, LACM, 4♂; same data except JAC, 1♂; Fryman Canyon, 5 miles west of US101 on Mulholland Drive, 34.1220, -118.3844, 347 m, 23-XII-2004, JA Cole, LACM, 4♂; Griffith Park, Fern Dell, end of Vermont Avenue, 34.1123, -118.2894, 222 m, 26-XII-2006, JA Cole, JF Eguizabal, LACM, 6♂; same data except JAC, 2♂; Griffith Park, Mount Hollywood Trail, 34.1240, -118.3009, 370 m, 15-XII-2001, JA Cole, AMNH, 1♂;

same data except LACM, 8♂; junction Las Flores Canyon Road and Schueren Road, 34.0625, -118.6486, 469 m, 24-25-VI-2012, JA Cole, LACM, 2♂; junction Las Flores Road and Gorge Road, 34.0507, -118.6391, 66 m, 25-VI-2012 JA Cole, LACM, 1♂; Sullivan Canyon, 34.061856, -118.496064, 26-VII-1969, BW Howard, LACM, 1♂, 1♀; Temescal Canyon Fire Road, Pacific Palisades, CA, 34.048064, -118.526471, 8-XII-1969, BW Howard, LACM, 1♀; Topanga State Park, Dead Horse Trail, 34.0915, -118.5939, 274 m, 12-VI-2007, JA Cole, JAC, 1♂; same data except 13-VI-2006, JA Cole, LACM, 1♂, 3♀; same data except 15-16-X-2006, JA Cole, JF Eguizabal, LACM, 10♂; same data except 15-VII-2005, JA Cole, LACM, 1♂; same data except 16-VI-2006, JA Cole, GL Miller, LACM, 2♀; same data except 28-V-2008, JA Cole, LACM, 3♀; same data except 3-7-VII-2006, JA Cole, JF Eguizabal, AMNH, 1♂, 1♀; same data except LACM, 5♂; same data except JAC, 1♂; same data except 3-VII-2006, JA Cole, JF Eguizabal, LACM, 4♂; same data except 4-5-VI-2006, JA Cole, L Gonzalez, LACM, 7♀; same data except JAC, 1♀; same data except 4-5-VI-2008, JA Cole, L Gonzalez, LACM, 1♀; same data except 7-VI-2006, JA Cole, LACM, 1♂, 4♀; same data except JAC, 1♀; same data except XII-2005, JA Cole, LACM, 2♂; UCLA Stunt Ranch Santa Monica Mountains Reserve, 34.0951, -118.6486, 374 m, 12-13-VI-2014, JA Cole, DA Gray, LACM, 2♂, 1♀; Topanga State Park, 34.09, -118.59, 365 m, 29-I-2004, DA Gray, CSUN, 1♂.

Aglaothorax amathitis Cole, Weissman, and Lightfoot, sp. nov.

Fig. 15 (distribution), Fig. 20 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 5 (male terminalia), Plate 8 (female subgenital plate), Plate 11 (male titillators), Plate 14 (male calling song).

Common Name. Bluffs Shieldback.

History of recognition. Populations from Palos Verdes, Los Angeles County, California treated as *A. morsei* (Rentz & Birchim 1968).

Type material. HOLOTYPE MALE: **USA, California, Los Angeles County,** Playa Del Rey, Ballona Wetlands, 33.96557N, 118.44508W, 4 m, 24-VI-1992, DB and BI Weissman, leg. S92-58, R92-75, T92-27, deposited in CAS, Entomology type # 20237. PARATYPES: (n=61) **USA, CA, Los Angeles Co.**, same data as holotype, CAS, 2♂, 2♀; El Segundo Dunes, 33.909722, -118.427222, 6-VI-1941, WD Pierce, LACM, 2♂, 2♀; El Segundo Sand Dunes, 33.909722, -118.427222, 13-VII-1938, WD Pierce, LACM, 1♂; same data except 17-VIII-1938, WD Pierce, LACM, 1♂; El Segundo, 33.909722, -118.427222, 2-VIII-1977, JN Hogue, CSUN, 1♀; same data except 30-V-1941, WD Pierce, LACM, 2♂, 3♀; Kenneth Hahn SRA, Baldwin Hills, 34.0042, -118.3592, 126 m, 26-VI-2006, JA Cole, JF Eguizabal, LACM, 4♂, 1♀; same data except 27-28-V-2008, JA Cole, AMNH, 2♂; same data except LACM, 9♂; same data except 27-28-VI-2006, JA Cole, JF Eguizabal, LACM, 8♂; same data except 28-V-2005, JA Cole, MFJ Storc, LACM, 1♂; same data except 29-30-V-2007, JA Cole, LACM, 1♂; same data except 7-VII-2021, JA Cole, J Bailey, LACM, 2♂; Ladera Linda Park, 12 miles south of I-405 off Western Boulevard, 33.7383, -118.3479, 149 m, 20-VI-2008, JA Cole, LACM, 5♂; Malaga Dune, Rancho Palos Verdes, 33.8004, -118.3858, 61 m, 19-20-VI-2008, JA Cole, AMNH, 1♂; same data except LACM, 8♂, 2♀; Rancho Palos Verdes Peninsula, Center 9/11 Memorial, 33.76917, -118.36583, 265 m, 7-VII-2021, JA Cole, J Bailey, LACM, 1♂.

Measurements. (mm, ♂n=12, ♀n=4) Hind femur ♂13.24–16.25, ♀17.69–22.16, pronotum total length ♂7.79–10.52, ♀8.30–10.15, prozona length ♂3.27–5.43, ♀4.19–5.25, metazona dorsal length ♂4.10–6.60 ♀4.11–4.96, pronotum constriction width ♂2.57–3.35, ♀3.19–3.76, metazona dorsal width ♂5.60–7.24, ♀6.00–7.83, head width ♂3.40–4.20, ♀4.50–5.41, ovipositor length ♀11.68–15.75.

Distribution. Palos Verdes Peninsula and Los Angeles Basin, Los Angeles County, California.

Habitat. Coastal bluffs and stabilized sand dunes. Naturally inhabits coastal sage scrub, riparian, and grassland, but also found in disturbed habitats and on ornamental vegetation near residential areas. Taken from Iceplant or Hottentot Fig (*Carpobrotus edulis* (L). L. Bolus), Lemonade Sumac (*Rhus integrifolia* (Nutt.) W.H. Brewer & S. Watson), Elderberry (*Sambucus* spp.), Rosemary (*Rosmarinus officinalis* L.), and Peruvian Pepper Tree (*Schinus mollae* L.). Although typically found on herbaceous vegetation, they may be arboreal where trees occur.

Seasonal occurrence. Wide adult activity season across spring and summer, from 12-V-1946 (no collector, LACM) to 27-IX-1980 (C. Nagano & E. Birdsall, LACM).

Stridulatory file. (n=6) length 3.10–4.00 mm, 80–104 teeth, tooth density 27.1±2.9 (22.5–30.3) teeth/mm.

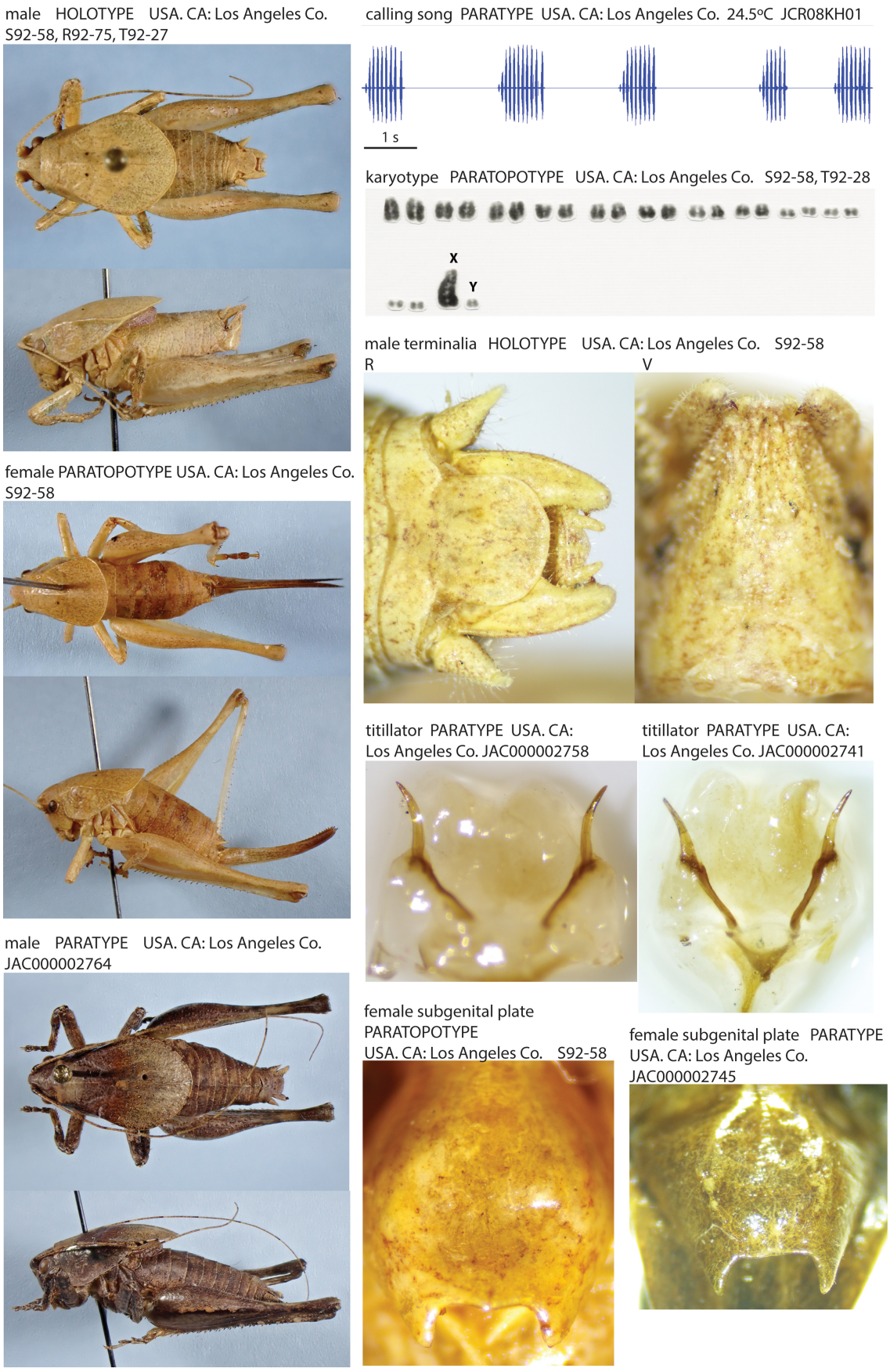


FIGURE 20. *A. amathitis* male and female habitus, calling song, male and female terminalia, and karyotype. Idiogram showing karyotype 2n♂=24, S92-58, T92-28.

Song. (n=29) Pulse trains 80±40 ms in length are repeated at a rapid rate of 9.70±0.93 s^{-1}. Mean peak frequency is 16.02±3.38 kHz; using high frequency recording equipment the peak frequency borders on ultrasonic at 20.50 kHz. Echemes that consist of 10±6 pulse trains (range 3–24 pulse trains/echeme) occur at a rate of 1–21 echemes/min^{-1}. The number of pulse trains/echeme is similar to *A. costalis* but the *A. costalis* pulse train rate is approximately one third faster at 15 s^{-1}.

Karyotype. (n=3) 2n♂=24 (22t+XtYt), paratopotype T92-28 (S92-58).

Recognition. Morphology, song, ecology, and geography. Male supra-anal plate rounded and tongue-like, paraproct with a subapical tooth, and titillators short, unlike Diminutiva Group species with the supra-anal plate heart-shaped or indented on the apical margin, the paraproct process tooth apical, and the titillators long and bowed. The male paraproct is cylindrical and twice as long as wide unlike *A. costalis*. The male supra-anal plate of *A. amathitis* is flat while those of *A. costalis* and *A. longipennis* are dorsally concave. The short male titillator arms do not have the basal notch found in *A. morsei* and *A. constrictans*. The female subgenital plate lateral processes are short, unlike Diminutiva Group species, with the posterior margin low and rounded rather than straight as in *A. costalis*. The *A. amathitis* pulse train rate of 9–11 s^{-1} is faster than that of *A. morsei* at 4–6 s^{-1}. The songs of *A. amathitis* and *A. longipennis* are similar, but the echemes of the former contain more pulse trains (3–24 vs. 2–6) that are produced a slower rate (9–11 vs. 11-15 s^{-1}). This species inhabits stabilized sand dunes in the Los Angeles Basin.

Etymology. Gr. *amathitis* dwelling in sand. Named after the coastal sand dune habitats of this species.

Notes. This new species occurs in and around undeveloped habitats in the Los Angeles Basin. Whereas *A. longipennis* occurs more widely than initially thought, *A. amathitis* is known from few localities, most of which are disturbed and subject to high human impact, like Malaga Dune in Palos Verdes and Kenneth Hahn State Recreation Area in Baldwin Hills. The coastal bluff and dunes habitats within the range of this species harbor many endemic and protected organisms, notable among them the federally endangered El Segundo Blue (*Euphilotes battoides allyni* Shields) and the Palos Verdes Blue (*Glaucopsyche lygdamus palosverdensis* Perkins & Emmel) butterflies. The type locality at Ballona Wetlands is now protected. Genetic resolution was only possible with fast evolving mtDNA markers (Fig. 3) suggesting recent divergence. Unlike with *A. longipennis* mitochondrial capture was not found in the *A. amathitis* lineage, which is expected in the absence of contemporary or historical sympatry with *A. dactyla*. An adult male from Malaga Dune at Rancho Palos Verdes succumbed to an *Ormia* tachinid fly parasitoid while in captivity.

Material examined. (n=7) In addition to Type Material above, **All USA, CA, Los Angeles Co.,** Ballona Wetlands, Playa Del Rey, 33.9602, -118.4482, 4 m, 2-3-VII-2012, JA Cole, 1♂ sound record; Dockweiler Beach, El Segundo Blue Restoration Area by Imperial and Vista Del Mar, 33.9222, -118.4333, 3-VII-2012, JA Cole, 1♂ sound record; Redondo Beach, 33.849182, -118.388408, 6-VIII-1938, no collector, LACM, 3♀; Windsor Hills, 33.988902, -118.353965, 114 m, 12-V-1946, LACM, 2♂.

Aglaothorax islandica (Rentz & Weissman, 1981)

Neduba (*Aglaothorax*) *morsei islandica*—Rentz & Weissman, 1981: 101.
Aglaothorax islandica **stat. rev.** (Revised to species level).
Neduba (*Aglaothorax*) *morsei santacruzae*—Rentz & Weissman 1981: 103 **New junior subjective synonym**.
Fig. 15 (distribution), Fig. 21 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 5 (male terminalia), Plate 8 (female subgenital plate), Plate 12 (male titillators), Plate 15 (male calling song).

Common name. Northern Channel Islands Shieldback.

History of recognition. Rentz & Weissman (1981) described two California Channel Islands endemics under *Neduba (Aglaothorax)*: *morsei santacruzae* from the University of California Research Station on Santa Cruz Island, and *morsei islandica* from Frenchy's Cove, West Anacapa Island. The disjunct distribution of the latter encompassed the islands immediately to the west and east of Santa Cruz Island. After consulting expanded series, we conclude that a single taxon occurs on the northern Channel Islands, for which genetic distance lends evidence of specific rank. We elevate *A. islandica* to species rank as a more appropriate species epithet and relegate *santacruzae* to a junior subjective synonym of *A. islandica*.

male PARATOPOTYPE
USA. CA: Ventura Co.



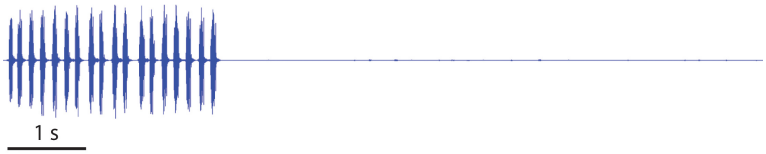
female PARATOPOTYPE
USA. CA: Ventura Co.



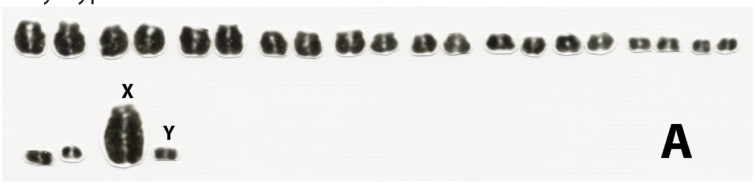
female *santacruzae* TOPOTYPE
USA. CA: Santa Barbara Co.



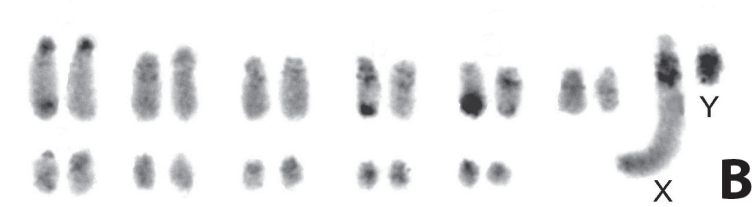
calling song USA. CA: Santa Barbara Co. 21.3ºC S18-30 R19-16



karyotype USA. CA: Santa Barbara Co. S82-40 T82-29

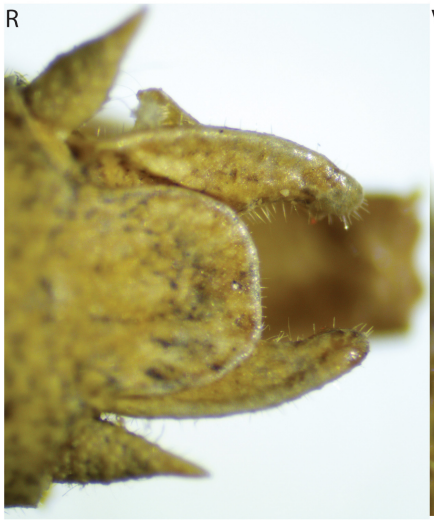


karyotype USA. CA: Santa Barbara Co. S18-30 T19-6

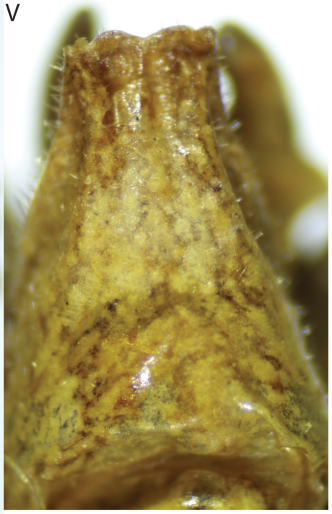


male terminalia PARATOPOTYPE USA. CA: Ventura Co. DCR111

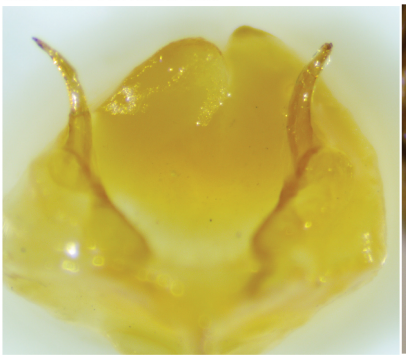
R



V



titillator PARATOPOTYPE
USA CA: Ventura Co.



female subgenital plate
PARATOPOTYPE

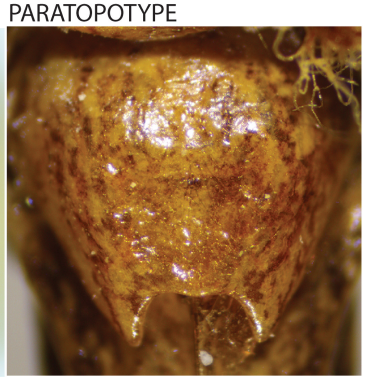


FIGURE 21. *A. islandica* male and female habitus, calling song, male and female terminalia, and karyotype. Idiograms of karyotype 2n♂=24 showing differences in preparation techniques: A. prepared by NU, B. F_1 prepared by EWS.

Type material. The holotype male of *A. islandica* from West Anacapa Island resides in CAS, type # 12440. Images of the type are available on OSFO (Cigliano *et al.* 2025). PARATYPES: (n=24) **USA, CA, Santa Barbara Co.,** Santa Cruz Island Reserve Field Station, 33.9969, -119.7260, 75 m, 1-VIII-1969, DC Rentz, DB Weissman, CAS, 2♂; same data except 14-VIII-1974, DB Weissman, CAS, 2♀; Santa Rosa Island, 0.5 miles north Black Mountain, 33.950003, -120.100964, 396 m, 9-VIII-1974, DB Weissman, CAS, 2♂, 1♀; Santa Rosa Island, Black Mountain, 33.950003, -120.100964, 396 m, DB Weissman, CAS, 1♀; **Ventura Co.**, West Anacapa Island, Frenchy's Cove, 34.01056, -119.425117, 23-VI-1971, DC Rentz, DB Weissman, CAS, 2♂, 1♀; same data except 24-VI-1971, DC Rentz, DB Weissman, CAS, 1♂; Middle Anacapa Island, 34.004449, -119.393171, 16-VI-1970, DB Weissman, CAS, 2♂, 1♀; same data except 17-VI-1970, DB Weissman, CAS, 4♂; same data except 22-VIII-1974, DB Weissman, CAS, 4♂, 1♀.

Measurements. (mm, ♂n=9, ♀n=8) Hind femur ♂13.59–16.75, ♀15.61–18.54, pronotum total length ♂8.45–9.85, ♀7.55–8.95, prozona length ♂3.66–4.18, ♀3.44–4.85, metazona dorsal length ♂4.70–5.85, ♀3.55–4.85, pronotum constriction width ♂2.72–3.60, ♀3.10–3.75, metazona dorsal width ♂5.79–7.48, ♀5.51–6.58, head width ♂3.80–4.40, ♀4.26–5.75, ovipositor length ♀11.36–12.95.

Distribution. Santa Barbara and Ventura Counties on three of the four northern California Channel Islands: Anacapa, Santa Cruz, and Santa Rosa. The species was never encountered on the windswept, low elevation San Miguel Island (Rentz & Weissman 1981).

Habitat. Coastal bluffs, chaparral, oak woodland, and dry riverbeds (Rentz & Weissman 1981). Several males were singing above 3 m in planted live oaks around the field station on Santa Cruz Island (S18-30).

Seasonal occurrence. Long adult season from spring through summer from 19-III-1982 (CW Melten, CAS) to 22-VIII-1974 (DB Weissman, CAS).

Stridulatory file. (n=6) length 3.50–3.75 mm, 89–100 teeth, tooth density 26.3±1.3 (24.1–27.7) teeth/mm.

Song. (n=3) Common song type of small *Aglaothorax* with slow series of pulse trains that may be counted by a human listener. Series of pulse trains 90±40 ms in length are produced at a rate of 6.55±0.75 s^{-1}. Mean peak frequency is 12.63±1.80 kHz. Echemes consist of 15±4 pulse trains (range 10–18). Echemes repeat at a rate of 6.6 min^{-1}.

Karyotype. (n=3) 2n♂=24 (22t+XtYt), T82-29 (S82-40), T19-6 (S18-30), both specimens from Santa Cruz Island Field Station Area.

Recognition. Male morphology, geography. This is the only *Aglaothorax* species found on the California Channel Islands. The male paraproct projections are about twice as long as wide and bear a well-developed mesal tooth that is located considerably far basad from the apex. This condition is shared by *A. hulodomus* and a few populations of *A. nesiazo*. The male supra-anal plate is flat and rounded or square with rounded caudal edges, similar to that of *A. morsei*. The male titillator arms are long for the Morsei Group and distinctly curved; the similar *A. hulodomus* and *A. nesiazo* have nearly straight titillator arms. The female subgenital plate has short triangular lateral processes as opposed to the long lateral processes of most Diminutiva Group species.

Notes. Populations on the Channel Islands are large, and considerable series were collected at oatmeal trails by DBW up Canyon de Islay on Santa Cruz Island in 2004 (S04-64, 10-VII-2004). At an identical oatmeal trail laid on 12-VII-2018 (S18-30), only five adult females and no adult males were collected. The five field-collected adult females of *A. islandica* (from S18-30, Santa Cruz Island) were housed together from 21-VII-2018 to 7-VIII-2018, as described on p. 6, when eggs were removed and kept at room temperature, in moist sand, until 29-X-2018. Eggs were then kept at 3ºC until 15-III-2019, when they were returned to room temperature. First hatching occurred 4-IV-2019 with first adults appearing 22-VI-2019. Hatching success was limited and we suspect that a 4.5-month chill period is probably not necessary since such low temperatures are rarely seen on Santa Cruz Island.

The northern California Channel Islands are an archipelago of near-shore fringing islands that, while connected to each other during the last glacial maximum, lack any evidence of a land bridge connecting them to the mainland (Salerno *et al.* 2023). Consistent with long-term geographic isolation, *A. islandica* is a basal member of the Morsei Group (Figs. 2–4), which is a clade of Transverse Range and Peninsular Range *Aglaothorax*. The only other nedubine katydid that occurs on the California Channel Islands is *Neduba propsti* (Rentz & Weissman 1981) on Santa Catalina Island (Cole *et al.* 2021; Rentz & Weissman 1981), an island that is not geologically related to the northern Channel Islands (Legg *et al.* 2004) and has also never been connected to mainland California. Reflecting long-term isolation, genetic resolution was strong (Figs. 2, 4) although two haplotypes rendered *A. islandica* polyphyletic with mtDNA (Fig. 3).

Material examined. (n=67) **All USA, CA, Santa Barbara Co.**, Santa Cruz Island, Canyon de Islay, 33.99588, -119.73811, 79-244 m, 12-VII-2018, DW & DB Weissman, CAS, 3♂, 6♀; same data except 10-VII-2004, DB Weissman, CAS, 18♂, 38♀; Santa Cruz Island Reserve Field Station, 33.9969, -119.7260, 75 m, 19-III-1982, CW Melten, CAS, 1♂; Santa Rosa Island, Black Mountain, 33.950003, -120.100964, 396 m, DB Weissman, CAS, 1♂.

Aglaothorax hulodomus Cole, Weissman, and Lightfoot, sp. nov.

Fig. 15 (distribution), Fig. 22 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 5 (male terminalia), Plate 8 (female subgenital plate), Plate 12 (male titillators), Plate 15 (male calling song).

Common name. Forest Home Shieldback.

History of recognition. None.

Type material. HOLOTYPE MALE: **USA, California, San Bernardino County,** San Bernardino Mountains, State Highway 18, 0.7 mile W & E of Skyforest, 34.23528N, 117.19149W, 1750 m, 26-VII-1989, DB & DW Weissman leg., S89-56, R89-64, T89-39, DNA09-35, 3.55 [stridulatory file length], 102 [stridulatory file tooth count] excised tegmen in gelcap below specimen, deposited in CAS, Entomology type #20238.

PARATYPES: (n=71) **USA, CA, Riverside Co.**, Cactus Spring Trailhead, 0.4 mi. S of SR74 on Pinyon Flats Sta. Rd., 33.5804, -116.4507, 1200 m, 28-29-VI-2004, JA Cole, LACM, 1♂; Chino Canyon, 1.5-3.5 mi. SW SR111, San Jacinto Mountains, 33.84662, -116.58295, 305 m, WR Icenogle, CAS, 1♂; Fern Valley, Idyllwild, 33.758631, -116.698074, 1737 m, 10-IX-1960, ER Tinkham, CAS, 1♂; same data except X-1958, ER Tinkham, CAS, 1♂; Idyllwild, 33.740021, -116.718908, 1646 m, 15-XII-1964, ER Tinkham, CAS, 1♀; same data except 28-VIII-1964, D Bryant, CAS, 1♂; Marion Canyon Campground, San Bernardino National Forest, 33.79278, -116.73222, 2012 m, 27-VIII-2020, JA Cole, J Bailey, LACM, 5♂; Pinyon Flat Campground, 14 miles southwest of Palm Desert on SR74, 33.5856, -116.4570, 1219 m, 28-29-VI-2004, JA Cole, LACM, 1♂; same data except 28-29-VI-2005, JA Cole, LACM, 6♂; same data except 3-4-VII-2008, JA Cole, LACM, 2♂; San Jacinto Mountains, 0.5 km N of Idyllwild on Hwy. 243, 33.744526, -116.718908, 1676 m, 16-VIII-1982, DB Weissman, CAS, 1♂; San Jacinto Mountains, 11.3 miles N of Idyllwild on Hwy. 243, 33.903975, -116.718908, 1615 m, 16-VIII-1982, DB Weissman, CAS, 6♂, 1♀; Santa Rosa Mountains, 33.431421, -116.227785, 1-XI-1952, ER Tinkham, CAS, 1♂; SR371 East of Anza, 33.55944, -116.60528, 1375 m, 26-VIII-2020, JA Cole, J Bailey, LACM, 2♂; SR74 roadside through Santa Rosa Indian Reservation, 33.56139, -116.56750, 1503 m, 26-VIII-2020, JA Cole, J Bailey, LACM, 1♂; Whitewater Canyon, 3 mi. N of Hwy. 10 on Whitewater Canyon Rd., 33.9579, -116.6463, 431 m, 20-21-VI-2006, JA Cole, GL Miller, LACM, 4♂, 1♀; Whitewater Canyon, 33.9579, -116.6463, 20-VI-1974, ER Tinkham, CAS, 1♂; **San Bernardino Co.**, same data as holotype, 1♂, 2♀; 0.4 mi. W Skyforest at Switzer Park Picnic Grounds, 34.235285, -117.186227, 1740 m, 20-VII-1992, DB Weissman, CAS, 1♀; 0.7 mi. W of Skyforest on Hwy. 18, 34.235284, -117.191491, 1707 m, 17-VIII-1982, DB Weissman, CAS, 2♂; Camp O-ongo, near Running Springs, 34.207786, -117.109205, 8-12-VIII-1966, CL Hogue, LACM, 1♂; same data except 1890 m, 16-22-VIII-1980, CL & JN Hogue, LACM, 1♂; San Bernardino Mts., Camp O-Ongo, 2.5 mi. NW of Running Springs, 34.22, -117.12, 1900 m, 21-VIII-1978, JN Hogue, CSUN, 1♀; same data except 22-28-VIII-1981, CL & JN Hogue, CSUN, 1♀; Forest Home, Mill Creek, 34.09009, -116.93140, 1859 m, X-1964, ER Tinkham, CAS, 1♂, 2♀; Hanna Flat Campground, San Bernardino National Forest, 34.28778, -116.97556, 2152 m, 10-11-VIII-2022, JA Cole, C Wong, LACM, 2♂; Mill Creek, 33.940314, -117.622585, no date, ER Tinkham, CAS, 1♀; Oak Glen beyond Penyoct Flat, 34.049457, -116.947804, 1487 m, X-1953, ER Tinkham, CAS, 1♂; San Bernardino Mountains, 0.8 mi. E Lake Arrowhead (City) on Highway 173, 34.248339, -117.175167, 1520 m, 20-VII-1992, DB Weissman, CAS, 4♀; San Bernardino Mountains, 34.125566, -116.876415, 10-IX-1957, ER Tinkham, CAS, 1♂; same data except 12-X-1952, ER Tinkham, CAS, 1♂, 1♀; San Bernardino Mountains, Mill Creek Road, 34.090712, -117.037165, 1463 m, 25-VII-1981, DC Lightfoot, DB Weissman, CAS, 1♂; San Bernardino, 34.088624, -117.280598, 13-X-1952, ER Tinkham, CAS, 1♂; Switzer Picnic Area, San Bernardino National Forest, 34.23284, -117.18608, 1724 m, 19-20-VII-2013, JA Cole, JF Eguizabal, AMNH, 1♂, 1♀; same data except LACM, 4 ♂; **San Diego Co.**, Mariposa Ranch, Anza, 33.46161, -116.63947, 1287 m, 20-21-VII-2019, A Abela, LACM, 1♀.

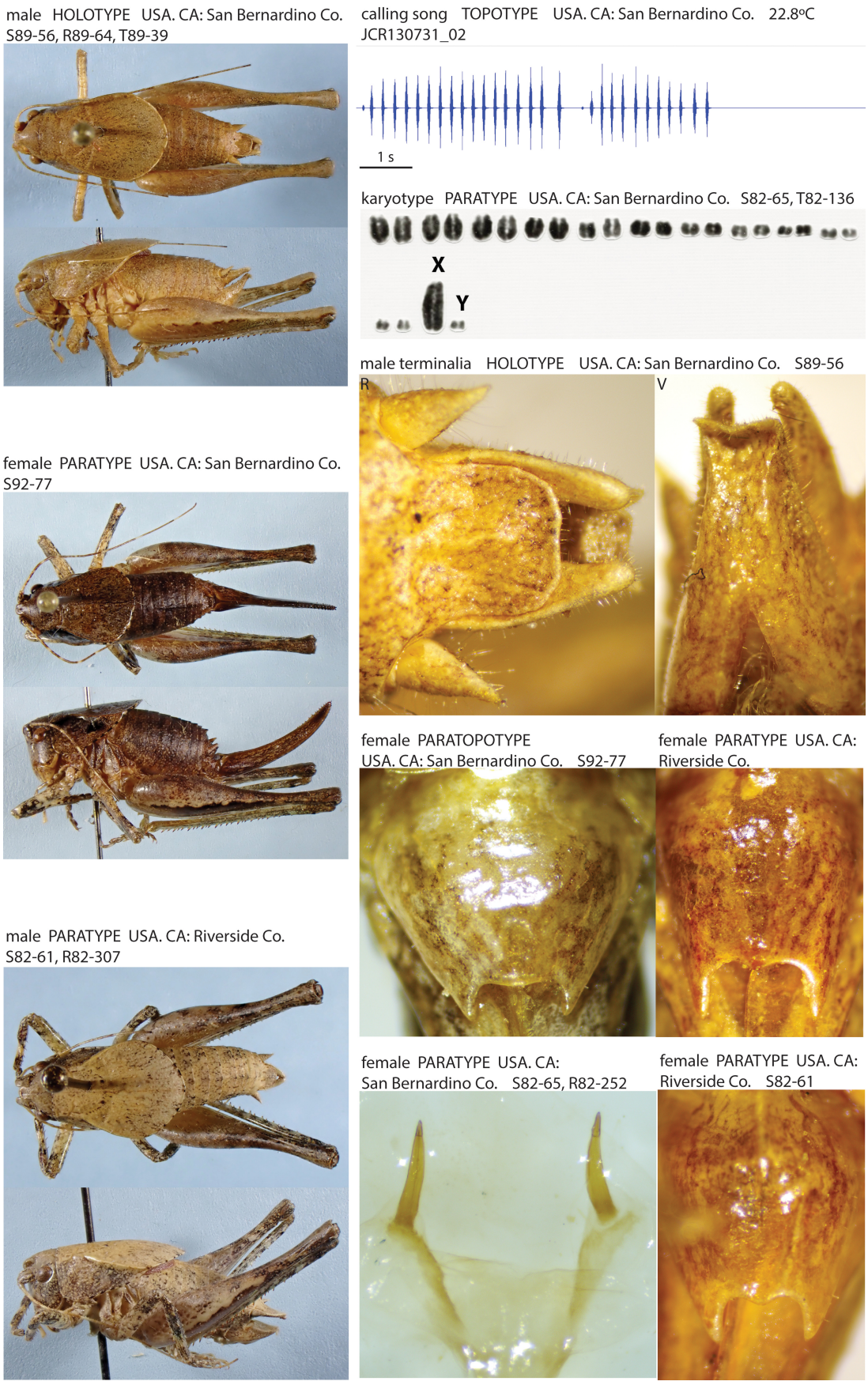


FIGURE 22. *A. hulodomus* male and female habitus, calling song, male and female terminalia, and idiogram of karyotype 2n♂=24.

Measurements. (mm, ♂n=9, ♀n=6) Hind femur ♂13.44–15.73, ♀16.83–19.35, pronotum total length ♂7.79–9.26, ♀7.65–9.05, prozona length ♂3.41–4.72, ♀4.03–4.90, metazona dorsal length ♂4.23–5.28, ♀3.27–4.48, pronotum constriction width ♂2.59–3.20, ♀3.05–3.52, metazona dorsal width ♂5.45–6.15, ♀5.41–6.17, head width ♂3.86–4.20, ♀4.60–5.10, ovipositor length ♀10.90–12.47.

Distribution. Moderate to high elevations in the Transverse and Peninsular Ranges of California including the San Bernardino, San Jacinto, and Santa Rosa Mountains. Populations exist at a wide range of elevations from 300 to 2150 m, the mode of elevation being 1600 m.

Habitat. Chaparral and understory of mixed woodland. Taken from Manzanita (*Arctostaphylos* spp.), *Ceanothus* spp., Yerba Santa (*Eriodictyon* spp.), and laurel sumac.

Seasonal occurrence. Adults from summer (20-VI-1974, ER Tinkham, CAS) through fall (13-X-1952, ER Tinkham, CAS). Nymphs apparently overlap adults over a considerable portion of the season, as a female nymph was found alongside adult males 20-VII-2013 (JA Cole & JF Eguizabal, LACM) that matured on 27-VII.

Stridulatory file. (n=9) length 3.30–3.90 mm, 91–113 teeth, tooth density 27.8±1.7 (24.6–30.0) teeth/mm.

Song. (n=37) Standard song structure for genus with slowly delivered pulse trains that are countable by a human listener. Pulse trains 60±10 ms in length produced at a rate of 5.33±0.82 s^{-1}. Mean peak frequency is 15.19±3.10 kHz, with ultrasonic peak frequencies detected up to 23.5 kHz. Echemes are variable and frequently long, consisting of 27±13 pulse trains (range 7–56 pulse trains/echeme). Echeme repetition is irregular; males may remain silent for a minute or more or repeat up to 8 min^{-1}.

Karyotype. (n=7) 2n♂=24 (22t+XtYt), paratype T82-136 (S82-65).

Recognition. Morphology, habitat. Male supra-anal plate rounded and paraproct processes with subapical tooth, characters that eliminate the Diminutiva Group from consideration, which are characterized by a heart-shaped caudally indented supra-anal plate and an apical tooth on the paraproct process. Male paraproct with an internal tooth that is positioned far from apex of process, which separates *A. hulodomus* from all other Morsei Group species except *A. islandica*, which is a Channel Islands endemic, and some *A. nesiazo*. The paraproct processes are about two times as long as wide in *A. hulodomus*, shorter than those of *A. nesiazo*, which also has a square supra-anal plate that is distinct from the rounded, flat supra-anal plate of *A. hulodomus*. From *A. costalis*, the male supra-anal plate is concave in that species but flat in *A. hulodomus*. The styli on the male subgenital plate are narrow and cylindrical in *A. hulodomus* but thick and conical in *A. conistylus,* and that species also has longer paraproct processes. The male titillator arms are short and barely curved laterally, nearly straight, and without a notch at the base; Diminutiva Group titillator arms are long, and *A. morsei* distributed to the west have a mesal notch at the base of the titillator arm. Female *A. hulodomus* have short, triangular lateral processes on the subgenital plate unlike the long, digitiform processes of most Diminutiva Group species.

Etymology. Gr. *hulodomus* forest home. Refers to the mountain woodland habitats of this species.

Notes. This eastern Transverse Range and northern Peninsular Range species replaces *A. morsei* to the east and south. This species was only recovered as monophyletic from concatenated data (Fig. 4). The genetic distance between *A. hulodomus* and *A. morsei* is substantial (Figs. 2–4) suggesting isolation by distance. Lineage sorting was incomplete between *A. hulodomus*, *A. conistylus*, and *A. nesiazo* (Figs. 2–3) which are geographically proximal, the first two species situated at the connection between the San Gabriel and San Bernardino Mountains at Cajon Pass. Some factors that may maintain low levels of gene flow are low dispersal ability and dissimilar habitat preferences: *A. morsei* inhabits riparian corridors and other mesic areas while *A. hulodomus* occurs in woodland understory. This species is sympatric with *A. gurneyi* in the San Bernardino Mountains but often separated by habitat, with *A. hulodom*us preferring more open woodland and chaparral while *A. gurneyi* inhabits dense woodland. We observed syntopy in ruderal habitats.

Material examined. (n=6) In addition to Type Material above, **All USA, CA, Riverside Co.,** Garnet Queen Creek at Santa Rosa Mountain Truck Trail, 33.543, -116.482, 1865 m, 3-IX-2005, JN Hogue, CSUN, 4♂, 1♀; **San Bernardino Co.,** Heaps Peak Arboretum, 34.23386, -117.16061, 1837 m, 19-20-VII-2013, JA Cole, JF Ramirez, 1♂ sound record.

Aglaothorax conistylus Cole, Weissman, and Lightfoot, sp. nov.

Fig. 15 (distribution), Fig. 23 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 5 (male terminalia), Plate 8 (female subgenital plate), Plate 12 (male titillators), Plate 15 (male calling song).

Common name. Alluvial Shieldback.

History of recognition. None.

Type material. HOLOTYPE MALE: **USA, California, Los Angeles Co.**, Sycamore Flat Campground, Angeles National Forest, 12.5 miles northwest of Big Pines off county road N4, 34.4128N, 117.8239W, 1309 m, 7-VII-2004, JA Cole leg., JAC000002979, 108 [stridulatory file tooth count], 3.85 [stridulatory file length, mm], genitalia in glycerin and excised tegmen in gelcap below specimen, deposited in CAS, Entomology type #20239.

PARATYPES: (n=20) **USA, CA, Los Angeles Co.,** same data as holotype, LACM, 2♂, 1♀; same data except 23-VI-2008, JA Cole, AMNH, 1♂; same data except LACM, 4♂; same data except 8-VII-2004, JA Cole, LACM, 2♂; Grassy Hollow off SR2, 2.5 miles west of Big Pines, Angeles National Forest, 34.37500, -117.72028, 2225 m, 4-VIII-2021, JA Cole, J Bailey, LACM, 3♂; San Gabriel Mountains, Camp Eaton (=Cumorah Crest) 3 km NE Newcomb Ranch, 34.348832, -117.978868, 3-VIII-2021, JA Cole, J Bailey, LACM, 1♀; same data except 1860 m, 10-15-VIII-2003, JN Hogue, CSUN, 1♂, 1♀; same data except 10-VIII-2005, JN Hogue, CSUN, 1♀; **Orange Co.,** jct. Hicks Haul Road, Blue Diamond Haul Road, and Santiago Canyon Road, 33.73721, -117.70137, 264 m, 22-IX-2019, J Bailey, LACM, 2♂; **San Bernardino Co.,** Applewhite Campground, San Bernardino National Forest, 34.26056, -117.49444, 1021 m, 19-20-X-2023, JA Cole, C Wong, LACM, 1♂.

Measurements. (mm, ♂n=7, ♀n=3) Hind femur ♂14.75–16.41, ♀14.54–18.65, pronotum total length ♂7.87–9.62, ♀7.25–9.00, prozona length ♂3.21–4.24, ♀3.90–5.60, metazona dorsal length ♂4.27–5.38, ♀3.20–3.40, pronotum constriction width ♂2.59–3.35, ♀2.82–3.39, metazona dorsal width ♂5.63–6.90, ♀5.10–6.10, head width ♂4.04–4.42, ♀4.40–4.85, ovipositor length ♀10.15–12.65.

Distribution. Eastern San Gabriel Mountains and adjacent basins, including the Antelope Valley and San Gabriel Valley.

Habitat. Chaparral, hillside scrub, and alluvial scrub. Taken from Rabbitbrush (*Ericameria nauseosa* (Pall. ex Pursh) G.L. Nesom & Baird) and low branches of Western Sycamore (*Platanus racemosa* Nutt.).

Seasonal occurrence. Limited records show adult activity from summer (23-VI-2008, JA Cole, LACM) through fall (20-X-2023, JA Cole and C Wong, LACM).

Stridulatory file. (n=5) length 3.20–4.10 mm, 89–108 teeth, tooth density 26.9±1.9 (24.1–28.4) teeth/mm.

Song. (n=7) Standard song for small *Aglaothorax* with pulse trains produced slowly enough to be counted. Pulse trains 60±20 ms in length are produced at a rate of 6.43±1.16 s^{-1}. Mean peak frequency 19.31±5.64 kHz, ranging as high as 27.10 kHz. Echemes consist of 22±9 pulse trains repeated at a rate of 10–20 min^{-1}. Increased sample size is likely to add song variation as in other species that produce this song type.

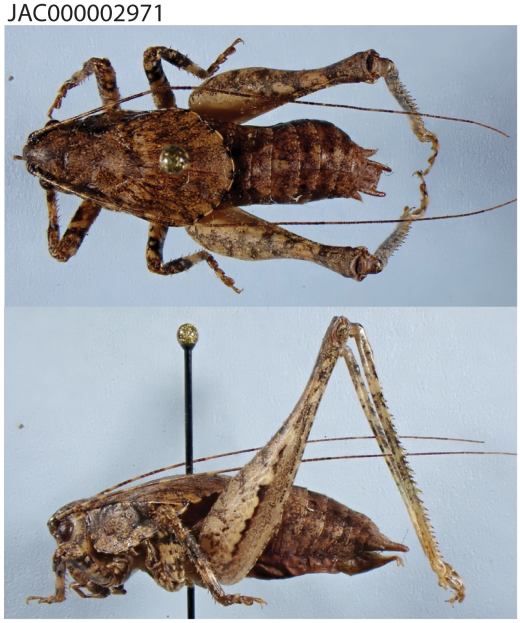
Karyotype. (n=2) 2n♂=24 (22t+Xt+Yt), paratypes JCT21-05, JCT21-09.

Recognition. Morphology, habitat. The male supra-anal plate is rounded and flat unlike the caudally indented or heart-shaped plate of the Diminutiva Group. The male subgenital plate has a narrow apex and thick, conical styli, which separate *A. conistylus* from other small *Aglaothorax* species in which the styli are narrow, cylindrical, and straight to curved. The male paraproct internal tooth position is apical to slightly subapical, which further eliminates species in which the tooth is positioned distinctly subapically like *A. hulodomus* and *A. morsei*. *A. nesiazo* usually have the tooth on the paraproct process positioned apically but also have square supra-anal plates, while the plate of *A. conistylus* is rounded. The titillator arms are distinctly curved laterally, unlike the nearly straight titillator arms of *A. hulodomus* and *A. nesiazo*, and lack a notch at the base as in *A. morsei*. The female subgenital plate has short, triangular lateral processes, unlike the long digitiform processes of sympatric *A. acrolophitus* and most other Diminutiva Group species.

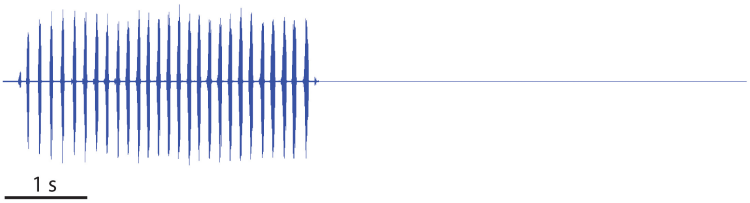
Etymology. Gr. *coni* a cone + *stylus* a pillar, stake. Refers to the cone shaped styli on the male subgenital plate.

Notes. *A. conistylus* is morphologically and ecologically distinct from two geographically adjacent (Fig. 15) *Aglaothorax* species: *A. morsei* and *A. hulodomus*. Concatenated genetic data found an *A. conistylus* grade between *A. morsei* to the west and *A. hulodomus* to the east (Fig. 4) that suggests isolation by distance. Calling songs are not significantly different in these separate lineages (Plates 14–15), suggesting a combination of geographical and ecological isolation. The habitats of *A. conistylus* are xeric and include steep, dry, sparsely vegetated hillsides in desert foothills and seasonally arid alluvial scrub. *A. morsei* prefers mesic canyon bottoms and *A. hulodomus* inhabits mixed woodland understory. This species is monophyletic based on nDNA markers (Fig. 2) but mtDNA found exemplars interspersed with other related Morsei Group lineages (Fig. 3) suggesting hybridization and gene flow between neighboring populations. Capture of *A. acrolophitus* mtDNA was also observed (Fig. 3) again suggesting hybridization, in this case between more distantly related taxa.

male PARATOPOTYPE USA. CA: Los Angeles Co. JAC000002971



calling song PARATOPOTYPE USA. CA: Los Angeles Co. 25.5ºC JCR04SF03



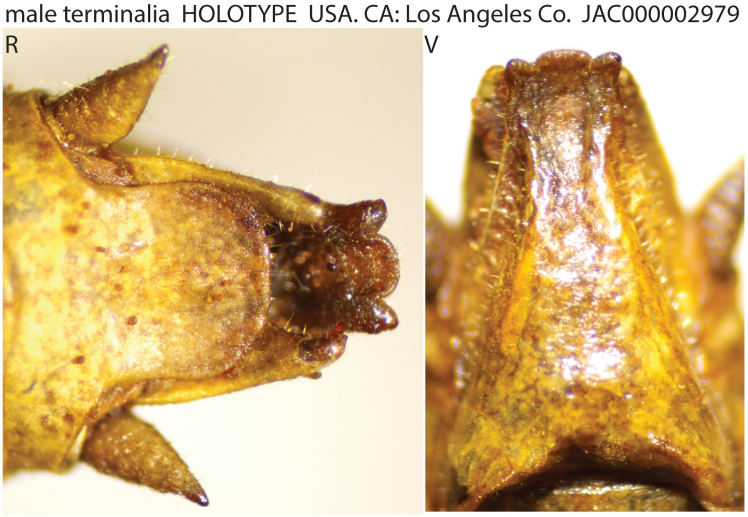
karyotype PARATYPE USA. CA: Los Angeles Co. JCT21-09



female PARATOPOTYPE USA. CA: Los Angeles Co. JAC000002980



male terminalia HOLOTYPE USA. CA: Los Angeles Co. JAC000002979



female PARATYPE USA. CA: Los Angeles Co. JAC000005723



titillators HOLOTYPE JAC000002979



female subgenital plate PARATOPOTYPE JAC000002980

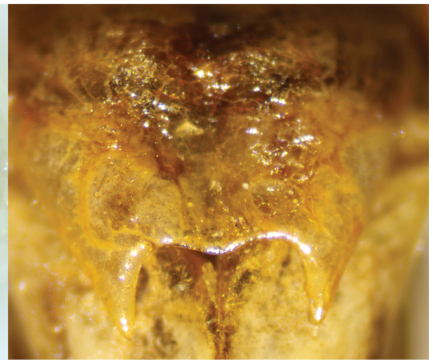


FIGURE 23. *A. conistylus* male and female habitus, calling song, male and female terminalia, and karyotype.

Material examined. See Type Material above. QUESTIONABLE PLACEMENT (n=1) **USA, CA, Los Angeles Co.**, Rio Hondo nr. SR60, Whittier Narrows, 34.029178, -118.049512, 22-V-1987, B Hebert, CSUN, 1♂.

Aglaothorax nesiazo Cole, Weissman, and Lightfoot, sp. nov.

Fig. 15 (distribution), Fig. 24 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 5 (male terminalia), Plate 8 (female subgenital plate), Plate 12 (male titillators), Plate 15 (male calling song).

Common name. Peninsular Shieldback.

History of recognition. None.

Type material. HOLOTYPE MALE: **USA, California, San Diego Co**unty, Torrey Pines State Park, 34.94546N, 117.25427W, 110 m, 9-VIII-2021, DB & DW Weissman, S21-21, R22-10, F1 [reared male], deposited in CAS, Entomology type #20374.

PARATYPES: (n=39) **USA, CA, San Diego Co.**, same data as holotype, CAS, 9♂, 12♀; 3-10 mi. SW of Borrego Springs on road S22, 33.048669, -117.041941, 410-1040 m, 8-VIII-1988, DB Weissman, DC Lightfoot, CAS, 1♂; Boulder Oaks Campground, Cleveland National Forest, 8 miles southeast of Pine Valley off I-8, 32.7299, -116.4839, 968 m, 27-VI-2004, JA Cole, LACM, 1♂; same data except 7-9-VII-2005, JA Cole, JF Eguizabal, AMNH, 1♂; same data except LACM, 2♂, 1♀; Camp Pendleton, Vandegrift Rd., 3 mi. S of Basilone, 33.210314, -117.392817, 10-VII-1976, DB Weissman, CAS, 1♂, 1♀; Campo, Highway 94, 32.606449, -116.468905, 792 m, 12-VII-1976, DB Weissman, CAS, 1♂; Mission Trails Regional Park, Brushy Gate, 32.83926, -117.03423, 180 m, 5-VIII-2021, JA Cole, J Bailey, LACM, 4♂, 1♀; Troy Canyon, Cleveland National Forest, 10 miles north of Boulder Oaks on Kitchen Creek Road, 32.8231, -116.4498, 1646 m, 19-20-VII-2003, JA Cole, MFJ Storc, AMNH, 1♂; same data except LACM, 1♂; same data except 7-VII-2005, JA Cole, JF Eguizabal, LACM, 2♂.

Measurements. (mm, ♂n=9, ♀n=7) Hind femur ♂11.85–14.60, ♀14.55–17.04, pronotum total length ♂7.10–8.55 ♀6.12–7.80, prozona length ♂2.71–3.93, ♀3.51–4.40, metazona dorsal length ♂3.57–4.70, ♀2.60–3.40, pronotum constriction width ♂2.39–2.90, ♀2.60–3.13, metazona dorsal width ♂4.90–6.03, ♀4.78–6.12, head width ♂3.15–3.92, ♀3.63–4.27, ovipositor length ♀9.06–11.34.

Distribution. Southern Peninsular Ranges of Southern California.

Habitat. Oak savannah and chaparral. On Scrub Oak (*Quercus dumosa*), Common Buckwheat (*Eriogonum fasciculatum*), and *Ceanothus* spp. Males may be heard deep within scrub oaks where they call from interior bare branches.

Seasonal occurrence. Records of adult activity span summer (27-VI-2004, JA Cole, LACM to 9-VIII-2021, DB & DW Weissman, CAS).

Stridulatory file. (n=9) length 2.80–3.35 mm, 76–108 teeth, tooth density 31.1±4.7 (26.2–38.6) teeth/mm.

Song. (n=7) Common song of small *Aglaothorax* with countable pulse trains. Pulse trains 70±20 ms in length are produced at a rate of 5.46±1.75 s^{-1}. Mean peak frequency is 16.61±3.42 kHz, the peak shifting as high as 22.40 kHz when high frequency recording equipment was used. Echemes are variable and consist of 30±15 (range 12–45) pulse trains repeated at a rate of 2–14 min^{-1}.

Karyotype. (n=3) 2n♂=24 (22t+XtYt), paratopotype, T21-23 (S21-21).

Recognition. Morphology, geography. Although the paraproct processes usually have an apical tooth, the male supra-anal plate is square and the titillators are short and barely bowed, eliminating the Diminutiva Group in which males have heart-shaped or caudally indented supra-anal plates. The long, slender, cylindrical paraproct processes eliminate *A. costalis*, *A. morsei*, and *A. hulodomus* from consideration. The male subgenital plate has thin, cylindrical styli unlike the thick cone-shaped styli of *A. conistylus*. The male titillator arms are short and nearly straight and without a basal notch, which eliminates *A. amathitis*, *A. conistylus*, *A. costalis*, *A. longipennis*, and *A. morsei*. From adjacent Baja California species to the south, *A. kelainops* and *A. sphenosternum* also have shorter paraproct processes, about 2 times as wide plus rounded supra-anal plates. Both sexes of *A. sphenosternum* may be separated by the wedge-like prosternal spines in contrast to the long, thin, spines of *A. nesiazo*. Females have short, triangular lateral processes on the subgenital plate, unlike most Diminutiva Group females. The female subgenital plate lateral processes are as long as wide, unlike *A. kelainops* and *A. constrictans* females which have the triangular lateral processes longer than wide.

Etymology. Gr. *nesiazo* peninsular. Refers to the California Peninsular Range distribution.

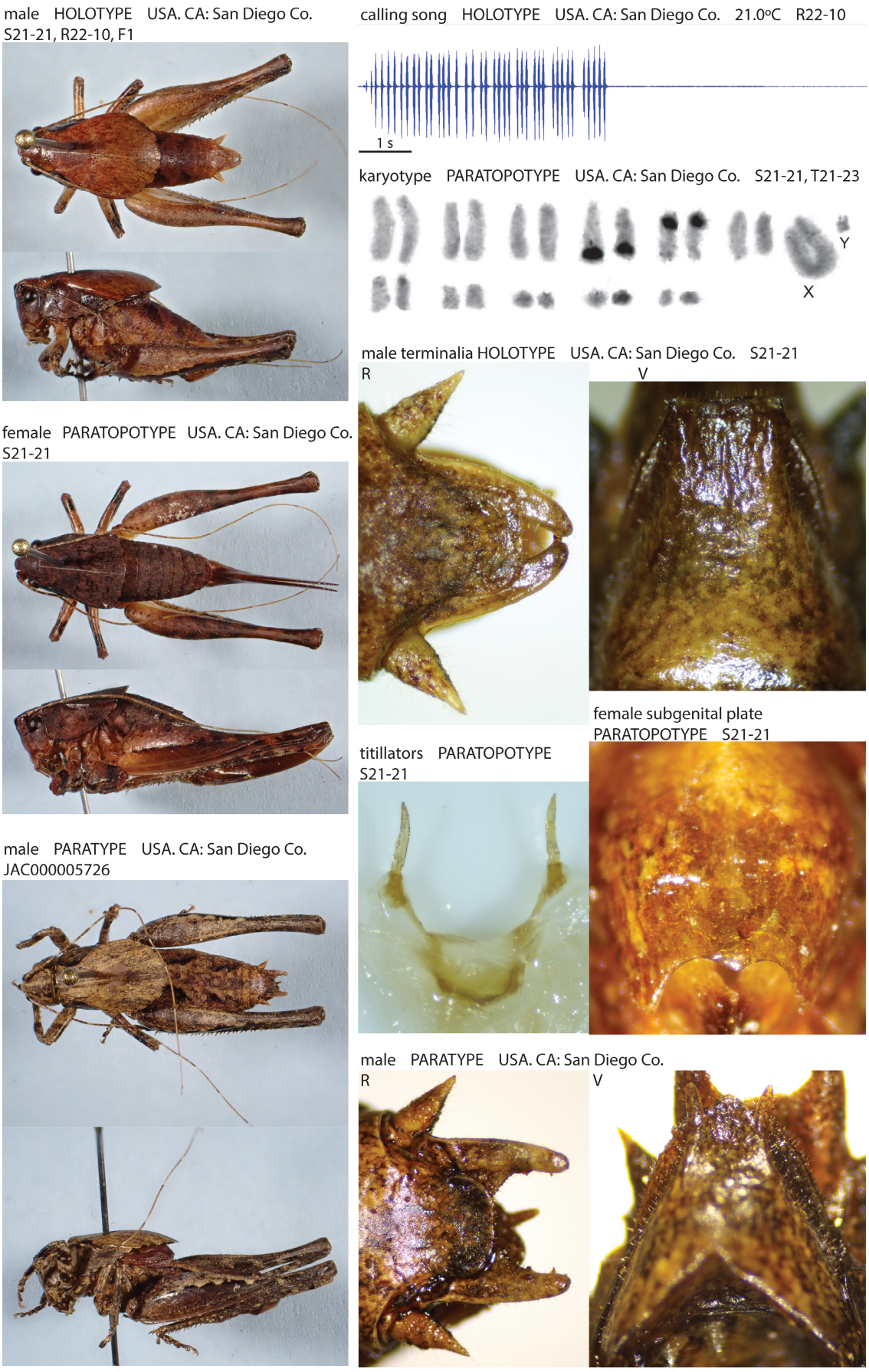


FIGURE 24. *A. nesiazo* male and female habitus, calling song, male and female terminalia, and karyotype. Idiogram shows karyotype 2n♂=24.

Notes. *A. nesiazo* belongs to a complex of Transverse and Peninsular Range species. Multiple mtDNA haplotypes exist (Fig. 3) and concatenated data found a grade between *A. hulodomus* to the north and three Baja California lineages to the south (Fig. 4). This phylogeographic pattern may be explained by isolation by distance as neighboring populations experience gene flow.

Three field collected adult females of *A. nesiazo* (from type locality S21-21), collected on 19-VIII-2021, were housed together at room temperature as described on p. 6, starting on 12-VIII-2021. Between 19-28-IX-2021, the sand was examined for eggs and a total of 37 were recovered. The eggs were subjected to two different treatments as follows:

1. Twenty-seven eggs were kept at room temperature (15–25ºC) and natural photoperiod until hatching commenced on 21-I-2022. Between 21-I-2022 and 9-III-2022, a total of 22 eggs hatched. The five unhatched eggs were continued at room temperature until they were chilled at 3ºC from 3-IX-2022 to 6-III-2023, before being returned to room temperature and natural photoperiod. Between 24–29-III-2023 another three eggs hatched, resulting in 25 out of 27 total eggs successfully hatched.

2. Ten eggs were kept at room temperature and natural photoperiod until 3-I-2022, without any hatching, when they were chilled at 3ºC. On 1-III-2022, the eggs were placed back at room temperature, and between 7-III-2022 and 22-III-2022 four eggs hatched. The six unhatched eggs were continued at room temperature until they were subsequently chilled for a second time, between 3-IX-2022 and 6-III-2023. They were then returned to room temperature with two eggs hatching on 24-III-2023, for a total of 6 out of 10 eggs successfully hatched.

It appears from treatment 1 that most eggs of *A. nesiazo* do not require a 3ºC chill period for hatching to occur, which makes sense as they occur in a coastal area of Southern California which may not always experience such winter temperatures. In fact, from treatment 2, chilling the eggs only seems to delay their hatching by the number of days that they are chilled. Most curious is the finding, in both treatments, that some 20% of total eggs require at least one chill period, and the passing of 18 months, before they hatched. We wonder how these findings reflect actual field conditions because they may indicate an unappreciated degree of flexibility of response to the variable weather and climate conditions that exist in Southern California's Mediterranean climate.

Material examined. See Type Material above. QUESTIONALBLE PLACEMENT: (n=1) **USA, CA, Riverside Co.,** Menifee Valley, 33.689188, -117.180867, 6-VII-1975, SI, SL Frommer, UCR, 1♂.

Aglaothorax bufonoides Cole, Weissman, and Lightfoot, sp. nov.

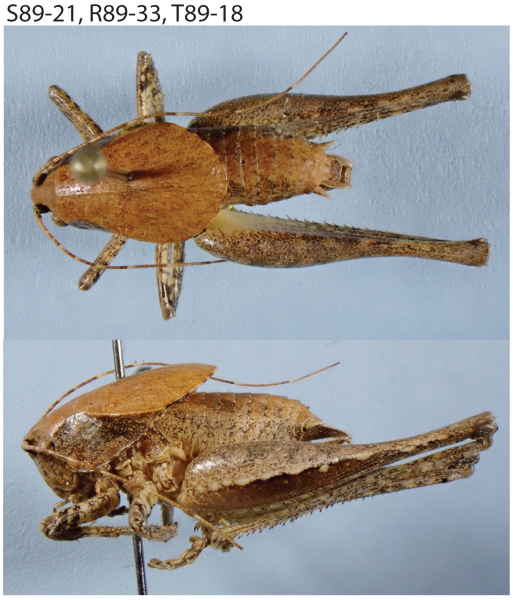
Fig. 15 (distribution), Fig. 25 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 5 (male terminalia), Plate 8 (female subgenital plate), Plate 12 (male titillators), Plate 15 (male calling song).

Common name. Toad Shieldback.

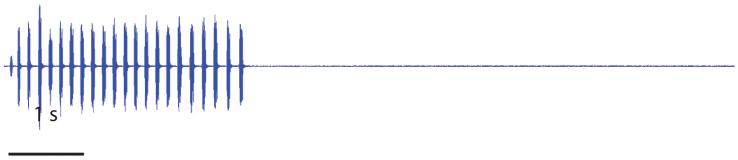
History of recognition. None.

Type material. HOLOTYPE MALE: México, Baja California, La Bufadora, 31.7243N, 116.7231W, 2-VI-1989, DB Weissman & DC Lightfoot, DB Weissman, S89-21, R89-33, T89-18, 3.45 [stridulatory file length, mm], 87 [stridulatory file tooth count] excised tegmen in gelcap below specimen, deposited in CAS, Entomology type #20375. PARATYPES: (n=46) **México, Baja California**, same data as holotype, CAS, 2♂, 1♀; same data as holotype except 29-VII-1986, DB Weissman, DC Lightfoot, CAS, 1♂; 12 km E Rosarito on dirt road to Table Mesa, 32.373719, -116.901529, 61 m, 19-VI-1980, DB Weissman, CAS, 1♂; 13 km E Rosarito on dirt road to Table Mesa, 32.373409, -116.890873, 61 m, 19-VI-1980, DB Weissman, CAS, 2♂; 2 km E La Bufadora at 0.16 km E km 20 on BCN 23, 31.723413, -116.692822, 28-VII-1978, DB Weissman, DC Lightfoot, CAS, 8♂, 4♀; 5 km E Rosarito on dirt road to Table Mesa, 32.349632, -117.013933, 61 m, 19-VI-1980, DB Weissman, CAS, 6♂; Highway 3, 5.5 km northeast of jct. Highway 1, 31.96361, -116.65833, 241 m, 29-VI-2019, JA Cole, DB Weissman, AMNH, 1♂; same data except LACM, 3♂; Highway 3, km marker 41, 31.62639, -116.46194, 195 m, 29-VI-2019, JA Cole, DB Weissman, LACM, 1♂; Highway 3, km marker 60, 32.21250, -116.51083, 463 m, 29-VI-2019, JA Cole, DB Weissman, LACM, 3♂; Hwy. 2, 5.7 km W El Condor at km 88.7, 32.476301, -116.222532, 1210 m, 19-VIII-1995, DB Weissman, DC Lightfoot, CAS, 2♂; km 60 on road to Sierra de San Pedro Martir National Park off Mex. Hwy. 1, 30.927296, -115.348406, 853 m, 26-VII-1978, DB Weissman, DC Lightfoot, CAS, 1♂; km 66 on road to Sierra de San Pedro Martir National Park off Mex. Hwy. 1, 30.927296, -115.348406, 27-VII-1978, DB Weissman, DC Lightfoot, CAS, 1♂; km 67 on road to Sierra de San Pedro Martir National Park, 30.927296, -115.348406, 21-VII-1977,

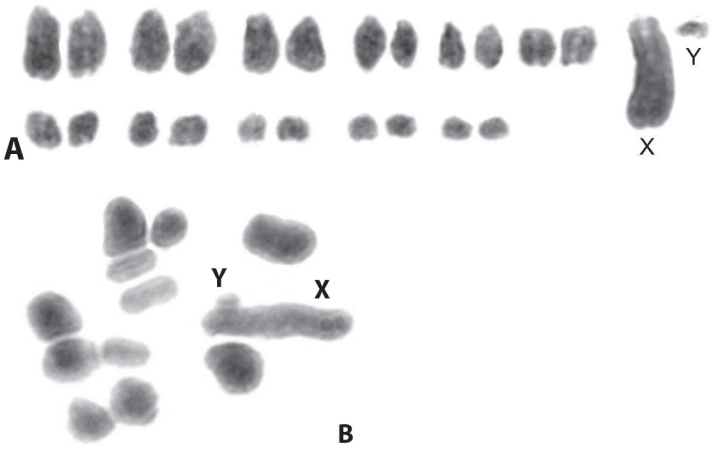
male HOLOTYPE México. Baja California.
S89-21, R89-33, T89-18



calling song PARATOPOTYPE México. Baja California. 23.5ºC
S89-21, R89-25



karyotype PARATYPE México. Baja California. JCT19-6



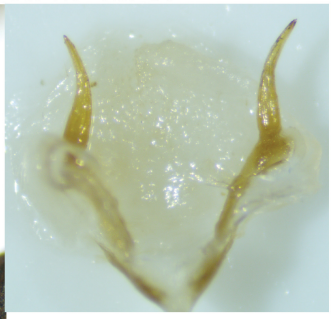
female PARATYPE
México. Baja California. S78-95



male terminalia HOLOTYPE
R



titillators PARATOPOTYPE
S89-21 R89-31



female subgenital plate PARATYPE
México. Baja California. S78-95



male terminalia PARATOPOTYPE México. Baja California. S89-21
R V

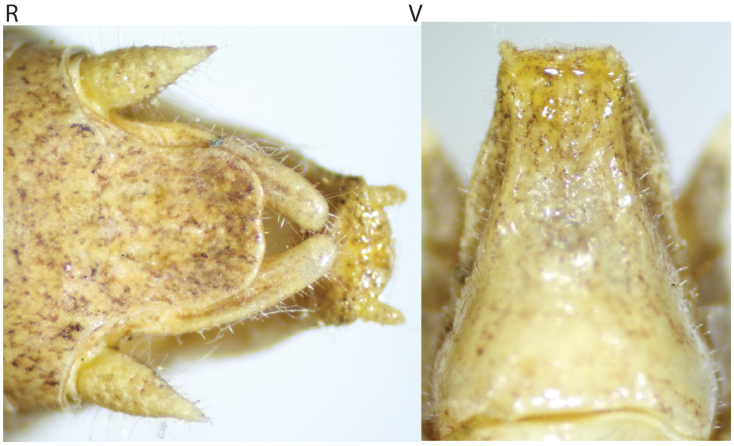


FIGURE 25. *A. bufonoides* male and female habitus, calling song, male and female terminalia, and karyotype. Idiogram A. karyotype 2n♂=24; B. Same male, metaphase I with small Y and large X sex chromosomes labeled.

DB Weissman, CAS, 1♂; km 73.8 on road to Sierra de San Pedro Martir Park off Mex. Hwy. 1, 30.927296, -115.348406, 1650 m, 4-VIII-1981, DB Weissman, DC Lightfoot, CAS, 1♂, 2♀; La Misión on Mexican Highway 1 Libre, 32.100855, -116.856278, 8-VII-1978, DB Weissman, DC Lightfoot, CAS, 2♂, 1♀; La Rumorosa at km 68.2 on Mex. Highway 2, 32.602043, -116.079469, 31-VII-1978, DB Weissman, DC Lightfoot, CAS, 2♂.

Measurements. (mm, ♂n=10, ♀n=5) Hind femur ♂13.80–16.15, ♀17.10–19.42, pronotum total length ♂7.61–9.13, ♀7.26–9.22, prozona length ♂3.40–4.22, ♀3.81–5.40, metazona dorsal length ♂3.83–5.35, ♀2.95–3.82, pronotum constriction width ♂2.58–3.17, ♀3.00–3.41, metazona dorsal width ♂5.35–6.45, ♀5.33–5.87, head width ♂3.14–4.05, ♀4.08–4.68, ovipositor length ♀11.30–13.50.

Distribution. Baja California, México. Geographically situated north of two other Baja California species, *A. kelainops* and *A. sphenosternum*, the latter two with divergent karyotypes. *A. bufonoides* has the widest range of the three species.

Habitat. Chaparral and oak woodland in valleys and on hillsides. On Mountain Mahogany (*Cercocarpus* spp.), Laurel Sumac, and *Keckiella* spp. The type locality is coastal bluff habitat.

Seasonal occurrence. Late spring (2-VI-1989, DB Weissman & DC Lightfoot, CAS) through summer (19-VIII-1995, DB Weissman & DC Lightfoot, CAS). It appears that despite the cooler, foggy coastal climate at La Bufadora, that population matures earlier than those more inland.

Stridulatory file. (n=4) length 3.00–3.90 mm, 87–110 teeth, tooth density 29.3±3.2 (25.2–32.0) teeth/mm.

Song. (n=12) Standard song for small *Aglaothorax* with pulse trains that occur slow enough for a human listener to count. Pulse trains of 60±10 ms produced at a rate of 5.31±1.19 s^{-1}. Mean peak frequency is 13.90±1.10 kHz. Echemes contain a variable number of pulse trains (mean 22±11, range 4–39 pulse trains), the echeme rate is 4–7 min^{-1}.

Karyotype. (n=13) 2n♂=24 (22t+XtYt), paratype JCT19-6, paratopotype S89-21, T89-10. Type locality T89-10 (S89-21) 2n♂=24, metaphase I clearly showing associated XY sex chromosomes and 11 pairs of autosomes.

Recognition. Morphology, karyotype. The male supra-anal plate is rounded and concave and the paraproct processes are twice as long as wide, with an apical or slightly subapical mesal tooth. *A. nesiazo* to the north in the Peninsular Ranges of California has a square supra-anal plate and long, slender paraproct processes, more than two times longer than wide. From Baja California congeners, *A. sphenosternum* has the prosternal spines wedgelike whereas *A. bufonoides* has typical long, thin spines. The male titillator arms are short and curved laterally, unlike the nearly straight arms of *A. nesiazo* distributed to the north and *A. kelainops* to the south. Females of *A. bufonoides* have the subgenital plate lateral processes as long as wide while those processes are longer than wide in *A. kelainops*. The karyotype of *A. bufonoides* is typical for small *Aglaothorax* at 2n♂=24; *A. kelainops* and *A. sphenosternum* have atypical karyotypes that are discussed below.

Etymology. G. *bufo* toad + *oid* like, form. Descriptive of the toad-like gestalt of the genus.

Notes. This is the most widespread *Aglaothorax* in Baja California. The species is alone on the Baja California peninsula in possessing the widespread small *Aglaothorax* karyotype of 2n♂=24. Populations with the three different karyotypes have not been found in any combination of sympatry, but ranges may be adjacent (Fig. 15). Songs are not divergent between the three Baja California taxa nor from coastal San Diego *A. nesiazo*. Phylogenetically, this species is related to *A. nesiazo* to the north, and two different haplotypes are in turn sister to each of two *Aglaothorax* with divergent karyotypes (Figs. 3–4): *A. kelainops* (2n♂=20) and *A. sphenosternum* (2n♂=22).

Material examined. See Type Material above. QUESTIONALBE PLACEMENT: (n=3) 4.2 mi. Arroyo Santo Tomas, 31.535497, -116.660687, EL Sleeper, CAS, 1♂; turnoff to Rancho Las Cruces 28 km S Santo Tomas on Mex. Highway 1, 31.38950, -116.32205, 19-VI-1977, DB Weissman, CAS, 2♂.

Aglaothorax kelainops Cole, Weissman, and Lightfoot, sp. nov.

Fig. 15 (distribution), Fig. 26 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 5 (male terminalia), Plate 8 (female subgenital plate), Plate 12 (male titillators), Plate 15 (male calling song).

Common name. Ojos Negros Shieldback.

History of recognition. None.

male HOLOTYPE México. Baja California.
S88-84, R88-135, T88-52



female PARATOPOTYPE
México. Baja California. S88-84



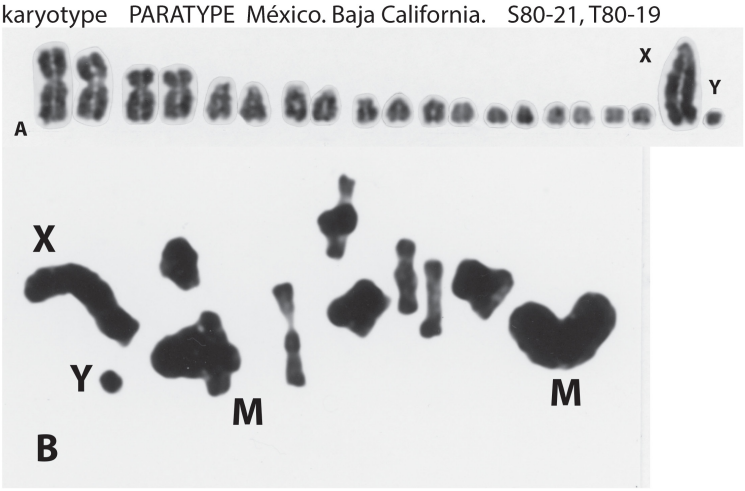
male PARATOPOTYPE
México. Baja California. S85-90, R85-204



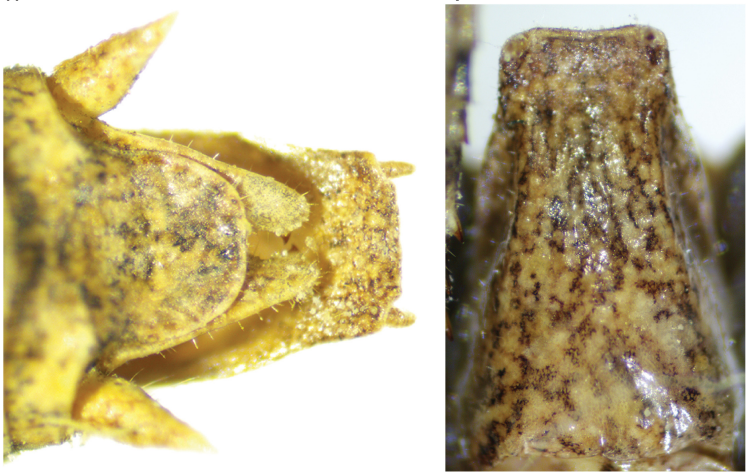
calling song HOLOTYPE México. Baja California. 25.0ºC
R88-135



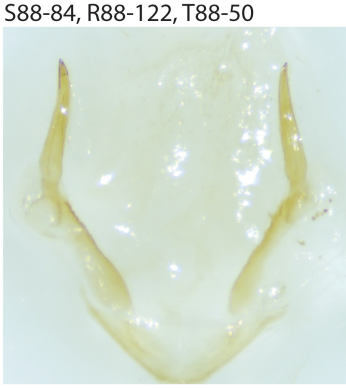
karyotype PARATYPE México. Baja California. S80-21, T80-19



male terminalia HOLOTYPE México. Baja California. S88-84
R V



titillator PARATOPOTYPE
S88-84, R88-122, T88-50



female subgenital plate
PARATOPOTYPE S88-84

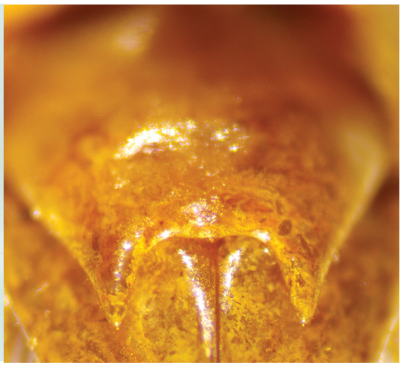


FIGURE 26. *A. kelainops* male and female habitus, calling song, male and female terminalia, and karyotype. Idiogram A. showing karyotype 2n♂=20, showing two largest autosomal pairs composed of metacentric chromosomes; B. Metaphase I in same male showing association of X and Y sex chromosomes; and two largest pairs of metacentric (M) autosomes.

Type material. HOLOTYPE MALE: **México, Baja California,** 41.3 km south of Ensenada on Highway 1, at km sign post 41.3, 31.49660N, 116.59972W, 9-VIII-1988, DB Weissman & DC Lightfoot leg., S88-84, R88-135, T88-52, 86 [stridulatory file tooth count], 3.3 [stridulatory file length], excised tegmen in gelcap below specimen, deposited in CAS, Entomology type #20377. PARATYPES: (n=18) **México, Baja California**, same data as holotype, CAS, 1♂, 1♀; 42 km S of Ensenada, 31.55439, -116.40891, 370 m, 19-VII-1985, DB Weissman, DC Lightfoot, DK Faulkner, CAS, 4♂, 1♀; 10 km N Santo Tomas at km 41 on Mex. 1, 31.62494, -116.46102, 18-VI-1980, DB Weissman, CAS, 1♂; 20 km S Maneadero at 0.32 km N, km 42 S Ensenada on Mex. 1, 31.54073, -116.40891, 28-VII-1978, DB Weissman, DC Lightfoot, CAS, 1♂, 2♀; 61.5 km south of Ensenada at Highway 1 km 61.5, 31.43738, -116.30825, 490 m, 2-VI-1989, DB Weissman, DC Lightfoot, CAS, 2♂; Highway 1, 30.4 km south of Ensenada, 31.63611, -116.47167, 177 m, 29-VI-2019, JA Cole, DB Weissman, LACM, 1♀; Highway 3, 4.3 km west of Ojos Negros, km marker 36, 31.87889, -116.30444, 762 m, 29-VI-2019, JA Cole, DB Weissman, AMNH, 1♂; same data except LACM, 2♂, 1♀.

Measurements. (mm, ♂n=11, ♀n=6) Hind femur ♂13.43–15.10, ♀16.00–18.15, pronotum total length ♂7.41–9.10, ♀7.21–8.80, prozona length ♂3.36–3.99, ♀3.96–5.16, metazona dorsal length ♂3.88–5.13, ♀2.78–3.90, pronotum constriction width ♂2.46–3.06, ♀2.95–3.70, metazona dorsal width ♂5.26–6.32, ♀5.39–6.25, head width ♂3.51–3.79, ♀3.85–4.60, ovipositor length ♀10.52–13.45.

Distribution. Northern Baja California, México.

Habitat. Chaparral on laurel sumac.

Seasonal occurrence. Late spring into summer (2-VI-1989, DB Weissman & DC Lightfoot, CAS to 9-VIII-1988, DB Weissman & DC Lightfoot, CAS).

Stridulatory file. (n=8) length 3.10–3.60 mm, 80–97 teeth, tooth density 26.2±0.9 (25.0–27.5) teeth/mm.

Song. (n=12) Common small *Aglaothorax* song with slow, countable pulse trains. Pulse trains 70±20 ms in length delivered at a rate of 6.42±0.68 s^{-1}. Mean peak frequency is 14.56±1.02 kHz. Variable echemes contain 19±7 (range 11–34) pulse trains that repeat at a rate between 7–13 min^{-1}.

Karyotype. (n=11) 2n♂=20 (4m+14t+XtYt), paratype T80-19 (S80-21). The presence of two metacentric autosomes, combined with an autosome chromosome number reduction from 22 to 18 when comparted with other widespread Morsei Group members, is most easily explained by Robertsonian fusions involving four telocentric pairs.

Recognition. Morphology, karyotype. Males have a rounded, concave supra-anal plate unlike the flat, square plate of *A. nesiazo* to the north in San Diego County, California. The male paraproct processes are about two times longer than wide, also unlike *A. nesiaz*o and *A. sphenosternum*. The prosternal spines are normally developed and spinelike compared with the conical spines of *A. sphenosternum*. The male paraproct processes have the internal tooth apical, unlike most Morsei Group species, and the supra-anal plate is not bilobed or indented on the caudal margin as in the Diminutiva Group. Male *A. kelainops* titillator arms are short and nearly straight, while those of *A. bufonoides* are smoothly curved laterally. The female subgenital plate lateral processes are longer than wide unlike *A. bufonoides* and *A. sphenosternum*, and *A. nesiazo* from Southern California. This is the only *Aglaothorax* with a 2n♂=20 karyotype.

Etymology. G. *kelain* black, murky + *ops* eyes. Named after the type locality near Ojos Negros in Baja California, México.

Notes. The Baja California peninsula harbors populations with three different karyotypes: *A. bufonoides* with the widespread 2n♂=24, this species with 2n♂=20, and *A. sphenosternum* with 2n♂=22 (see species account below, p. 67). *A. kelainops* is related to a subset of *A. bufonoides* populations (Figs. 3–4). Divergent karyotypes are a recurring theme in peripheral populations of *Aglaothorax*, echoed by *A. diminutiva* at the north limit of the range (see species account below, p. 71), *A. segnis* at the extreme east (p. 28), and *A. kelainops* and *A. sphenosternum* (p. 67) at the southern extreme of the distribution in northern Baja California, México. Taken together, if Robertsonian fusions are rare events, and given that *A. sphenosternum* does not share a recent common ancestor with *A. kelainops*, reduction of chromosome number from the common karyotype 2n♂=24 to 2n♂=20 involves intermediate 2n♂=22 populations that have not been observed.

Material examined. See Type Material above.

Aglaothorax sphenosternum Cole, Weissman, and Lightfoot, sp. nov.

Fig. 15 (distribution), Fig. 27 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 5 (male terminalia), Plate 8 (female subgenital plate), Plate 12 (male titillators), Plate 15 (male calling song).

Common name. Wedge-breasted Shieldback.

History of recognition. None.

Type material. HOLOTYPE MALE: **México, Baja California,** 11 miles east of Ojos Negros on road to Laguna Hanson, 31.90864N, 116.07022W, 1160 m, 9-VIII-1988, DB Weissman, DC Lightfoot, S88-85, R88-124, T88-58, 3.0 [stridulatory file length, mm], 104 [stridulatory file tooth count], excised tegmen in gelcap below specimen, deposited in CAS, Entomology type #20376. PARATYPES: (n=8) **México, Baja California**, 11 mi. E of Ojos Negros on road to Laguna Hanson, 31.908643, -116.070218, 1160 m, 9-VIII-1988, DB Weissman, DC Lightfoot, CAS, 2♂, 3♀; Laguna Hanson Road, 18 km east of Ojos Negros, 31.91139, -116.11694, 1033 m, 28-VI-2019, JA Cole, DB Weissman, LACM, 3♂.

Measurements. (mm, ♂n=7, ♀n=1) Hind femur ♂12.78–13.80, ♀15.13, pronotum total length ♂7.65–8.47, ♀7.25, prozona length ♂3.42–4.56, ♀3.63, metazona dorsal length ♂3.80–4.63, ♀3.62, pronotum constriction width ♂2.60–2.84, ♀2.69, metazona dorsal width ♂5.26–6.57, ♀5.05, head width ♂3.46–3.90, ♀4.05, ovipositor length ♀9.01.

Distribution. Northern Baja California, México.

Habitat. Chaparral. On Yerba Santa, Laurel Sumac, and *Salvia* spp.

Seasonal occurrence. Sparse records span summer (28-VI-2019, JA Cole & DB Weissman, CAS to 9-VIII-1998, DB Weissman & DC Lightfoot, CAS).

Stridulatory file. (n=3) length 2.90–3.10 mm, 92–107 teeth, tooth density 33.6±1.7 (31.7–34.7) teeth/mm.

Song. (n=6) Standard small *Aglaothorax* song type with a slow pulse train rate. Pulse trains 70±10 ms are repeated at a rate of 6.08±0.44 s^{-1}. Mean peak frequency is 15.48±0.35 kHz. Echemes contain a variable number (mean 14 ± 7, range 4–26) of pulse trains repeated at rates between 7 and 14 min^{-1}.

Karyotype. (n=5) 2n♂=22 (2m+18t+XtYt), holotype T88-58 (S88-85). The presence of one pair of metacentric autosomes, combined with an autosome number reduction from 22 to 20 when compared with other widespread Morsei Group members, is most easily explained by a Robertsonian fusion involving two telocentric pairs.

Recognition. Morphology, karyotype. Both sexes may be diagnosed by the broad, conical prosternal spines, in contrast to the long, thin, spines typical of other Morsei and Diminutiva Group species. In addition, males have a concave supra-anal plate, which contrasts with the flat, square plate of *A. nesiazo* to the north. Male *A. sphenosternum* also have long, thin, cylindrical paraproct processes, unlike San Diego County, California *A. nesiazo* or the two other Baja California species *A. bufonoides* and *A. kelainops*. The apical paraproct tooth eliminates *A. costalis*, *A. morsei*, and *A. hulodomus* from consideration. The male titillator arms are short and nearly straight, unlike the arms of *A. bufonoides* that are smoothly curved laterally. The male stridulatory file tooth density is higher than both other Baja California species at 33.6 ± 1.7 teeth/mm versus 29.3 ± 3.2 in *A. bufonoides* and 26.2 ± 0.9 in *A. kelainops*. Female *A. sphenosternum* have the subgenital plate lateral processes as long as wide, whereas *A. kelainops* females have those processes slightly longer than wide. This is the only *Aglaothorax* with a 2n♂=22 karyotype.

Etymology. G. *spheno* wedge + *sternum* breast, breastbone. Descriptive of the conical prosternal spines that help diagnose this species.

Notes. Like *A. kelainops* (see species account above p. 64), this species is genetically related to a subset of *A. bufonoides*, albeit to a different subset of populations (Figs. 3–4). A chromosome evolution hypothesis that explains the reduction in chromosome number from 2n♂=24 to 2n♂=22 is Robertsonian fusion, during which two pairs of telocentric autosomes underwent centric fusion. Once evolved, such divergent karyotypes may create reproductive isolation through reduction in hybrid fitness (Shaw *et al.* 1998; White 1978). Reproductive isolation via chromosome differences may explain the biogeography, where closely situated populations do not overlap in sympatry (Fig. 15). Songs are statistically identical, thus reinforcement of premating isolation via calling songs has not occurred as in other nedubines with (*Neduba duplocantans* Cole, Weissman, and Lightfoot 2021; Cole *et al.* 2021) and without (*Aglaothorax costalis*; Cole 2016, also see species account above p. 43) chromosome differences.

Material examined. See Type Material above. QUESTIONABLE PLACEMENT: (n=2) **México, BCN,** 11.2 km E Ojos Negros on road to Laguna Hanson, 31.908726, -116.139372, 1200 m, 2-VIII-1981, DB Weissman, DC Lightfoot, CAS, 1♂; 17.9 km E Ojos Negros on road to Laguna Hanson, 31.90864, -116.068237, 1463 m, 29-VII-1978, DB Weissman, DC Lightfoot, CAS, 1♂.

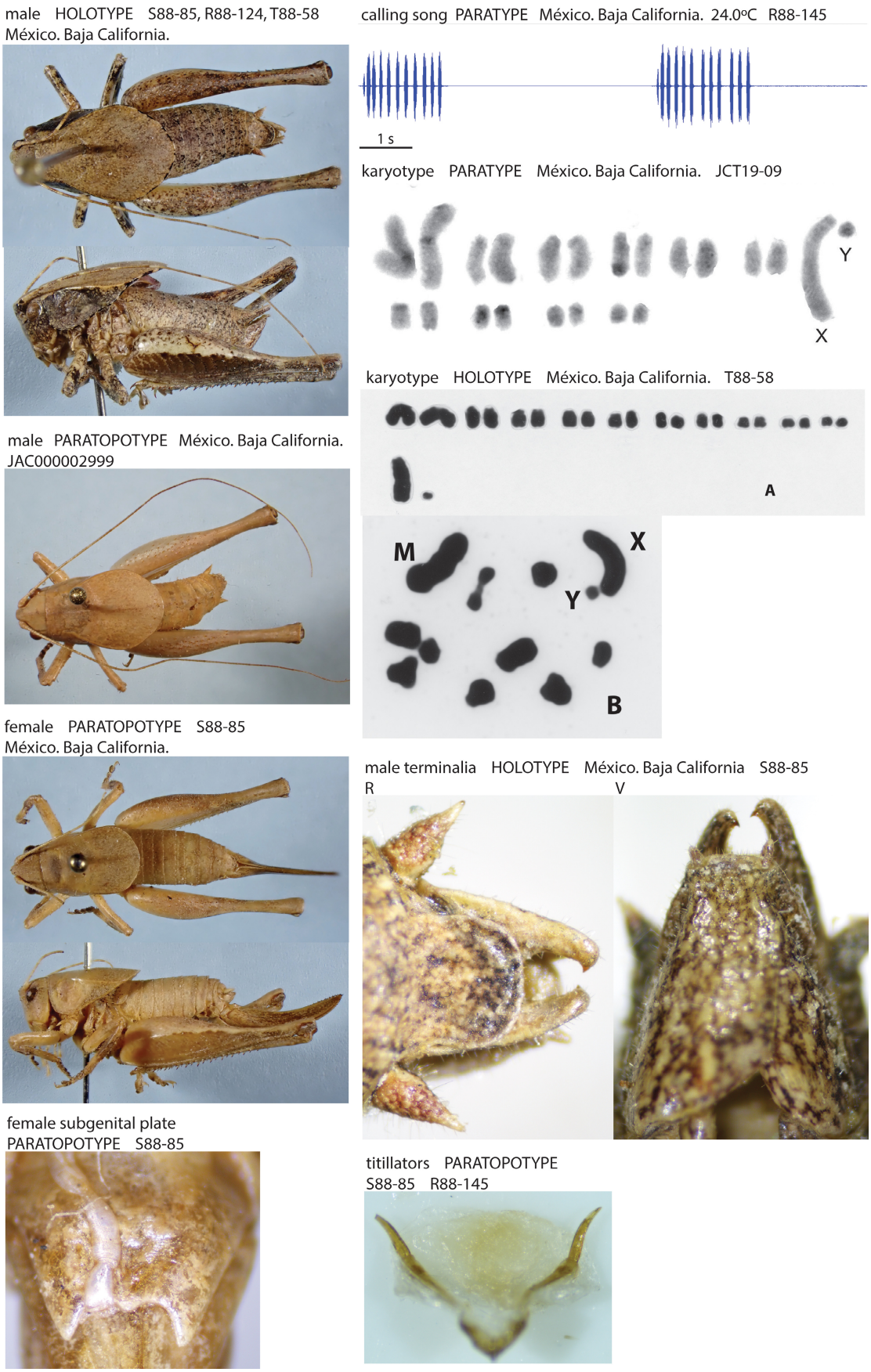


FIGURE 27. *A. sphenosternum* male and female habitus, calling song, male and female terminalia, and idiogram A. Karyotype 2n♂=22 showing largest autosomal pair M composed of metacentric chromosomes; B. Sex chromosomes X and Y, in same male, are marked and associated (without apparent chiasmata), to ensure proper segregation at anaphase.

TABLE 4. Comparative chaetotaxy of the Diminutiva Group.

species	n	forefemur dorsal surface	foretibia auditory foramen	foretibia ventro-anterior margin	foretibia ventro-posterior margin	midfemur dorsal surface	midtibia dorso-anterior margin	midtibia dorso-posterior margin	midtibia ventro-anterior margin	midtibia ventro-posterior margin
diminutiva	7	0–4	1	6–7	6–7	0–3	2–3	2–3	6–8	5–7
♀	7	0–4	1	6	6	2–3	2–3	3	7	6–7
constrictans	18	0-4	0–1	6	5–6	1–3	2–3	2–3	5–8	5–7
♀	13	1–4	0–1	6	6	1–3	1–3	2–3	6–8	6–7
dactyla	17	0–4	1	6	6–7	1–3	2–3	1–3	6–7	5–7
♀	11	0–4	1	6	6	0–3	1–3	3	7	6–7
acrolophitus	15	0–3	0–1	6	6–7	0–3	1–3	2–3	6–8	5–7
♀	11	0–4	1	5–6	5–6	0–3	1–3	2–4	7	5–7
oreibates	6	3–5	1	6–7	6	1–3	2–3	3	6–7	5–7
♀	5	1–5	1	6	6	0–4	2–4	2–4	6–7	6–7
poecilonotum	6	0–3	1	6	6	1–3	2–3	3–4	6–7	6–7
♀	5	1–3	1	5–6	6	1–3	2–3	3	6–7	6–7

Diminutiva Group

The Diminutiva Group is, like the Morsei Group, a clade of small *Aglaothorax*. The prosternal spines are typically long and divergent, occasionally reduced and nipple-like. Like the other *Aglaothorax* species Groups, chaetotaxy is more variable within species than between (Table 4). The male supra-anal plate of this group is characteristically heart-shaped, indented along the posterior margin and expanded posterolaterally into two lobes (Figs. 28–33, Plate 6). The male subgenital plate has a wide posterior margin that is rounded to transverse and with long cylindrical styli (Figs. 28–33). The male paraprocts have the internal tooth situated apically (Figs. 28–33, Plate 6). In all but one species (*A. constrictans*) the male titillator arms are long, slender, and strongly curved laterally, often bowed (Plate 13). The female subgenital plate in all but one species (again *A. constrictans*) has long, digitiform lateral processes (Figs. 28–33, Plate 9). The female ovipositor is shorter than the hind femur, approximately 3/4 its length, and regularly upcurved (Figs. 28–33).

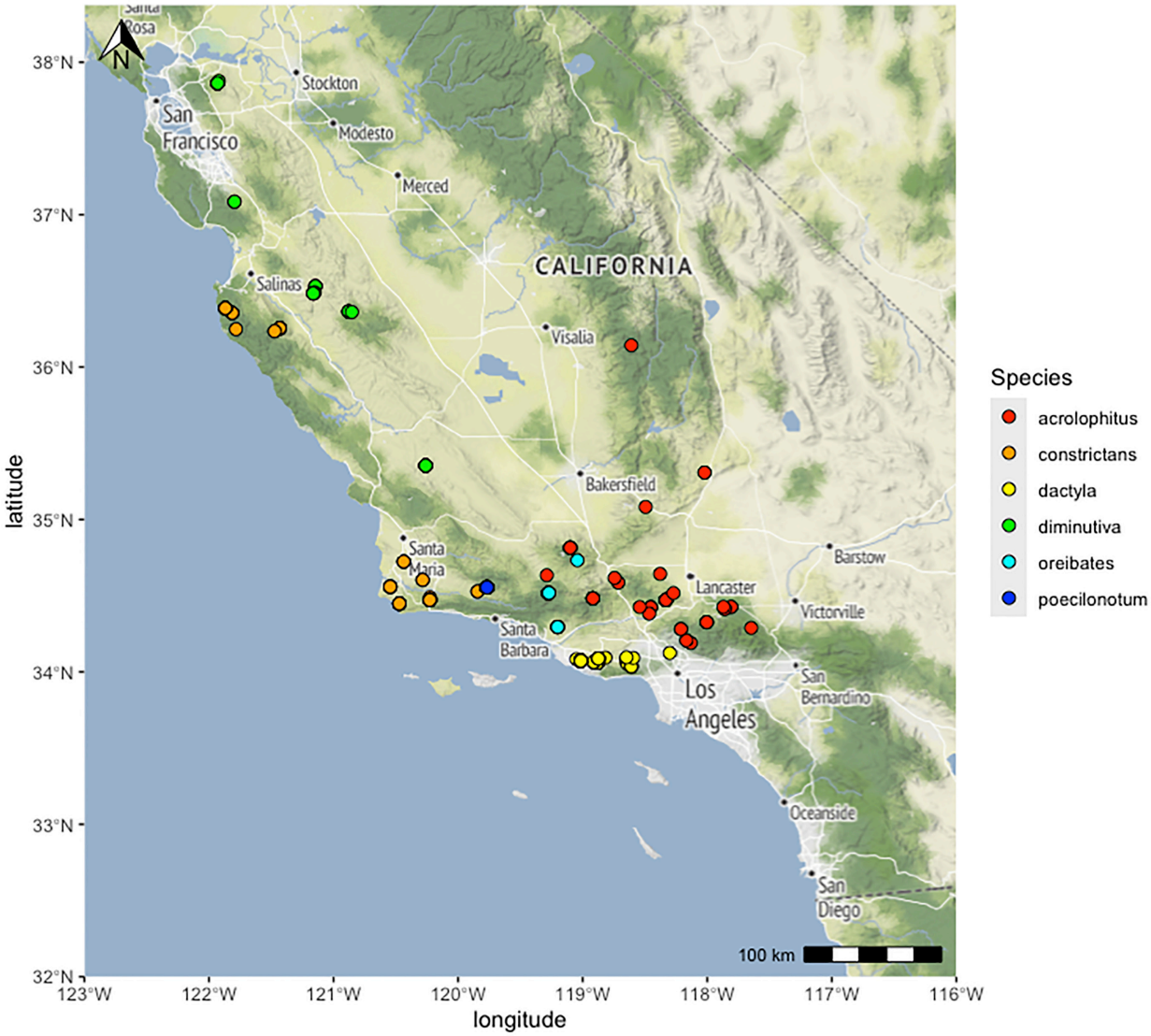


FIGURE 28. Distribution of Diminutiva Group species.

Diminutiva Group males produce a calling song with irregular, often long echemes (bouts) of widely spaced pulse trains (Plate 15). Male choruses may synchronize or alternate pulse train production. The acoustical activity of several species may begin late at night and continue until dawn, becoming more frequent as the night progresses.

The Diminutiva Group is most speciose in the South Coast Ranges of California, but a widespread species occurs in the Tehachapi Mountains at the eastern extreme of the Transverse Ranges where they join the southern

Sierra Nevada (Fig. 28). The Transverse Ranges represent a region of sympatry with members of the Morsei Group marked by extensive mitochondrial capture (Fig. 3). Apart from incidences of capture, the Diminutiva Group species are well resolved phylogenetically (Figs. 2–4).

Aglaothorax diminutiva (Rentz & Birchim, 1968)

Neduba (*Aglaothorax*) *diminutiva*—Rentz & Birchim 1968: 63

Fig. 28 (distribution), Fig. 29 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 6 (male terminalia), Plate 9 (female subgenital plate), Plate 13 (male titillators), Plate 15 (male calling song).

Common name. Diminutive Shieldback.

History of recognition. Described in *Neduba* (*Aglaothorax*) from Mount Diablo, Contra Costa County, California (Rentz & Birchim 1968). Support for species status came from a divergent karyotype (Ueshima & Rentz 1979). Three subspecies were then described from Southern California: *constrictans*, *dactyla*, and *malibu* (Rentz & Weissman 1981), the first of these without female specimens and the second from a female holotype. Below, we elevate the first two subspecies to species rank and synonymize the third under *A. dactyla*.

Type material. The holotype male is deposited at Academy of Natural Sciences at Philadelphia. Images of the holotype are available at OSFO (Cigliano *et al.* 2025). TOPOTYPES EXAMINED: (n=11) **USA, CA, Contra Costa Co.**, Mount Diablo State Park, 37.862703, -121.93107, 1160 m, 1-IX-2002, DB Weissman, CAS, 1♀; same data except 13-VIII-1994, DB Weissman, CAS, 1♂; same data except 37.881038, -121.916706, 1142 m, 11-VIII-1990, DB, DW Weissman, CAS, 5♀; Mount Diablo State Park, Juniper Camp, 37.862703, -121.93107, 886 m, 17-VIII-1965, DC, KA Rentz, CAS, 1♂; same data except 28-VIII-1982, DB Weissman, CAS, 1♂; Mount Diablo State Park, Muir Picnic Area, 37.8764, -121.9208, 1001 m, 20-21-VII-2005, JA Cole, LACM, 1♂; Mount Diablo State Park, summit, 37.862703, -121.93107, 1220 m, 13-VIII-1991, DB Weissman, CAS, 1♀.

Measurements. (mm, ♂n=8, ♀n=7) Hind femur ♂12.21–13.68, ♀13.85–16.27, pronotum total length ♂7.00–8.23 ♀7.00–7.75, prozona length ♂2.79–3.49, ♀3.21–4.36, metazona dorsal length ♂4.00–4.83, ♀2.84–4.35, pronotum constriction width ♂2.34–2.96, ♀2.60–3.50, metazona dorsal width ♂5.00–5.57, ♀4.85–5.40, head width ♂3.56–3.95, ♀4.25–4.69, ovipositor length ♀11.21–12.24.

Distribution. Interior South Coast Ranges of California. Type material is from the northernmost extent of these mountains in the Diablo Range, but we have determined specimens from throughout the interior South Coast Ranges.

Habitat. Chaparral and oak woodland understory. On Sage (*Salvia* spp.), Mountain Mahogany, Coast Live Oak (*Quercus agrifolia* Née), Scrub Oak (*Quercus* spp.), and Poison Oak.

Seasonal occurrence. Adult activity from spring (12-VI-2008, JA Cole, LACM) through summer (6-IX-2002, JA Cole, LACM).

Stridulatory file. (n=6) length 2.80–3.40 mm, 83–110 teeth, tooth density 32.0±1.6 (29.6–34.3) teeth/mm.

Song. (n=18) The common small *Aglaothorax* song with slowly produced, widely spaced pulse trains that occur slow enough that a human listener may count them. Pulse trains 70±40 ms in length are delivered at a rate of 4.34±0.88 s^{-1}. Mean peak frequency is 15.14±4.54 kHz; high frequency recording equipment detected ultrasonic peak frequencies as high as 33.00 kHz. Echemes contain a variable number of pulse trains, typically a high number (mean 39±22, range 12–83 pulse trains). The echeme repetition rate range is 1–6 min^{-1}. Acoustical activity intensifies as the night wears on. At the type locality, in Juniper Camp, a few paltry calls were heard before 2330 h. Upon awakening at 0130 h, some 15 males were calling in the same area. In San Luis Obispo County, singing did not begin in earnest until after 2330 h on 12-VI-2008, and in San Benito County on 10-VIII-2017, singing was frequent only after midnight.

Karyotype. (n=2), 2n♂=23(20t+Xm+Xt+Ym), topotype T82-114 (S82-113). Ueshima and Rentz (1979) show the X_1 as a submetacentric, a condition confirmed at anaphase II in T82-114 (not shown in Fig. 28). The same karyotype was found from a population at Pinnacles National Park (Ueshima & Rentz 1979), confirming placement with this species. The sex determination is unique among *Aglaothorax*, a neo-X_1X_2Y system also shared with five species of *Neduba*: *N. arborea* Cole, Weissman, and Lightfoot, *N. duplocantans* Cole, Weissman, and Lightfoot, *N. inversa* Cole, Weissman, and Lightfoot, *N. prorocantans* Cole, Weissman, and Lightfoot, and *N. sierranus* (Rehn & Hebard) (Cole *et al.* 2021).

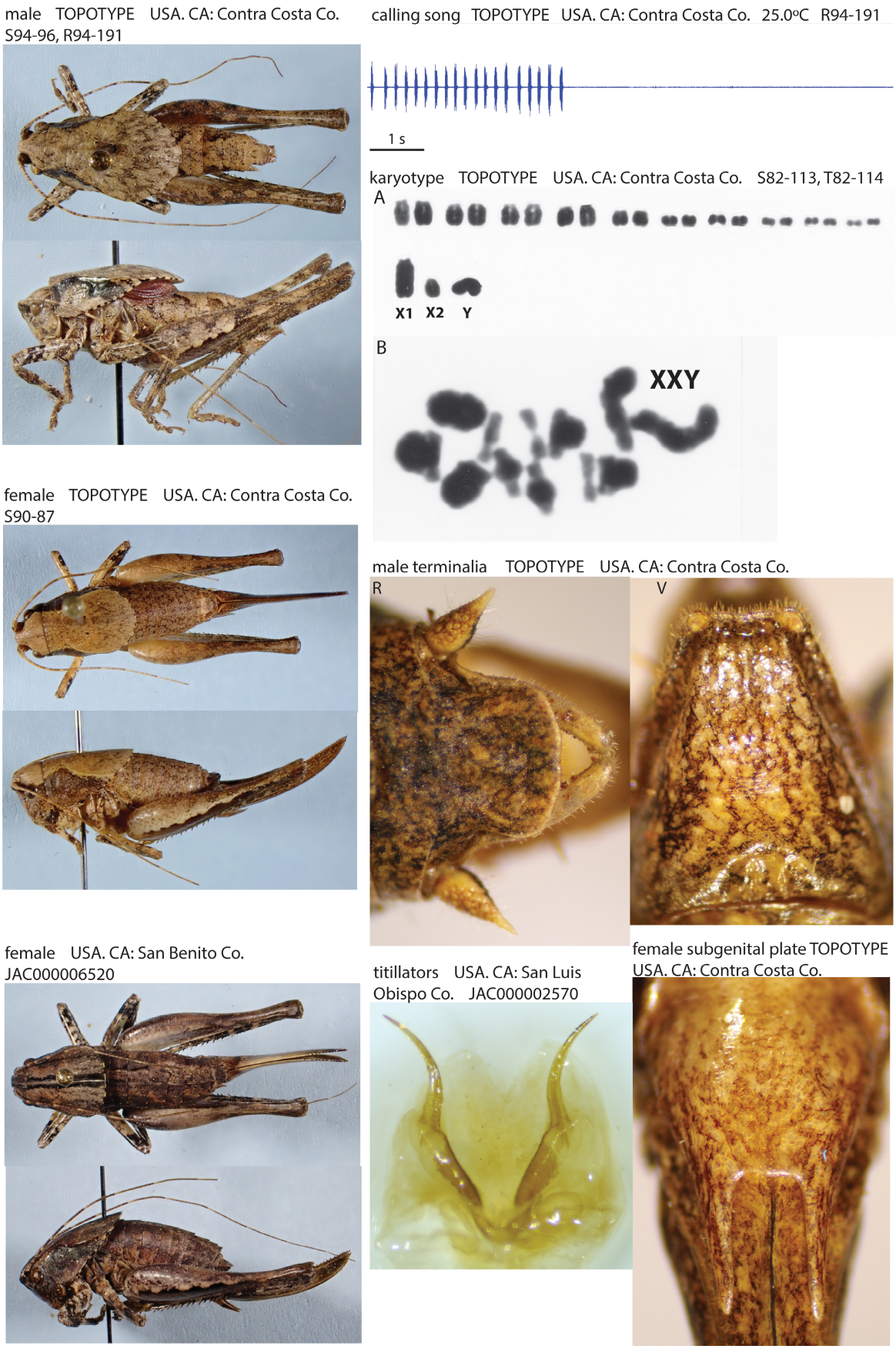


FIGURE 29. *A. diminutiva* male and female habitus, calling song, male and female terminalia, and karyotype. A. Idiogram, *A. diminutiva,* type locality T82-114 (S82-113) showing X_1X_2Y sex chromosome system; B. Metaphase I in same male showing association of all 3 sex chromosomes, with submetacentric X_1 and submetacentric Y apparent.

Recognition. Morphology, geography, karyotype. The male supra-anal plate is heart shaped, expanded after the base and indented along the caudal margin, and the titillator arms are long and bowed, character states that exclude all Morsei Group species. Likewise characteristic of the Diminutiva Group and exclusive of much of the Morsei Group, the male paraproct process has an apical tooth. Also occurring in the South Coast Ranges is *A. constrictans*, but in that species males have short, slightly curved titillator arms and females have short triangular subgenital plate lateral processes that are barely longer than wide. Female *A. diminutiva* have the subgenital plate lateral processes much longer than wide, and the processes meet the transverse caudal margin of the plate with a slight angle. Female *A. constrictans* have short, triangular subgenital plate processes that are scarcely longer than wide. Other Diminutiva Group species have the processes broadly rounded mesally onto the caudal margin of the plate. The processes of *A. diminutiva* are shorter and wider than those of *A. dactyla*. This is the only *Aglaothorax* species along the interior South Coast ranges and has the most northern distribution of any member of the genus. The *A. diminutiva* karyotype is unique among small *Aglaothorax* at 2n♂=23.

Notes. Mount Diablo is a region of high endemism, particularly for Orthoptera where it is also the type locality of the endemic *Neduba diabolica* (Scudder) as well as the more wide-ranging *Capnobotes attenuatus* (Scudder). The lifespan of wild caught adults may be long: a female captured by DBW on 1-IX-2002 at the type locality lived until 8-XII and laid many eggs. *Ormia* parasitoid flies emerged within 5–7 days from each of five males brought back to the laboratory from Laguna Mountain Recreation Area, San Benito County. These males were collected late in the season in mid-August. We speculate as to whether the prevalence of early evening *Ormia* activity may be a factor that explains late night calling.

Material examined. (n=24) **All USA, CA, San Benito Co.,** Pinnacles Nat. Mon., Chalone Camp, 36.530796, -121.145198, 8-VII-1967, DC, KA Rentz, CAS, 1♂; Pinnacles Nat. Mon., Chalone Campground, 36.530796, -121.145198, 12-VIII-1982, DB Weissman, CAS, 1♂; Pinnacles National Monument, 36.530796, -121.145198, 427 m, 25-VII-1982, PH Sullivan, LACM, 1♀; Pinnacles National Park, Pinnacles Campground, 36.48970, -121.15072, 311 m, 6-VII-2023, JA Cole, C Wong, 1♂ song record; Pinnacles National Park, Pinnacles View Area, 36.48309, -121.16313, 306 m, 6-7-VII-2023, JA Cole, C Wong, LACM, 2♂; same data except JAC, 1♂, 1♀; Short Fence Trailhead, Coalinga Road, Laguna Mountain Recreation Area, BLM, 36.36403, -120.87840, 670 m, 10-11-VIII-2017, JA Cole, AMNH, 1♂; same data except LACM, 4♂; Upper Sweetwater Campground, Coalinga Road, Laguna Mountain Recreation Area, BLM, 36.36067, -120.85256, 848 m, 10-11-VIII-2017, JA Cole, 1♂ song record; **San Luis Obispo Co.,** La Panza Campground, Los Padres National Forest, 12 miles northeast of Pozo, 35.3538, -120.2606, 732 m, 12-13-VI-2008, JA Cole, LACM, 2♂; same data except JAC, 2♂; same data except 9-10-VI-2002, JA Cole, AMNH, 1♂; same data except LACM, 2♂; same data except JAC, 1♂; **Santa Clara Co.,** Uvas Canyon County Park, 15 miles west of Morgan Hill on Croy Road, 37.0855, -121.7954, 349 m, 6-IX-2002, JA Cole, LACM, 1♂; same data except JAC, 1♂.

Aglaothorax constrictans (Rentz & Weissman, 1981) stat. rev.

Neduba (*Aglaothorax*) *diminutiva constritcans*—Rentz & Weissman, 1981: 92
Aglaothorax constrictans **stat. rev.** (Revised to species level).
Fig. 28 (distribution), Fig. 30 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 6 (male terminalia), Plate 9 (female subgenital plate), Plate 13 (male titillators), Plate 15 (male calling song).

Common name. Constricted Shieldback.

History of recognition. Described as a subspecies of *Neduba (Aglaothorax) diminutiva* from male material only (Rentz & Weissman 1981). We elevate this taxon to species rank based on aberrant morphology for the Diminutiva Group in both males and females, and due to the appreciable genetic distance from other Diminutiva Group lineages.

Type material. The type series was collected from a dune area near the lighthouse at Bixby Ranch, Point Conception, Santa Barbara County, California. Images of the holotype and a paratype are available at OSFO (Cigliano *et al.* 2025). PARATYPES EXAMINED (n=13): **USA, CA, Santa Barbara Co.,** Point Conception, Bixby Ranch, dunes nr. Lighthouse, 34.44860, -120.47155, 8-VI-1971, DC Rentz, DB Weissman, CAS, 1♂; same data except 8-VII-1971, DC Rentz, DB Weissman, CAS, 1♂; same data except 8-VIII-1974, DC Rentz, DB Weissman, CAS, 11♂.

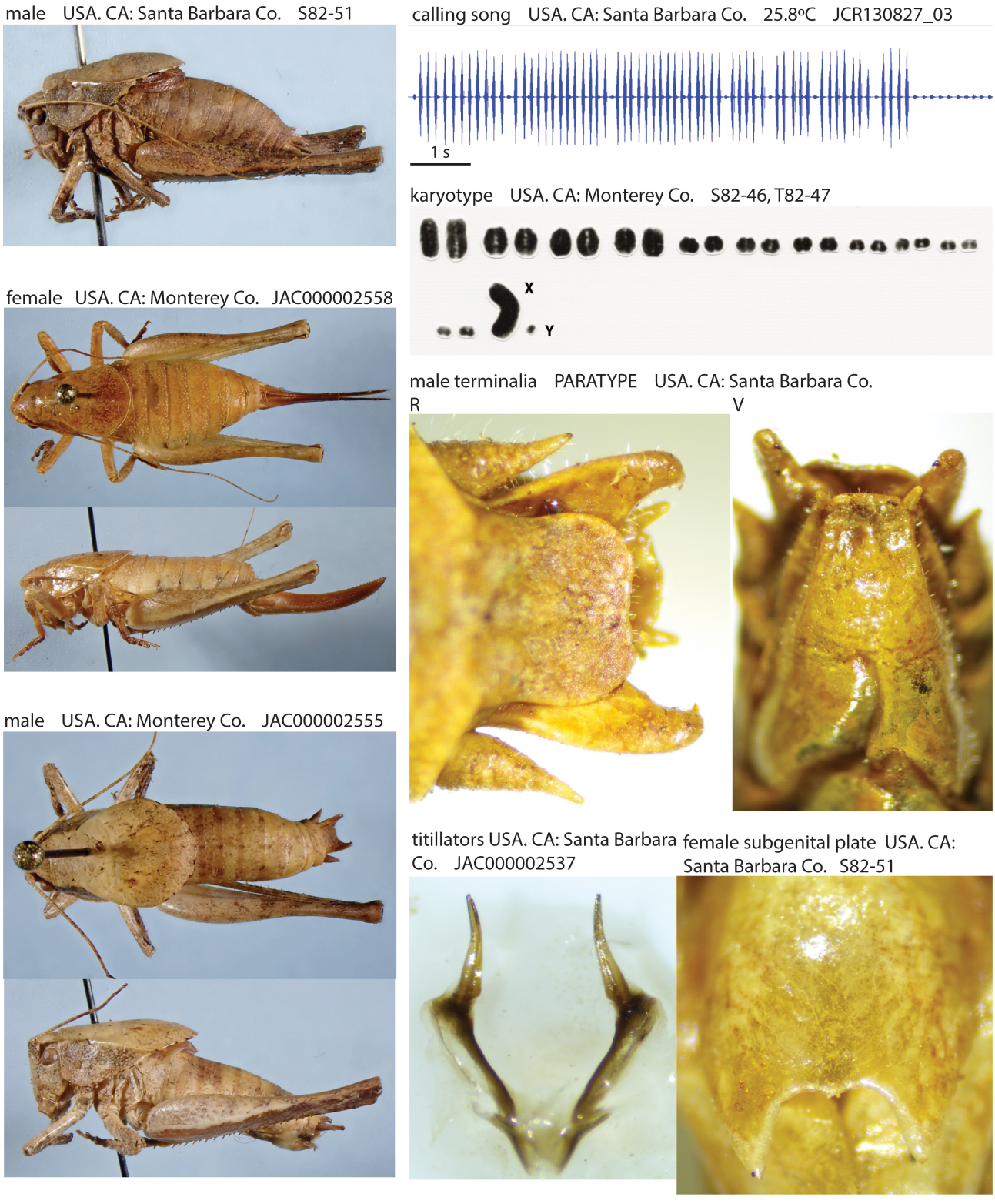


FIGURE 30. *A. constrictans* male and female habitus, calling song, male and female terminalia, and karyotype. Idiogram shows karyotype 2n♂=24.

Measurements. (mm, ♂n=18, ♀n=13) Hind femur ♂12.45–15.05, ♀14.70–18.37, pronotum total length ♂7.20–9.15, ♀7.16–9.50, prozona length ♂3.34–3.94, ♀1.34–4.76, metazona dorsal length ♂3.84–5.24, ♀3.35–5.85, pronotum constriction width ♂2.40–5.47, ♀2.45–3.55, metazona dorsal width ♂5.15–6.51, ♀5.05–6.58, head width ♂3.40–3.95, ♀4.00–4.60, ovipositor length ♀10.55–11.79.

Distribution. South Coast Ranges of California bordering the Pacific Ocean. Distribution extends from Point Conception north through the Santa Lucia Range.

Habitat. Coastal dunes, coastal sage scrub, chaparral, and oak savanna from the beachfront to mountain slopes.

Seasonal occurrence. Adult activity spans late spring (4-VI-2006, JA Cole, LACM) through summer (8-IX-2002, JA Cole, LACM).

Stridulatory file. (n=16) length 3.00–3.90 mm, 84–107 teeth, tooth density 28.7±2.3 (23.3–32.1) teeth/mm.

Song. (n=19) Common small *Aglaothorax* song with widely spaced, individually countable pulse trains. Length of pulse trains is 50±20 ms. Pulse trains repeat at a rate of 5.31±0.69 s^{-1}. Mean peak frequency is 14.35±0.77 kHz. Long, variable echemes contain on average 38±19 (range 12–89) pulse trains. Silent intervals between echemes range from 7 to 29 s.

Karyotype. (n=4) 2n♂=24 (22t+XtYt), paratype T82-47 (S82-51).

Recognition. Typical for the Diminutiva Group, the male supra-anal plate is heart-shaped, expanded laterally and indented on the caudal margin, and the paraproct processes have an apical tooth. Otherwise, the morphology of this species is aberrant for the Diminutiva Group, the male titillators and female subgenital plate instead resembling those of the Morsei Group. Male titillator arms are short and barely curved as opposed to long and distinctly curved, the condition found in all other Diminutiva Group species. Females have short, triangular subgenital plate processes instead of long, digitiform processes as in the rest of the Diminutiva Group. For males, the apical position of the mesal tooth on the paraproct process excludes most Morsei Group species from consideration; *A. amathitis*, *A. costalis*, *A. longipennis*, and *A. morsei* all have a subapical tooth on the paraproct process along with a rounded supra-anal plate. The male titillator arms are notched at the base, a character state shared only with *A. morsei*. The female subgenital plate lateral processes are longer than wide unlike all Morsei Group females except *A. kelainops*.

Notes. This species is genetically a member of the Diminutiva Group (Figs. 2–4) but possesses morphology that is characteristic of the Morsei Group. Genetically, the closest relative is *A. diminutiva* which occurs in the South Coast Ranges to the east. Shared morphology may be the result of historical gene flow. Currently the ranges of *A. constrictans* and *A. diminutiva* are separated by the Salinas Valley. Other Morsei Group and Diminutiva Group lineages are found in the area where the Transverse and Peninsular Ranges meet in Ventura and Santa Barbara Counties, California, but we have not found any occurrences of sympatry. This species was, however, sympatric with both *Neduba carinata* Walker and *N. lucubrata* Cole, Weissman, & Lightfoot at Bottcher's Gap in the Ventana Wilderness of the South Coast Ranges of California, this occurrence representing the highest count of sympatric nedubine species that we have encountered. The Nature Conservancy protected 25,000 acres of the Bixby Ranch type locality at Point Conception in 2017.

Material examined. (n=51) **All USA, CA, Monterey Co.,** 0.9 miles E of Arroyo Seco and G17, intersection on Arroyo Seco, 36.25466, -121.43208, 192 m, 12-VIII-1982, DB Weissman, CAS, 6♂, 4♀; Arroyo Seco Rd., 0.6 mi. W of intersection with G6, 36.235139, -121.473392, 274 m, 29-VII-1983, DB Weissman, CAS, 1♂, 1♀; Big Sur, SR1, 36.3547, -121.8136, 685 m, 20-VIII-2012, JA Cole, 1♂ sound recording; Bottcher's Gap, Los Padres National Forest, 19 miles north of Big Sur off SR1 on Palo Colorado Road, 36.3550, -121.8138, 652 m, 20-21-VIII-2012, JA Cole, LACM, 1♀; same data except JAC, 1♀; Bottcher's Gap, Los Padres National Forest, 19 miles north of Big Sur off SR1 on Palo Colorado Road, 36.3550, -121.8138, 652 m, 7-8-IX-2002, JA Cole, LACM, 1♂; Palo Colorado Rd., 3 mi. E of SR1, 36.3864, -121.8687, 327 m, 20-VIII-2012, JA Cole, LACM, 5♂, 1♀, 2 pairs in copula; same data except JAC, 1♂, 1♀; Pfeiffer Big Sur State Park, 36.248852, -121.782732, 5-VII-1986, DB & BI Weissman, CAS, 1♂; **Santa Barbara Co.,** Gaviota Pass Rest Area, 34.489433, -120.225984, 22 m, 14-VIII-1986, B Hebert, CSUN, 1♀; Gaviota State Park, 34.47222, -120.22722, 4 m, 20-21-VIII-2013, JA Cole, AMNH, 1♂; same data except LACM, 8♂, 1♀; same data except JAC, 3♂; Harris Grade Road, 5 miles north of Lompoc, 34.7238, -120.4368, 216 m, 3-VI-2006, JA Cole, JAC, 1♂; same data except, 4-VI-2006, JA Cole, LACM, 1♂; same data except JAC, 1♀; junction Santa Rosa Rd. and US101, 34.603319, -120.284877, 14-VII-1976, CAS, 2♂; Santa Ynez Mountains, 0.8 mi. W Cold Arch Bridge on Hwy. 154, 34.528049, -119.843848, 320 m, DB Weissman, DC Lightfoot, CAS, 1♂, 1♀; Vandenberg Air Force Base, 2.7 mi. NW of intersection 13th and Airfield on 13th, 34.764161, -120.579461, 90 m, 13-VIII-1982, DB Weissman, CAS, 4♂, 1♀, CAS.

Aglaothorax dactyla (Rentz & Weissman, 1981) stat. rev.

Neduba (*Aglaothorax*) *diminutiva dactyla*—Rentz & Weissman, 1981: 94.
Neduba (*Aglaothorax*) *diminutiva malibu*—Rentz & Weissman 1981: 95 **New junior subjective synonym.**
Fig. 28 (distribution), Fig. 31 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 6 (male terminalia), Plate 9 (female subgenital plate), Plate 13 (male titllators), Plate 15 (male calling song).

Common name. Clawed Shieldback.

History of recognition. Described as a subspecies of *Neduba* (*Aglaothorax*) *diminutiva* from the western Santa Monica Mountains with populations to the east of Malibu Creek named *N. (A.) d. malibu* (Rentz & Weissman 1981). Transferred to *Aglaothorax* where this species is currently classified (Cigliano *et al.* 2025). The Santa Monica Mountains Diminutiva Group lineage shows strong genetic separation from other clades in the Group, especially from type *A. diminutiva*. Although we found phylogeographic separation west and east of Malibu Creek, expanded sample size negates prior morphological diagnosis of subspecies. Coupled with an absence of song and karyotype differences, we recognize *A. dactyla* at species rank and synonymize *A. d. malibu* under *A. dactyla*.

Type material. The holotype female of *N.* (*A.*) *d. dactyla* was collected from the junction of State Highway 23S and Mulholland Highway, Los Angeles County, California and is housed at CAS. The holotype male of *N.* (*A.*) *d. malibu* was collected at Big Rock Canyon Road 0.4 miles north of Pacific Coast Highway in Malibu, Los Angeles County, California, and is also housed at CAS. Images of the types are available at OSFO (Cigliano *et al.* 2025).

PARATYPES EXAMINED: (n=2) *dactyla* **USA, CA, Los Angeles Co.,** Cal Hwy 23 Mulholland Hwy., 34.0873, -118.8742, 556 m, 21-VI-1971, DB Weissman, CAS, 1♀; **Ventura Co.,** Point Mugu State Beach dune area, 34.083332, -119.050003, 4 m, 19-VII-1972, DB Weissman, CAS, 1♂; TOPOTYPES EXAMINED: (n=9); *dactyla* **USA, CA, Los Angeles Co.,** Malibu, Eino's, corner of Mulholland and Decker (23S), 34.08855, -118.87360, 2-VII-1976, DB Weissman, CAS, 1♂; SR23S & Mulholland Hwy., 34.0873, -118.8742, 548 m, 14-VIII-1982, DB Weissman, CAS, 3♂; same data except 17-VI-2008, JA Cole, LACM, 1♂; same data except JAC, 1♀; *malibu* **USA, CA, Los Angeles Co.**, Malibu, Big Rock Canyon Rd. at Rockport, 34.035842, -118.609528, 28-VI-1976, DB Weissman, CAS, 1♂; Malibu, intersection of Big Rock and Inland Roads, 34.035842, -118.609528, 5-VII-1982, DB Weissman, CAS, 2♂.

Measurements. (mm, ♂n=17, ♀n=11) Hind femur ♂13.65–16.07, ♀15.70–19.35, pronotum total length ♂8.04–9.76, ♀7.05–9.95, prozona length ♂2.90–4.19, ♀3.24–5.05, metazona dorsal length ♂4.58–5.95, ♀3.40–5.00, pronotum constriction width ♂2.25–3.05, ♀2.61–3.40, metazona dorsal width ♂5.60–6.65, ♀5.03–6.75, head width ♂3.35–3.88, ♀4.07–4.81, ovipositor length ♀11.00–14.30.

Distribution. Santa Monica Mountains, California.

Habitat. Coastal sage scrub, grassland, chaparral, oak woodland. Frequents hillsides, hilltops, and dry (south) slope chapparal. On California Sage (*Artemisia californica* Less.), Mulefat (*Baccharis* sp.), Laurel Sumac, *Ceanothus* spp., Monkeyflower, Western Sycamore, Coast Live Oak, Scrub Oak, White Sage (*Salvia leucophylla* Greene), and Poison Oak.

Seasonal occurrence. Spring (3-V-1997, JA Cole, LACM) through summer (24-VIII-1976, PH Sullivan, CAS). Nymphs and adults occurred alongside one another at the early date record.

Stridulatory file. (n=6) length 3.20–3.90 mm, 81–106 teeth, tooth density 27.8±2.7 (25.3–32.8) teeth/mm.

Song. (n=46) Common small *Aglaothorax* song with slowly produced pulse trains that are countable by a human listener. Pulse trains 50±20 ms in length are produced at a rate of 5.05±0.79 s^{-1}. Mean peak frequency is 15.84±4.43 kHz, with peak frequencies as high as 26.60 kHz detected with ultrasonic recording equipment. Echemes are highly variable in length and group 36±20 (5–92) pulse trains. The echeme repetition rate is 1–12 min^{-1}. Males are synchronous chorusers. Followers may join leaders and overlap pulse trains precisely, making it difficult to gauge the number of males singing in an area. Across distance, choruses may be heard to spread like waves as males at increasing distances join the chorus center.

Karyotype. (n=3) 2n♂=24 (22t+XtYt), topotype T82-123 (S82-56).

Recognition. Morphology, geography. The male supra-anal plate is heart-shaped, sometimes only slightly, but the caudal margin of the plate is always indented, the paraproct processes have an internal apical tooth, and the titillator arms are long and bowed, characters that separate *A. dactyla* from Morsei Group species. Sympatric and nearby allopatric Morsei Group species have rounded supra-anal plates, a subapical tooth on the paraproct process, and short, barely curved titillator arms. The long, bowed titillators also separate *A. constrictans* from consideration,

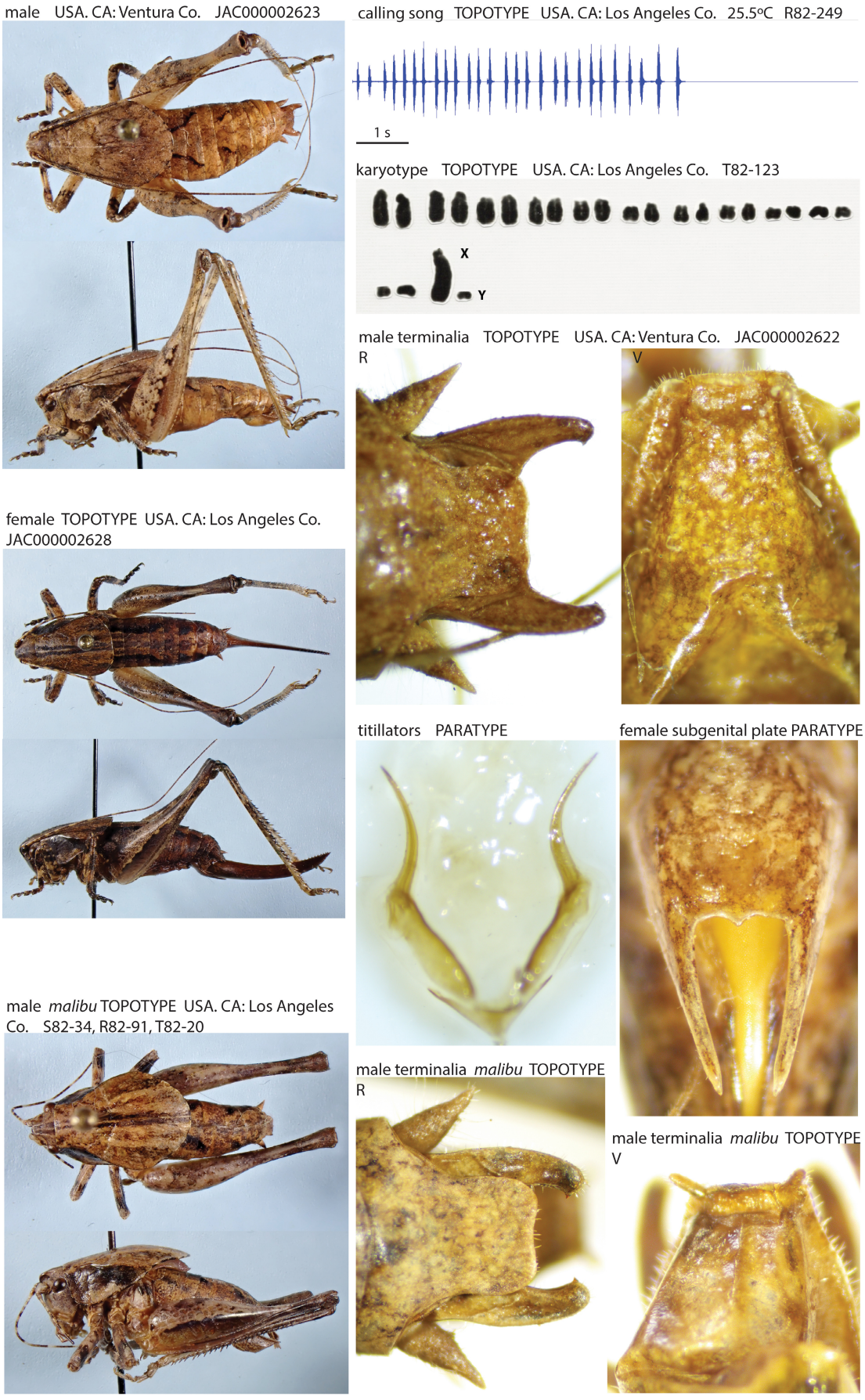


FIGURE 31. *A. dactyla* male and female habitus, calling song, male and female terminalia, and karyotype. Idiogram shows karyotype 2n♂=24.

which has short titillator arms and *A. oreibates*, which has long titillators that show less lateral curvature. The female subgenital plate has the longest and most slender digitiform lateral processes of any *Aglaothorax*; the processes of *A. acrolophitus* and *A. poecilonotum* are shorter, thicker at the base, and more strongly tapered.

Notes. Complete syntopy of *A. dactyla* and *A. costalis* in a garden were noted in their original description, where their specific distinction was evident from obvious song differences (Rentz & Weissman 1981). We have since observed syntopy throughout the Santa Monica Mountains: both species may be found on the same plants and choruses of their divergent songs may be heard alongside one another. The history of mitochondrial capture by *A. costalis* and *A. longipennis* (Fig. 3) illustrates incomplete reproductive isolation. The contact zone between *A. dactyla* and *A. costalis* is an example of reinforcement of premating isolation. Females of both species avoid songs of heterospecifics (Cole 2016), which is made possible by evolution of a rapid pulse train rate in *A. costalis*. In addition to song, the two species show partial ecological and temporal isolation. *A. dactyla* prefers the dry upland or south facing slopes while *A. costalis* is more common in lowland, mesic, and riparian areas. Adult activity commences and ceases earlier in the season in *A. dactyla* than in *A. costalis*. East of Malibu Creek, *A. dactyla* is broadly sympatric with *A. longipennis* but that pair are more strongly separated by habitat and have not been observed in syntopy.

Material examined. (n=51) **All USA, CA, Los Angeles Co.,** Backbone Trailhead, at junction Stunt, Schueren, and Saddle Peak Rds., 34.0812, -118.6454, 721 m, 9-24-VI-2012, JA Cole, JAC, 2♂, 2♀; Calamigos Ranch, 34.09278, -118.81694, 550 m, 1-VII-1961, DL Gibo, CSUN, 1♀; Charmlee County Park, 34.0608, -118.8771, 427 m, 23-24-VIII-1976, PH Sullivan, CAS, 1♀; Charmlee Wilderness Park, 3.8 miles north of SR1 on Encinal Canyon Road, 34.0608, -118.8771, 427 m, 29-30-VI-2006, JA Cole, JF Eguizabal, LACM, 1♂; same data except 2-VI-2005, JA Cole, JF Eguizabal, LACM, 1♀; same data except JAC, 1♂; same data except 3-4-V-1997, JA Cole, LACM, 1♂, 1♀; Griffith Park, Mount Hollywood Trail, 34.1240, -118.3009, 370 m, 7-V-2002, JA Cole, JF Eguizabal, 1♂ sound record; junction Big Rock Drive and SR1, 34.0377, -118.6088, 5 m, 17-VI-2008, JA Cole, 1♂ sound record; junction Las Flores Canyon Rd. and Schueren Rd., 34.0625, -118.6486, 469 m, 24-25-VI-2012, JA Cole, JAC, 1♂; junction Las Flores Rd. and Gorge Rd., 34.0507, -118.6391, 66 m, 25-VI-2012, JA Cole, LACM, 1♂; Leo Carrillo State Park, Nicholas Flat, at end of Decker School Rd., 34.0638, -118.9128, 457 m, 3-VI-2008, JA Cole, LACM, 1♂, 1♂ sound record; same data except 5-VI-2007, JA Cole, LACM, 1♂; same data except 8-VI-2008, JA Cole, LACM, 1♂; Topanga State Park, Dead Horse Trail, 34.0915, -118.5939, 274 m, 27-28-V-2008, JA Cole, 1♂ sound record; UCLA Stunt Ranch Santa Monica Mountains Reserve, 34.0951, -118.6486, 374 m, 12-13-VI-2014, JA Cole, DA Gray, LACM, 1♂; **Ventura Co.,** Point Mugu State Park, Sycamore Canyon, 34.0728, -119.0145, 4 m, JA Cole, LACM, 7♂, 1♀; same data except 11-VI-2007, JA Cole, LACM, 1♀; same data except 14-15-VI-2007, JA Cole, 1♂ sound record; same data except JA Cole, JF Eguizabal, LACM, 1♂; same data except 16-17-VI-2008, JA Cole, LACM, 1♀; same data except JAC, 1♀; same data except 18-VI-2007, JA Cole, 1♂ sound record; same data except 2-3-VI-2008, JA Cole, LACM, 4♂; same data except JAC, 1♂; same data except 28-29-V-2007, JA Cole, 1♂ sound record; same data except 4-VI-2007, JA Cole, AMNH, 1♂, 1♀; LACM, 2♂; same data except 5-6-VI-2006, JA Cole, LACM, 3♂, 1♀; JAC, 1♂; same data except 9-VI-2005, JA Cole, LACM, 1♀.

Aglaothorax acrolophitus Cole, Weissman, and Lightfoot, sp. nov.

Fig. 28 (distribution), Fig. 32 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 6 (male terminalia), Plate 9 (female subgenital plate), Plate 13 (male titllators), Plate 15 (male calling song).

Common name. Mountaineer Shieldback.

History of recognition. None.

Type material. HOLOTYPE MALE: **USA, California, Kern County,** Tehachapi, Water Canyon Road, 0.15 miles south of intersection with Highland, 35.30774N, 118.02174W, 1463 m, 28-VIII-1983, DB Weissman, S83-115, R83-293, T83-45, 97 [stridulatory file tooth count], 3.7 [stridulatory file length, mm], excised tegmen in gelcap below specimen, deposited in CAS, Entomology type #20378. PARATYPES: (n=39) **USA, CA, Kern Co.,** Tehachapi, Water Canyon Rd., 0.15 miles S of intersection with Highline Rd., 35.307739, -118.021738, 1463 m, 28-VIII-1983, DB Weissman, CAS, 1♂; **Los Angeles Co.**, Agua Dulce Canyon, Agua Dulce Canyon Road, 2 miles south of Agua Dulce, 34.4729, -118.3311, 679 m, 17-VI-2003, JA Cole, AMNH, 1♂, 1♀; same data except LACM, 5♂, 5♀; Arroyo Seco, Gabrielino Recreation Trail, end of Windsor, 34.2065, -118.1670, 355 m, 4-IX-2021, JA Cole, JF Eguizabal, LACM, 1♂; Chilao Campground, Angeles National Forest, 25 miles NE of La Canada Flintridge

on SR2 (Angeles Crest Highway), 34.3262, -118.004, 1615 m, 27-IX-1999, JA Cole, JF Eguizabal, LACM, 2♂; same data except 7-VIII-2013, JA Cole, LACM, 2♂; Devil's Punchbowl County Park, 34.4138, -117.8587, 1470 m, 17-VIII-1982, DB Weissman, LACM, 1♂; end of Stonehill Way, Canyon Country, 34.4246, -118.4532, 294 m, 26-27-V-2013, JA Cole, LACM, 3♂; Forest Road 7N01 and San Francisquito Canyon Road, 34.6431, -118.3783, 1080 m, 30-31-VII-2017, JA Cole, LACM, 1♀; Placerita Nature Center, 34.382775, -118.465917, 21-XII-1982, PH Sullivan, CAS, 1♂; Templin Highway off I-5, 34.6165, -118.7439, 700 m, 29-30-VI-2006, JA Cole, JF Eguizabal, LACM, 1♀; **Ventura Co.,** McGill Campground, Los Padres National Forest, 34.81505, -119.10014, 2271 m, 8-9-VIII-2017, JA Cole, LACM, 4♂; Squaw Flat Road at trailhead to Sespe Creek, 8 miles north of Fillmore on Goodenough Road, 34.4826, -118.9179, 799 m, 11-VII-2021, JA Cole, AMNH, 1♂; same data except LACM, 3♂, 2♀; same data except 3-4-VII-2012, JA Cole, LACM, 4♂;

Measurements. (mm, ♂n=13, ♀n=11) Hind femur ♂11.80–14.17, ♀13.25–17.05, pronotum total length ♂6.50–9.04, ♀5.95–8.30, prozona length ♂2.75–4.04, ♀2.73–4.91, metazona dorsal length ♂3.60–5.55, ♀3.10–4.54, pronotum constriction width ♂2.40–3.00, ♀2.60–3.80, metazona dorsal width ♂4.89–6.16, ♀4.40–5.90, head width ♂3.44–4.20, ♀3.77–4.75, ovipositor length ♀9.95–13.37.

Distribution. Northern Transverse Ranges of California. Populations span a considerable west-east distance from the San Emigdio Mountains in the west to the Tecachapi Mountains in the east and apparently north into the southern Sierra Nevada.

Habitat. Chaparral and mixed woodland. Prefers thick tangles of vegetation. On Manzanita, *Ceanothus* spp., Chaparral Yucca (*Hesperoyucca whipplei* (Torr.) A. Baker), and Peruvian Pepper Tree (*Schinus mollae* L.). May occur in exurban developments that encroach upon native habitat e.g. in Canyon Country, Los Angeles County, California.

Seasonal occurrence. Adult activity from spring (26-V-2013, JA Cole, LACM) into winter (21-XII-1972, PH Sullivan, CAS). Nymphs were common 17-VI-2003 (JA Cole, LACM).

Stridulatory file. (n=13) length 2.70–3.70 mm, 76–98 teeth, tooth density 29.5±3.2 (23.8–35.9) teeth/mm.

Song. (n=30) Common small *Aglaothorax* song type with a slow pulse train rate. Pulse trains 60±20 ms are produced at a rate of 5.25±0.70 s^{-1}. Mean peak frequency is 14.08±1.31 kHz. Variable length echemes contain a large number of pulse trains, on average 31±16 (range 8–78) pulse trains. The echeme repetition rate is 6 min^{-1}.

Karyotype. (n=4) 2n♂=24 (22t+XtYt), holotype T83-45 (S83-115).

Recognition. Morphology, geography. Male supra-anal plate heart-shaped, paraproct with apical internal tooth, and titillators long and strongly bowed, excluding the Morsei Group that possesses in most species a subapical internal tooth on the male paraproct arm, a rounded or square supra-anal plate, and short titillator arms. Male *A. constrictans* also have a heart-shaped supra-anal plate but have short titillator arms. Male *A. oreibate*s have titillator arms with less lateral curvature and a basal constriction. Female subgenital plate with long digitiform processes unlike the short, triangular processes of Morsei Group species and *A. constrictans*. The *A. acrolophitus* female subgenital plate lateral processes are stout at the base and taper to a blunt apex unlike the sharp, slender processes of female *A. dactyla*. The inner margins of the female subgenital plate processes met in a rounded angle in *A. acrolophitus* but at a right angle in *A. diminutiva*. Males of *A. dactyla* and both males and females of *A. poecilonotum* may be morphologically indistinguishable but are geographically separated in the Santa Monica and Santa Ynez Mountains, respectively.

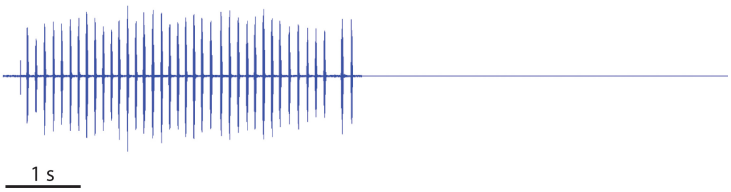
Etymology. *Gr. acrolophitus* a mountaineer. Inspired by the wide distribution across the Transverse Ranges of California.

Notes. Populations that belong to this species are distributed across a wide geographic range (Fig. 27). This is the only small *Aglaothorax* that enters the Sierra Nevada Mountains, where *Neduba* spp. replace *Aglaothorax* in chaparral and mixed woodland habitats (Cole *et al.* 2021). Adult activity and nymphal development may overlap by several weeks. At Agua Dulce Canyon, Los Angeles County, nymphs and adults were common feeding on the stalks and fruits of chaparral yucca. A parasitoid *Ormia* fly emerged 8-VI-2013 from a male collected from a northern Los Angeles County exurban habitat in Canyon Country on 26-27-V-2013. The introgression of *A. acrolophitus* mtDNA into both *A. conistylus* and *A. morsei* has occurred along regions of sympatry in the San Gabriel Mountains. In areas of overlap *A. acrolophitus* was apparently rare. JAC collected large series of *A. morsei* for female preference testing several times at Arroyo Seco, Gabrieleño Recreation Trail, Los Angeles County, California. On only one occasion, 3-IX-2021, was a male of *A. acrolophitus* captured.

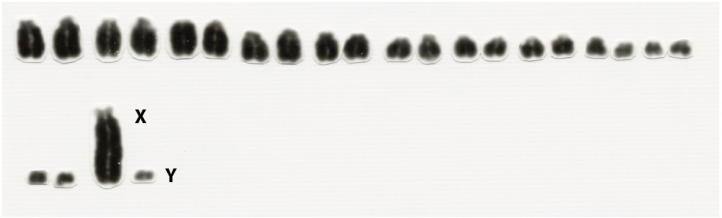
male HOLOTYPE USA. CA: Kern Co. S83-115, R83-293, T83-45



calling song PARATOPOTYPE USA. CA: Kern Co. 21.0ºC R83-292

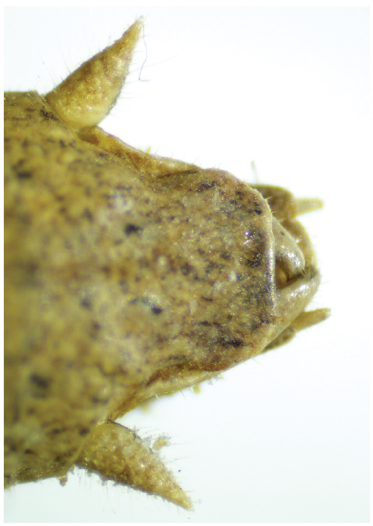


karyotype HOLOTYPE USA. CA: Kern Co. S83-115, T83-45

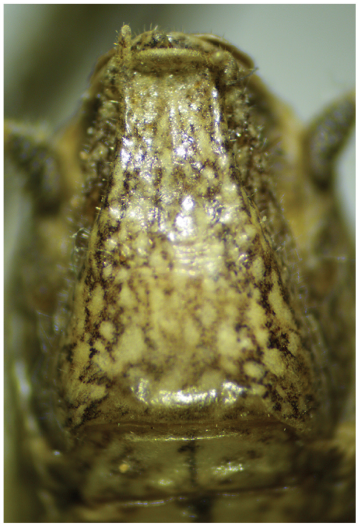


male terminalia HOLOTYPE USA. CA: Kern Co. S83-115

R



V



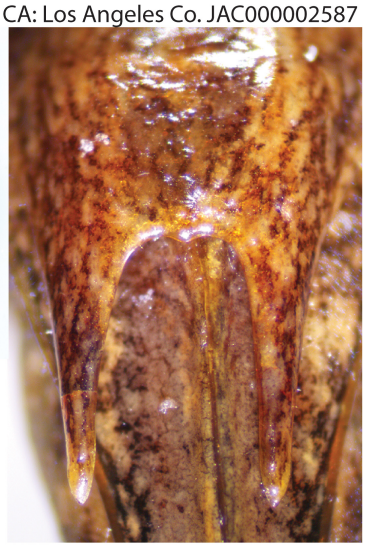
female PARATYPE USA. CA: Los Angeles Co. JCR000002592



titillators PARATYPE USA. CA: Ventura Co. JAC000002576



female subgenital plate PARATYPE CA: Los Angeles Co. JAC000002587



male PARATYPE USA. CA: Los Angeles Co. JCR000002940

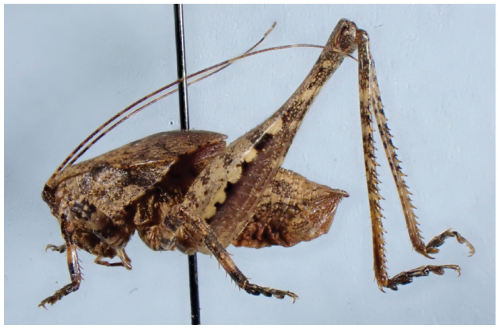


FIGURE 32. *A. acrolophitus* male and female habitus, calling song, male and female terminalia, and karyotype. Idiogram shows karyotype 2n♂=24.

Material examined. (n=7) **All USA, CA, Kern Co.,** Water Canyon Road, 1.4 miles below entrance to Tehachapi Mountain Park, 35.08258, -118.49486, 1571 m, 20-VII-2015, JA Cole, DB Weissman, JAC, 1♂; **Los Angeles Co.,** Clear Creek, San Gabriel Mountains, 34.288893, -117.646722, 1113 m, 15-VII-1970, RH Crandall, LACM, 1♂; county road N4, 3 miles east of Big Rock Springs, 34.4264, -117.8078, 1407 m, 7-VII-2004, JA Cole, LACM, 1♂; same data except 8-VII-2004, JA Cole, LACM, 1♂; Devil's Punchbowl County Park, 34.4138, -117.8587, 1470 m, 3-4-VIII-1974, PH Sullivan, CAS, 1♀; Templin Highway and FR6N53, 34.5858, -118.7142, 899 m, 16-VI-2012, JA Cole, 1♂ sound record; **Ventura Co.**, Pine Mountain Summit, 34.634152, -119.28817, 2027 m, 4-IX-1983, no collector, LACM, 1♂. QUESTIONABLE PLACEMENT: (n=8) USA, CA, **Los Angeles Co.**, Altadena, 34.189728, -118.131182, 1080 m, 29-VI-1989, RH Crandall, taken by sphecid, LACM, 1♀; Arroyo Seco, Gabrielino Recreation Trail, end of Windsor, 34.2065, -118.16700, 355 m, 17-IV-2017, JA Cole, K Halsey, JAC, 1♂ nymph; Bouquet Canyon, 34.425829, -118.541475, 700 m, 23-VII-1937, N Westerland, LACM, 1♂; Juniper Hills, Devil's Punchbowl Road (County Road N6), 2 miles east of Longview Road, 34.4267, -117.8697, 1316 m, 14-VI-2015, JA Cole, GE Bell, T Farwell, JAC, 1♂ nymph; San Gabriel Mountains, Big Tujunga Canyon near Fusier Canyon, 34.281, -118.211, 700 m, 2-V-2015, K Singh, malaise trap, CSUN, 2♀ nymphs; Sierra Highway, 0.5 miles west of Boiling Point, 34.5174, -118.2713, 920 m, 17-VI-2003, JA Cole, 1♂ song recording; **Tulare Co.**, Sierra Nevada, Sequoia Nat. For., Greenhorn Mts., Camp Nelson, 36.142724, -118.609256, 1525 m, 14-VIII-1982, SL Gibson, 1♂.

Aglaothorax oreibates Cole, Weissman, and Lightfoot, sp. nov.

Fig. 28 (distribution), Fig. 33 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 6 (male terminalia), Plate 9 (female subgenital plate), Plate 13 (male titillators), Plate 15 (male calling song).

Common name. Ventura Shieldback.

History of recognition. None.

Type material. HOLOTYPE MALE: **USA, California, Ventura County,** Highway 33, 34.51633N, 119.27758W, 649 m, 11-VII-2018, DB & DW Weissman, S18-26, R19-17, T19-11, D175, SING1000 [DNA extraction], MLNS Catalog # R19-017 [sound archive], 8444746 [specimen barcode], deposited in CAS, Entomology type #20380. PARATYPES: (n=14) **USA, CA, Ventura Co.**, same data as holotype, CAS, 4♂, 1♀; Harmon Canyon, 948 Scenic Way Drive, Ventura, 34.29458, -119.20121, 219 m, 23-V-2016, JA Cole, AMNH, 1♂; same data except LACM, 3♂, 1♀; same data except, JAC, 1♂; Wheeler Gorge Camp, 34.51824, -119.27108, 1870 m, 11-VII-2018, DB & DW Weissman, CAS, 3♀.

Measurements. (mm, ♂n=6, ♀n=5) Hind femur ♂15.45–17.31, ♀15.15–18.64, pronotum total length ♂9.24–10.91, ♀7.44–9.25, prozona length ♂3.85–4.51, ♀3.88–5.24, metazona dorsal length ♂5.08–6.41, ♀3.15–4.01, pronotum constriction width ♂2.85–3.57, ♀2.85–3.35, metazona dorsal width ♂6.51–7.43, ♀5.01–6.37, head width ♂4.10–4.40, ♀4.18–4.83, ovipositor length ♀10.75–14.00.

Distribution. Western Transverse Ranges of California.

Habitat. Coastal sage scrub and chaparral, including exurban areas adjacent to natural habitat.

Seasonal occurrence. Scant records show a long season with spring (23-V-2016, JA Cole, LACM) through fall (18-X-2020, A. Abela, LACM) adult activity.

Stridulatory file. (n=2) length 3.8 mm, 98–101 teeth, tooth density 26.2±0.6 (25.8–26.6) teeth/mm.

Song. (n=8) Typical small *Aglaothorax* song with widely spaced pulse trains produced slowly enough to count. Pulse trains 60±20 ms in length are produced at a rate of 5.14±0.34 s^{-1}. Mean peak frequency is 11.91±0.86 kHz. Variable length echemes contain 19–42 (mean 28±7) pulse trains. Silent intervals between echemes are brief and last 12±3 (range 5–16) s.

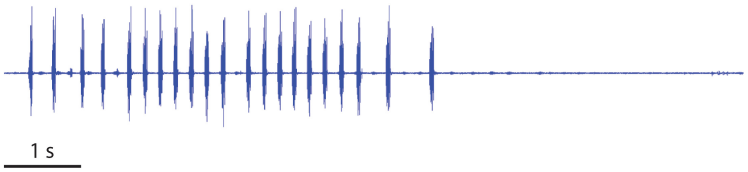
Karyotype. (n=5) 2n♂=24 (22t+XtYt), paratopotype T19-5 (S18-26).

Recognition. Morphology, DNA, geography. Body size averages large for the Diminutiva Group. The heart-shaped male supra-anal plate and apical mesal tooth on the male paraproct processes separate most Morsei Group species. The long titillator arms, characteristic of the Diminutiva Group in general, serve to eliminate *A. constrictans* and Morsei Group species, which possesses short titillator arms. The gentle lateral curve and narrowed base of the titillators separate this species from *A. dactyla*, *A. diminutiva*, and *A. poecilonotum*, which have strongly curved titillator arms without a basal constriction. The female subgenital plate of *A. oreibates* has lateral processes that are

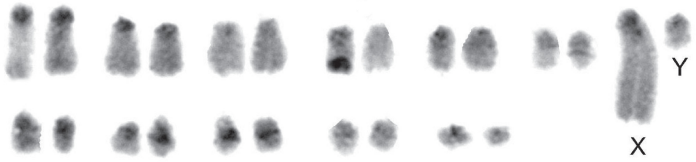
male HOLOTYPE USA. CA: Ventura Co. CAS8444746



calling song PARATOPOTYPE USA. CA: Ventura Co. 21.3ºC S18-26, R19-15

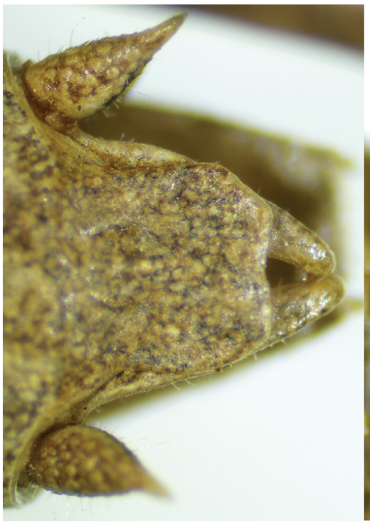


karyotype PARATOPOTYPE USA. CA: Ventura Co. S18-26, T19-5

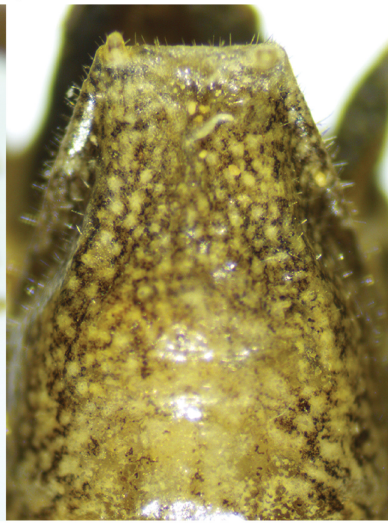


male terminalia HOLOTYPE USA. CA: Ventura Co. CAS8444746

R



V



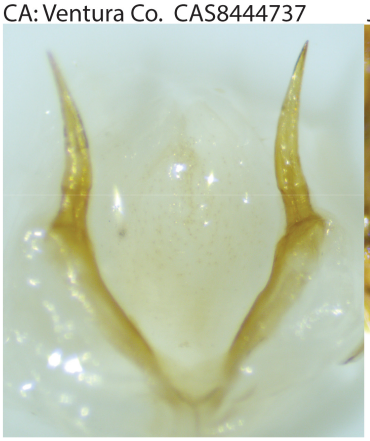
female PARATYPE USA. CA: Ventura Co. JAC000002644



male PARATYPE USA. CA: Ventura Co. JAC000002641



titillators PARATOPOTYPE USA. CA: Ventura Co. CAS8444737



female subgenital plate PARATYPE JAC000002644

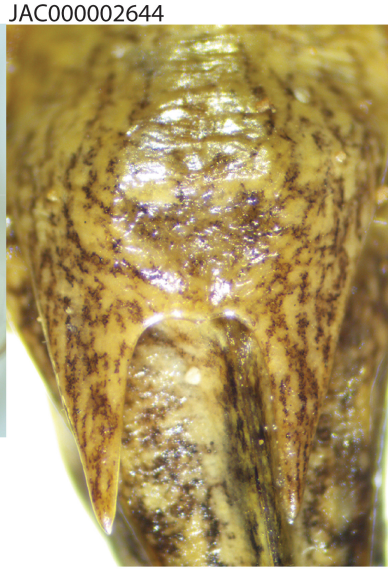


FIGURE 33. *A. oreibates* male and female habitus, calling song, male and female terminalia, and karyotype. Idiogram shows karyotype 2n♂=24.

of moderate length, thick at the base and tapered to a blunt apex. This condition eliminates *A. dactyla* in which females have longer, narrower, and sharper lateral processes. The lateral processes meet the subgenital plate caudal margin at a curve, unlike the right angle of *A. diminutiva*. Females may be morphologically indistinguishable from those of *A. acrolophitus* and *A. poecilonotum*, but *A. oreibates* is not known from the north slope of the Transverse Ranges or the Santa Ynez Mountains.

Etymology. Gr. *ore* a mountain + *bates* one that walks or haunts.

Notes. The type series were raised from eggs laid by two wild caught females collected on oatmeal trails on 11-VII-2018 from S18-26 and S18-28, and treated as described on p. 6. From 21-VII until 17-VIII, they laid some 15–20 eggs which were kept at room temperature, in moist soil, until 29-X-2018, and then refrigerated at 3ºC where they remained until 15-III-2019, when they were returned to room temperature. First hatching occurred on 2-IV-2019 with 12 eggs total hatching by 22-IV-2019. The first adults appeared 10-VI-2019.

Material examined. In addition to Type Material above, **USA, CA, Ventura Co.,** Lockwood Valley, 34.732482, -119.042048, 18-X-2020, A Abela, LACM, 1♀.

Aglaothorax poecilonotum Cole, Weissman, and Lightfoot, sp. nov.

Fig. 28 (distribution), Fig. 34 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 6 (male terminalia), Plate 9 (female subgenital plate), Plate 13 (male titillators), Plate 15 (male calling song).

Common name. Santa Ynez Shieldback.

History of recognition. None.

Type material. HOLOTYPE MALE: USA, California, Santa Barbara County, Upper Oso Campground, Los Padres National Forest, 34.55469N, 119.76960W, 349 m, 10-VIII-2021, DB & DW Weissman, S21-22, R22-8, F1 [reared], deposited in CAS, Entomology type #20379. PARATOPOTYPES (n=45) **USA, CA, Santa Barbara Co.**, same data as holotype, CAS, 6♂, 21♀; Upper Oso Campground, Los Padres National Forest, 22 miles northwest of Santa Barbara off SR154 (Paradise Rd.), 34.5544, -119.7683, 376 m, 11-12-VI-2008, JA Cole, LACM, 10♂; same data except 7-8-VI-2002, JA Cole, AMNH, 2♂; same data except LACM, 5♂, 1♀.

Measurements. (mm, ♂n=6, ♀n=5) Hind femur ♂12.13–14.43, ♀13.65–16.55, pronotum total length ♂6.85–8.59, ♀6.47–8.38, prozona length ♂3.15–4.20, ♀3.26–4.79, metazona dorsal length ♂3.55–5.05, ♀2.60–4.18, pronotum constriction width ♂2.36–2.80, ♀2.50–3.40, metazona dorsal width ♂5.10–6.11, ♀4.60–6.15, head width ♂3.41–3.90, ♀3.77–4.41, ovipositor length ♀10.34–11.83.

Distribution. Santa Ynez Mountains of Santa Barbara County, California.

Habitat. Oak woodland understory and riparian. On *Ceanothus* spp., Scrub Oak, and Sage (*Salvia* spp.).

Seasonal occurrence. Adult activity from late spring (7-VI-2002, JA Cole, LACM) through summer (10-VIII-2021, DB Weissman, CAS). A captive reared nymph matured on 30-IV, which may be earlier than during a typical season in nature.

Stridulatory file. (n=5) length 2.9–3.5 mm, 88–103 teeth, tooth density 30.3±4.2 (25.7–35.5) teeth/mm.

Song. (n=5) Common song type of small *Aglaothorax*. Pulse trains of length 40 ms are repeated at a rate of 4.42±0.45 s^{-1}. Mean peak frequency is 18.74±3.02 kHz; high frequency recording equipment places the peak frequency within the ultrasonic at 22.80 kHz. Echemes are variable in length and contain 11–40 (mean 26±11) pulse trains. Silent intervals between echemes are brief at 8±4 s (range 5–12.5 s). At the type locality males were first heard singing at 2100 h and peak acoustical activity began after 2330 h.

Karyotype. (n=3) 2n♂=24 (22t+XtYt) paratype T21-18 (S21-22).

Recognition. Morphology, geography. The male paraproct process has an apical mesal tooth unlike the generally subapical tooth of most Morsei Group species. The male titillator is long and bowed, unlike the short slightly curved titillator arm of *A. constrictans* and the morse Group. The strong lateral curve to the titillator and lack of a basal constriction on the titillator arms together eliminate *A. oreibates* from consideration, which has less lateral curvature and a basal constriciton. The *A. poecilonotum* female subgenital plate has digitiform lateral processes that are broad at base and rather blunt at the apex, unlike the long, narrow, and sharp processes of *A. dactyla*. The *A. poecilonotum* subgenital plate lateral processes round onto the caudal margin of the plate unlike the right angle observed in female *A. diminutiva*. Female *A. poecilonotum* may be morphologically indistinguishable from those of *A. acrolophitus* and *A. oreibates*. The range of *A. poecilonotum* is restricted to the Santa Ynez Mountains.

male HOLOTYPE USA. CA: Santa Barbara Co. S21-22, R22-8



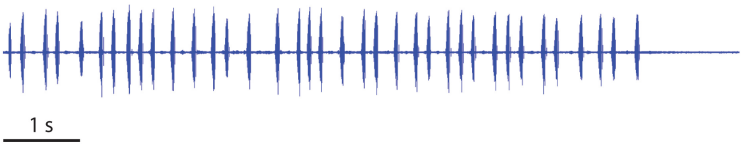
female PARATOPOTYPE USA. CA: Santa Barbara Co. S21-22



male PARATOPOTYPE USA. CA: Santa Barbara Co. JAC000002603



calling song PARATOPOTYPE USA. CA: Santa Barbara Co. 24.5ºC JCR08UO01

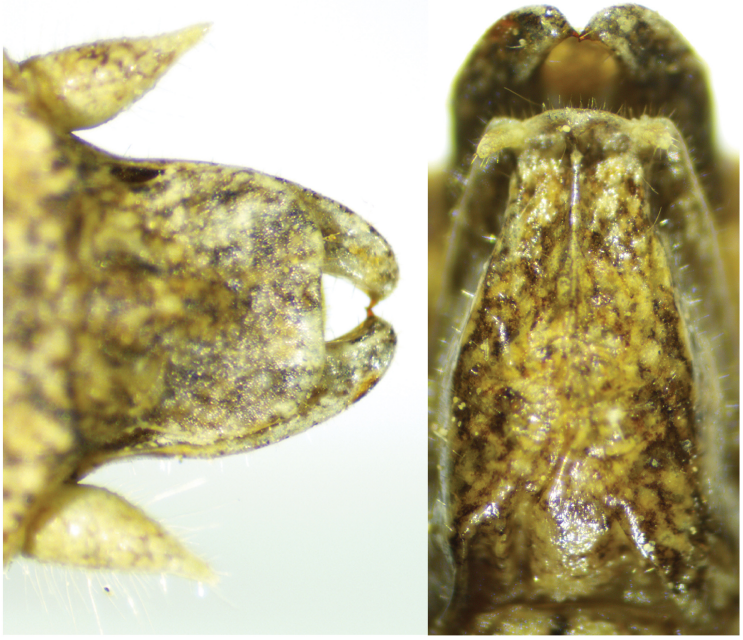


karyotype PARATOPOTYPE USA. CA: Santa Barbara Co. S21-22, T21-18

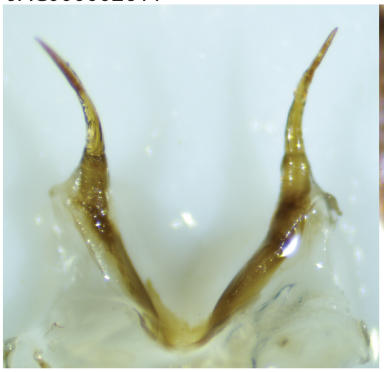


male terminalia HOLOTYPE USA. CA: Santa Barbara Co. S21-22

R V



titillators PARATOPOTYPE JAC000002611



female subgenital plate PARATOPOTYPE S21-22



FIGURE 34. *A. poecilonotum* male and female habitus, calling song, male and female terminalia, and karyotype. Idiogram shows karyotype 2n♂=24.

Etymology. Gr. *poecilo* variegated, many colored + *notum* the back. Descriptive of the variable color patterns exhibited among individuals, of which one of the color patterns is also variegated.

Notes. There was little singing when the type series was collected on 10-VIII-2021 (S21-22), but many adult females and two adult males were attracted to a long oatmeal trail. Five field-collected adult females were housed together at room temperature as described on p. 6 starting on 10-VIII-2021. On 28-IX-2021, the sand was examined for eggs and a total of 30 were harvested. All eggs were kept at room temperature (between 15–25ºC) and natural photoperiod until hatching commenced on 4-I-2022. Between 4-I-2022 and 30-I-2022, a total of 17 eggs hatched. The 13 unhatched eggs were continued at room temperature until they were chilled at 3ºC from 3-IX-2022 to 6-III-2023, before being returned to room temperature and natural photoperiod. Between 6-III-2023 and 25-III-2023, another eight eggs hatched, for a total of 25 out of 30 eggs successfully hatched.

Material examined. See Type Material above.

Diminutiva Group populations that need further study. A single male with full metadata from Pico Canyon, Newhall Ranch, Los Angeles County, California, has long bowed titillaors consistent with the Diminutiva Group, sings with the standard 5 s^{-1} pulse train rate, and exhibits mitonuclear conflict: nDNA groups this individual with *A. longipennis* + *A. amathitis* while mtDNA falls outside of both small *Aglaothorax* clades. An expanded sample size is required to arrive at a diagnosis given the character conflict in this population. The population may have hybrid characteristics as in the nearby Santa Monica Mountains. A collection of malaise trap samples from the Santa Suzana Mountains is morphologically a member of the Diminutiva Group and occupies a locality in the vicinity of both *A. acrolophitus* and *A. dactyla*. Without song or DNA data, we withhold placing this population to species.

Material examined. (n=12) **USA, CA, Los Angeles Co.,** Pico Canyon, 2 miles west of Newhall, 34.37740, -118.58448, 438 m, 11-XI-2023, J Bailey, LACM, 1♂; same data except 34.384720, -118.566078, 26-VI-1969, J Lyon, LACM, 1♂; Santa Susana Mountains, dry tributary of Browns Canyon, 34.289, -118.594, 390 m, 12-V-2-VI-2022, RW Cohen, malaise trap, CSUN, 1♂, 1♀; same data except 19-IV-12-V-2022, 2♂, 1♀; same data except 2-23-VI-2022, 1♀; same data except 23-VI-19-VII-2022, 1♂; same data except 24-V-28-VI-2023, 1♀; same data except 7-VIII-14-IX-2023, 2♂.

Discussion

Phylogeny. *Aglaothorax* gene trees showed widespread incongruence (Figs. 2–3) that reduced overall topological support in the concatenated analysis (Fig. 4). Many taxa did not form monophyletic groups. The "fear of paraphyly" (*sensu* Coyne & Orr 2004) is a well-known problem in species-level phylogenetics: gene trees are likely paraphyletic or polyphyletic early in the speciation process before lineage sorting has taken place (Maddison 1997). Increased gene sampling may not solve this problem as a plurality of loci may not have monophyletic gene trees (Freudenstein *et al.* 2017).

Aglaothorax gene tree incongruence largely took the form of mitochondrial capture. Capture of *A. dactyla* mtDNA by *A. costalis* was previously reported in contact zones in the Santa Monica Mountains (Cole 2016). Our expanded taxon sampling reinforced this pattern: mitochondrial capture now involves six Transverse Range species and always involves Diminutiva Group mtDNA introgression into Morsei Group lineages. In the Santa Monica Mountains *A. dactyla* mtDNA has been captured by both *A. costalis* in the west and *A. longipennis* in the east. In parallel in the San Gabriel Mountains, *A. acrolophitu*s mtDNA has been captured by *A. morsei* in the west and *A. conistylus* in the east.

Our topologies emphasize the importance of geography in *Aglaothorax* speciation. The populations of several species formed phylogenetic grades across geography: *A. morsei*, *A. conistylus*, and *A. hulodomus* in the Morsei Group are one such grade (Fig. 4) that spans from west to east across the San Gabriel and San Bernardino Mountains in geographical order (Fig. 15).

Morphology. *Aglaothorax* species are remarkably morphologically plastic. Expanded sample sizes found that many character states used previously in keys and diagnostic tables (Rentz & Birchim 1968; Rentz & Weissman 1981) were not in fact fixed within lineages. Character states tended to recur in several lineages, for example an apical internal tooth on the male paraproct which is found in *A. segnis* (Fig. 10) and *A. strobilion* (Fig. 11) in the Ovatus Group; *A. bufonoid*es (Fig. 24), *A. kelainops* (Fig. 25), *A. sphenosternum* (Fig. 26), and some *A. nesiazo* (Fig. 23) in the Morsei Group; and fixed in all species of the Diminutiva Group (Figs. 28–33). We found combinations of several recurring character states that were diagnostic, although variation will continue to pose diagnostic problems, especially with singletons or small series.

Aglaothorax ovatus male
USA. CA: Los Angeles Co.



Aglaothorax ovatus female
USA. CA: Los Angeles Co.



Aglaothorax giganteus male
TOPOTYPE USA. CA: Inyo Co.



Aglaothorax giganteus female
TOPOTYPE USA. CA: Inyo Co.



Aglaothorax gurneyi male
TOPOTYPE USA. CA: San Bernardino Co.



Aglaothorax segnis male
TOPOTYPE USA. NV: Lincoln Co.



Aglaothorax tinkhamorum male
TOPOTYPE USA. CA: Riverside Co.



Aglaothorax armiger male
TOPOTYPE USA. NV: Clark Co.



Aglaothorax armiger female
TOPOTYPE USA. NV: Clark Co.



Aglaothorax khioneos male
PARATYPE USA. CA: Inyo Co.



Aglaothorax khioneos female
TOPOTYPE USA. CA: Inyo Co. photo: James Bailey



PLATE 1. Living habitus of Ovatus Group.

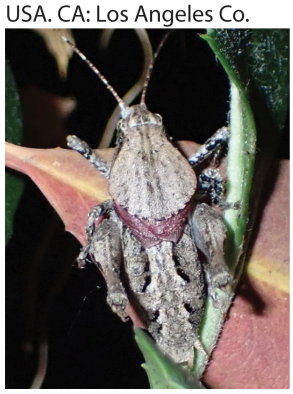
Aglaothorax morsei male
USA. CA: Los Angeles Co.



Aglaothorax costalis male
USA. CA: Los Angeles Co.



Aglaothorax longipennis male
USA. CA: Los Angeles Co.



Aglaothorax amathitis male
USA. CA: Los Angeles Co. photo: James Bailey



Aglaothorax hulodomus male
PARATYPE USA. CA: Riverside Co.



Aglaothorax conistylus female
USA. CA: Los Angeles Co.



Aglaothorax conistylus male PARATYPE
USA. CA: Los Angeles Co. photo: James Bailey



Aglaothorax nesiazo male
USA. CA: San Diego Co. photo: James Bailey



Aglaothorax nesiazo female
USA. CA: San Diego Co. photo: James Bailey



Aglaothorax bufonoides
male PARATYPE México. BC



Aglaothorax sphenosternum male
PARATYPE México. Baja California



PLATE 2. Living habitus of Morsei Group.

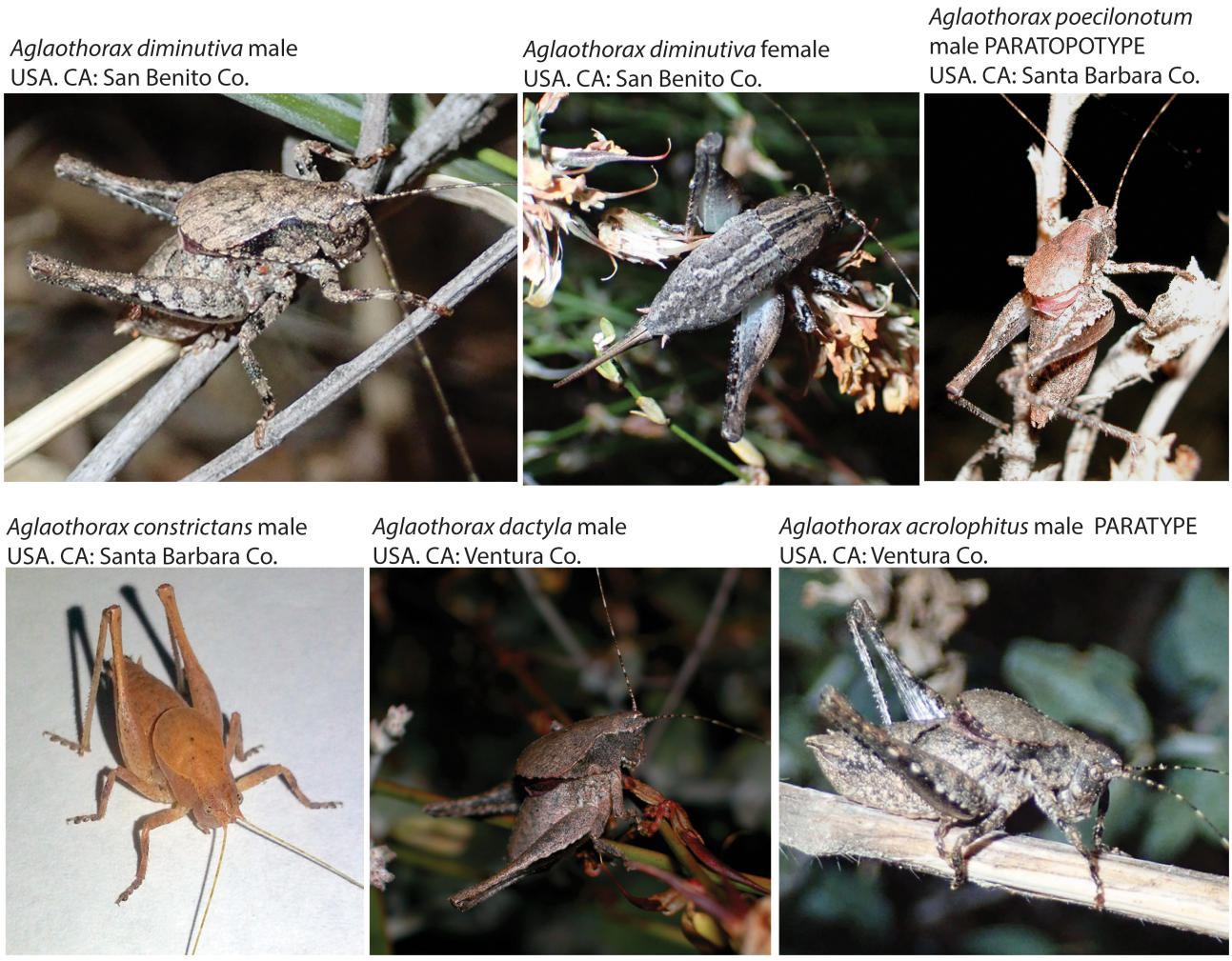


PLATE 3. Living habitus of Diminutiva Group.

Concerning functional morphology, female nedubines are unique among North American tettigoniine katydids in possessing ovipositors that have serrations or teeth on both dorsal and ventral valves near the apices (Cole *et al.* 2021; Lightfoot *et al.* 2011). Rentz & Birchim (1968) speculated that females use their toothed ovipositors to place their eggs in wood or other plant tissue rather than directly into the ground as do many tettigoniine genera. We were thus surprised by how readily *A. islandica*, *A. nesiazo*, *A. oreibates*, and *A. poecilonotum* females oviposited into sand in the laboratory. Subsequently JAC observed female *Neduba steindachneri* (Herman) ovipositing in soft soil of a dirt trail in Kittitas County, Washington on 7-VIII-2024. If endophytic oviposition does occur, this behavior is not obligate.

Our results generate several questions that may now be investigated in the laboratory given that we have shown how to get females to oviposit and how to get eggs to hatch, at least for taxa that live in frost-free environments. Specifically, do a certain small percentage of eggs require at least one period of chill to hatch? Must some eggs pass through two winters before hatching? What is the relationship between rainfall and egg development and hatching? How long can some eggs remain viable in the soil during a prolonged drought? Do any species of Nedubini oviposit into wood or plant tissue? And lastly, what is the function, if any, of the teeth on the ovipositor?

Song evolution. Like *Neduba* (Cole *et al.* 2021), *Aglaothorax* is remarkable for the overall lack of song evolution. With one notable exception, songs show no appreciable divergence within species Groups. Ovatus Group species sing with frequent echemes that consist of few pulse trains delivered at 8–10 s^{-1}. The widespread song type among the Morsei and Diminutiva Group is one of irregularly produced, often prolonged echemes that contain a variable number of pulse trains produced at a rate of 5 s^{-1}. The exception is a song evolution event associated with the western Santa Monica Mountains contact zone between *A. costalis* and *A. dactyla*. The latter species maintains

the widespread 5 s^{-1} pulse train rate while the former has evolved a threefold increase in pulse train rate to 15 s^{-1} (Cole 2010).

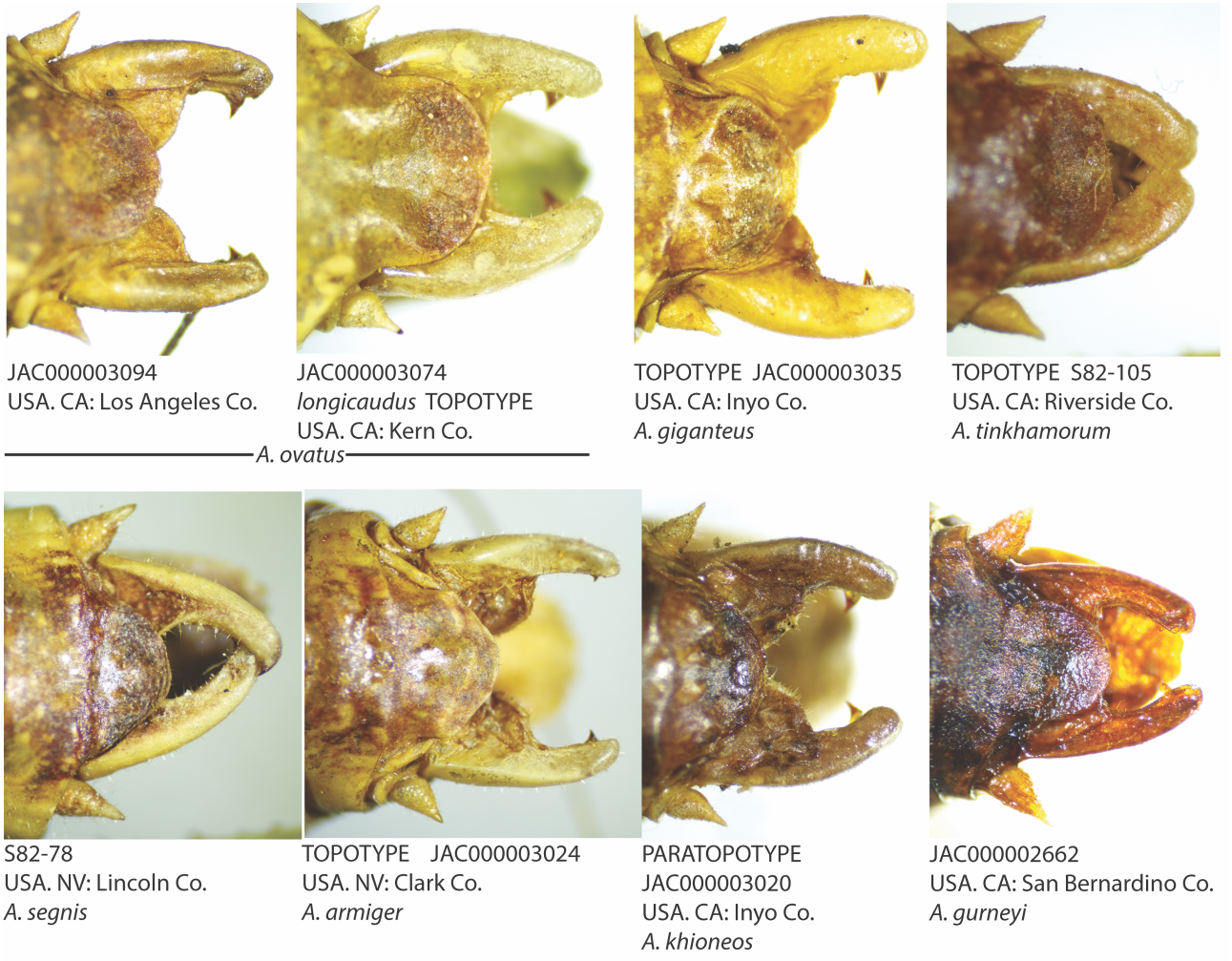


PLATE 4. Male terminalia of Ovatus Group, dorsal view.

Karyotype evolution. Five karyotypes are found among *Aglaothorax* species. Of these, the karyotypes 2n♂23: 20t+XmXtYm in *A. diminutiva* (Fig. 28); 2n♂20: 4m+14t+XtYt in *A. kelainops* (Fig. 25); and 2n♂22: 2m+18+XtYt in *A. sphenosternum* (Fig. 26) are unique. The remaining two are the widespread 2n♂24: 22t+XtYt karyotype found throughout the Dimunitiva and Morsei Groups, but also in *A. gurneyi* and *A. segnis* in the Ovatus Group, and 2n♂23: 22t+Xt that is found in the rest of the Ovatus Group.

We emphasize two main chromosome evolution patterns. The first is that incidences of chromosome evolution are scattered in *Aglaothorax*; each *Aglaothorax* species Group contains a few species with divergent karyotypes. In contrast, the relate genus *Neduba* consisted of two major clades, one of which was invariable as to karyotype while the other exhibited no less than eight karyotypes. The second pattern is that divergent *Aglaothorax* karyotypes are found in geographically peripheral populations: *A. diminutiva* occupies the northwestern distribution extreme in the South Coast Ranges at Mount Diablo, Contra Costa County, California; *A. segnis* occupies the easternmost extent of the Mojave Desert in eastern Nevada; and *A. kelainops* and *A. sphenosternum* make up the southernmost populations extending down the Baja California Peninsula. *A. gurneyi* is an exception, not geographically peripheral but ecologically unique, inhabiting a sky island of mixed woodland in the San Gabriel and San Bernardino Mountains, California. In contrast, *Neduba* chromosome evolution occurred among populations associated with a single geographic region, the Sierra Nevada.



PLATE 5. Male terminalia of Morsei Group, dorsal view.

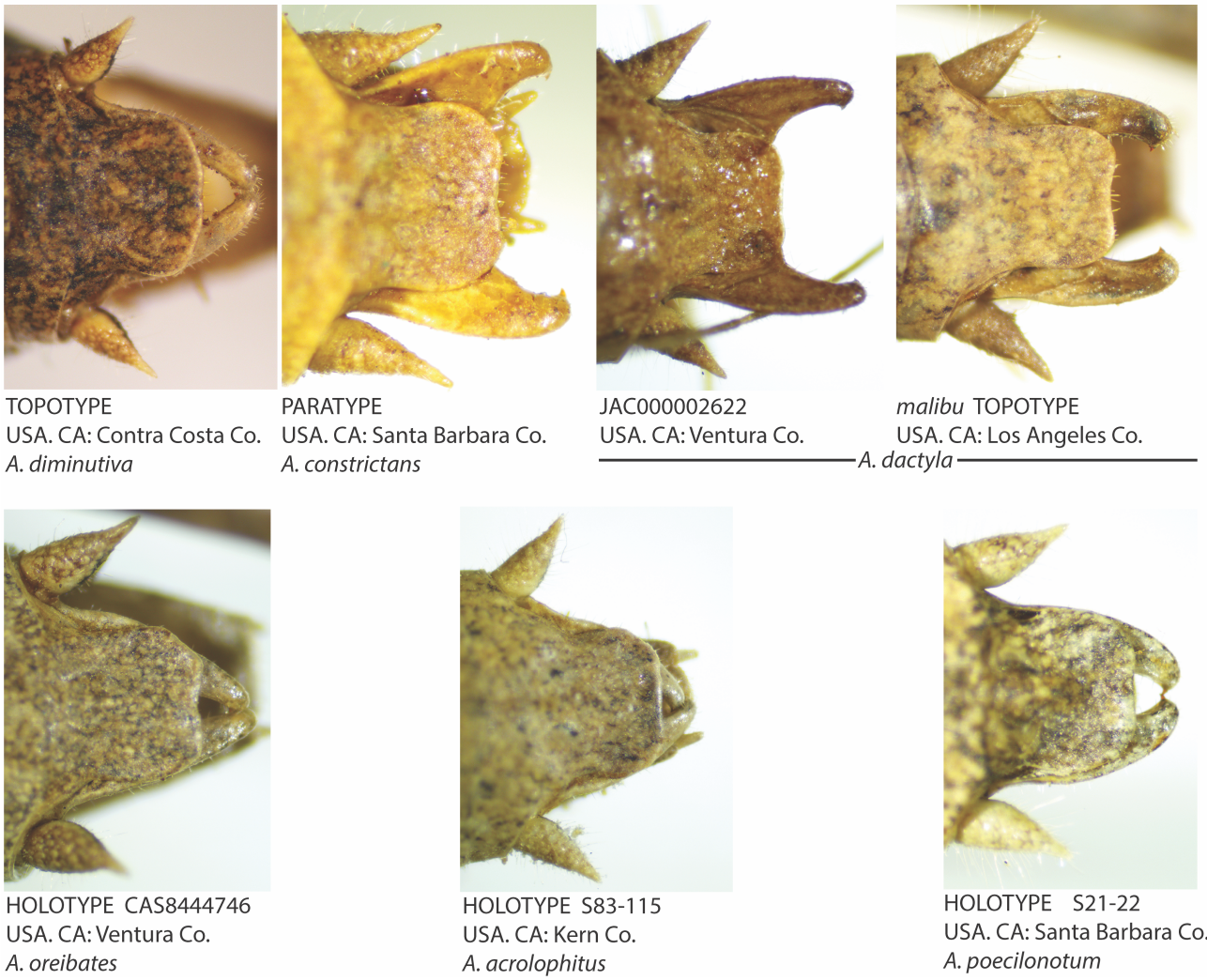


PLATE 6. Male terminalia of Diminutiva Group, dorsal view.

Speciation. Nedubini are a paleoendemic lineage (Cole & Chiang 2016) that has considerable neoendemic radiation, given the short branch lengths within species Groups in our phylogenetic hypotheses (Figs. 2–4). Synthesizing the above evidence, we conclude that *Aglaothorax* speciation is largely allopatric, with geographic barriers and geographic distance constituting the main isolation mechanisms among *Aglaothorax* species. The flightless condition of *Aglaothorax* species combines with the varied topography of California and the Basin and Range provinces to drive local divergence. *Neduba* speciation evoked a similar isolation by distance hypothesis (Cole *et al.* 2021). Ancient and/or contemporary gene flow between adjacent populations may be explained by a stepping stone population model (Kimura 1953; Kimura & Weiss 1964) that has in several cases obscured ancestor-descendent relationships (Figs. 2–4).

In addition to geographic isolation, divergent songs and karyotypes may constitute isolating barriers in a few cases. Premating isolation via female discrimination against heterospecific calling songs is known from the contact zone between *A. costalis* and *A. dactyla* (Cole 2016) and perhaps also between sympatric *A. dactyla* and *A. longipennis*. We conclude that reinforcement of premating isolation is a rare event (see Marshall *et al.* 2002) that occurred due to a chance set of circumstances, as several other species have apparently hybridized (Fig. 3) without accompanying song evolution.

In yet other cases, chromosome differences may constitute isolation barriers (Shaw *et al.* 1998; White 1978). We observed divergent karyotypes at peripheral populations. Chromosomal speciation may be peripatric, where small effective population sizes at range peripheries may enable fixation of novel karyotypes (Barton 1980) that confer postzygotic isolation (Hauffe & Searle 1998; King 1993). As with *Neduba*, stasipatric speciation (White 1978) is

an alternate hypothesis that may simultaneously explain chromosome evolution and speciation in *Aglaothorax*. The species with divergent karyotypes in Baja California present the strongest case, with close-set parapatric boundaries that may have resulted from *in-situ* chromosome evolution in an effectively instantaneous speciation event (White 1978).

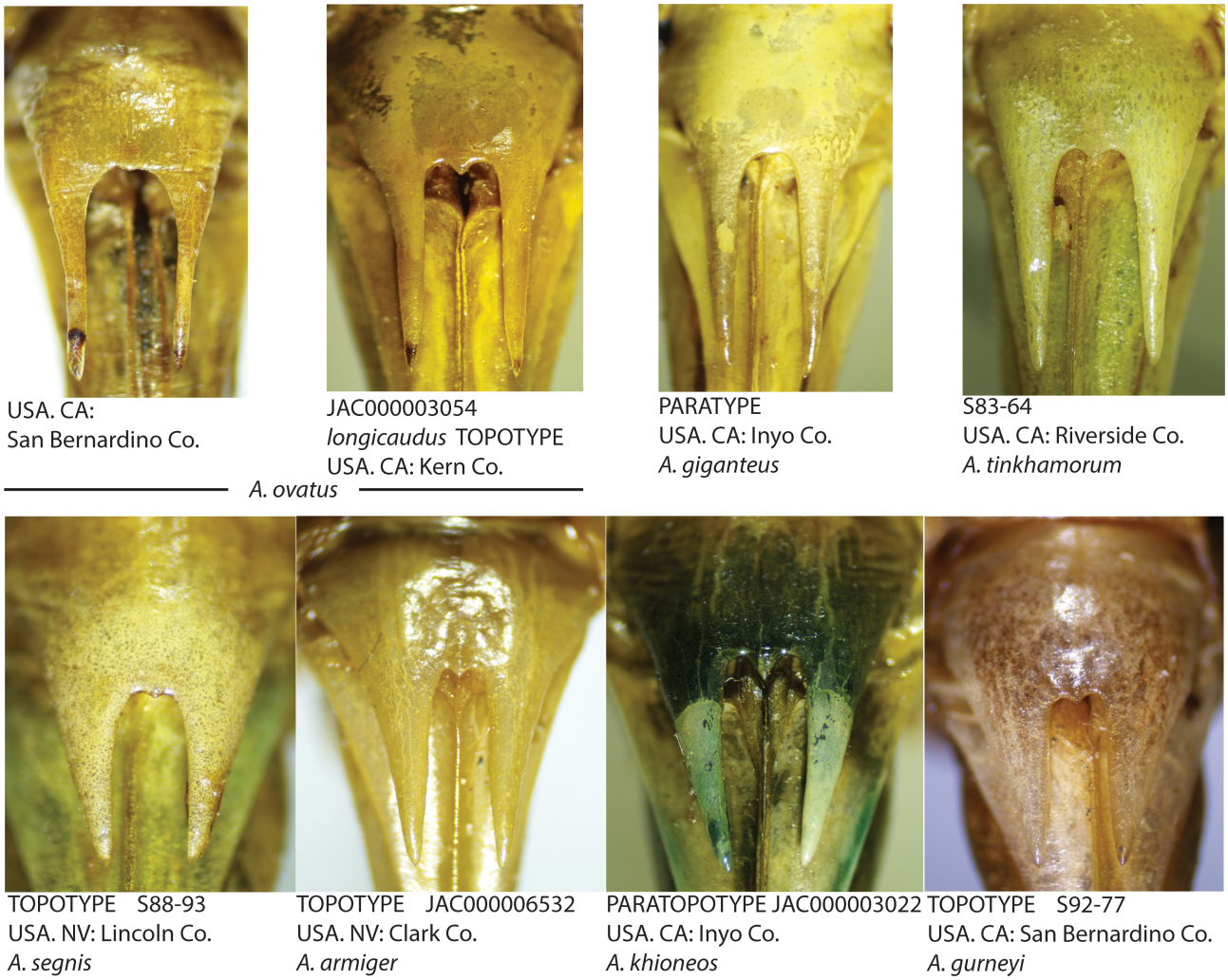
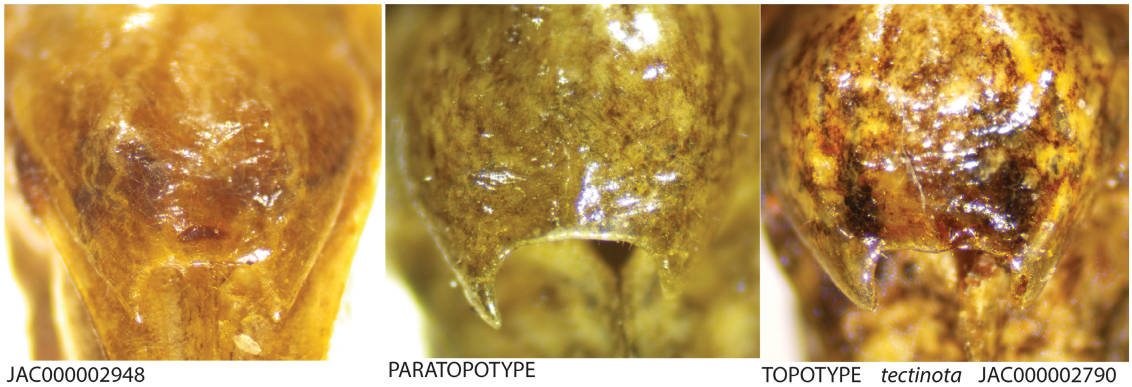


PLATE 7. Female subgenital plates of Ovatus Group, ventral view.

We treat *Aglaothorax* taxa at species rank based on contemporary, fixed syndromes of morphology and, in several cases fixed, divergent songs or karyotypes, all of which are evidence of metapopulation tokogeny that is consistent with species status, despite several cases of gene flow. Genomic studies have revealed pervasive gene flow (Mallet 2005) and hybridization between biological species, particularly early in the speciation process, and the biological species concept (Coyne & Orr 2004) and the genotypic cluster species concept (Mallet 1995) among others allow for a modicum of gene flow. Future tokogeny decides the fate of the lineages. Speciation may proceed as lineages further diverge, isolation barriers arise or strengthen, or isolation by distance holds. Alternatively, de-speciation or differential fusion (Templeton 1981) may occur if isolating barriers disappear or if gene flow overwhelms them.

Conservation. *Aglaothorax* have been neglected biologically not because of rarity in the strict sense but because of their sessile nature, crypsis, secretive habits, and their sporadic occurrence. As inhabitants of coastal sage scrub, chaparral, and hot deserts, *Aglaothorax* species are presumably resilient to extreme conditions. Populations are apparently tolerant to considerable drought, as we found active populations throughout the extensive California drought from 2012 to 2017. *Aglaothorax* must also be adapted to a regular fire regime, although this has not been studied. Given their lack of flight capability and apparently low dispersal, persistence of populations through burns is presumably facilitated by underground survival in the egg stage.

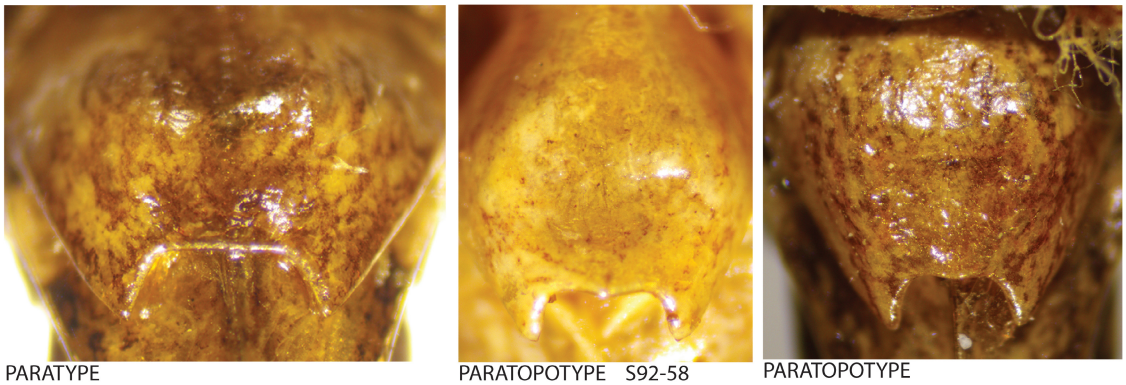


JAC000002948
USA. CA: Los Angeles Co.
A. morsei

PARATOPOTYPE
USA. CA: Ventura Co.

TOPOTYPE *tectinota* JAC000002790
USA. CA: Los Angeles Co.

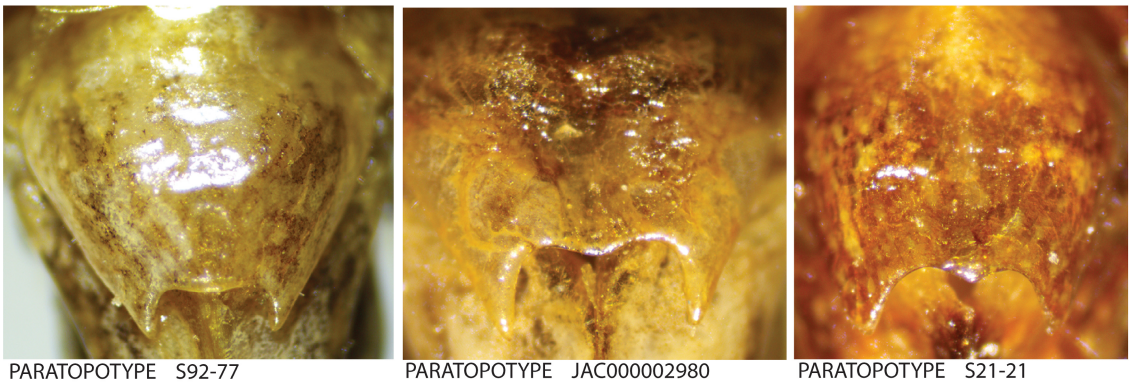
A. costalis



PARATYPE
USA. CA: Los Angeles Co.
A. longipennis

PARATOPOTYPE S92-58
USA. CA: Los Angeles Co.
A. amathitis

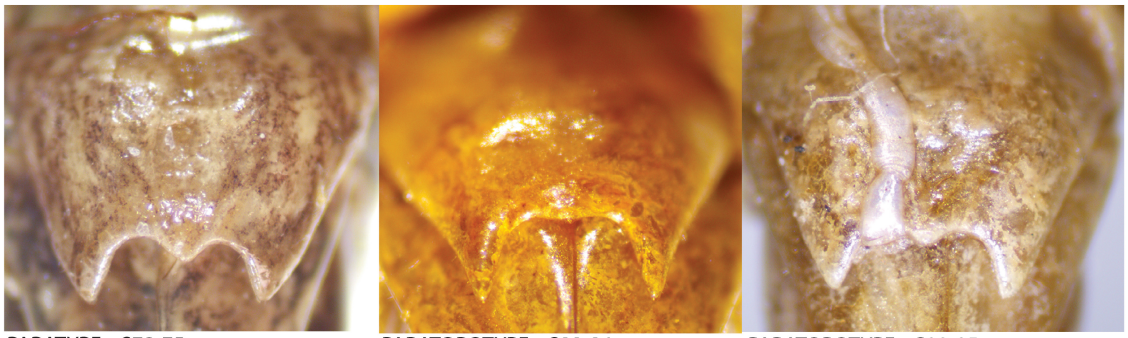
PARATOPOTYPE
USA. CA: Ventura Co.
A. islandica



PARATOPOTYPE S92-77
USA. CA: San Bernardino Co.
A. hulodomus

PARATOPOTYPE JAC000002980
USA. CA: Los Angeles Co.
A. conistylus

PARATOPOTYPE S21-21
USA. CA: San Diego Co.
A. nesiazo



PARATYPE S78-75
México. Baja California.
A. bufonoides

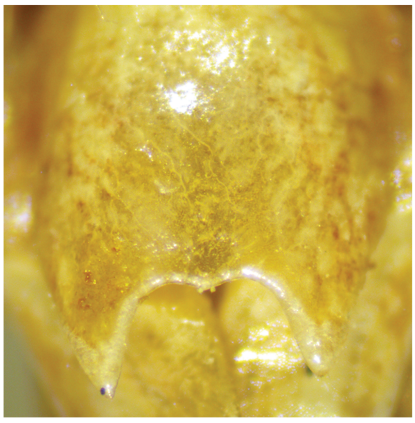
PARATOPOTYPE S88-84
México. Baja California.
A. kelainops

PARATOPOTYPE S88-85
México. Baja California.
A. sphenosternum

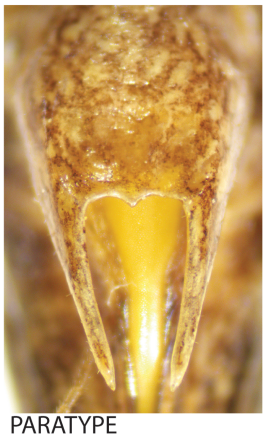
PLATE 8. Female subgenital plates of Morsei Group, ventral view.



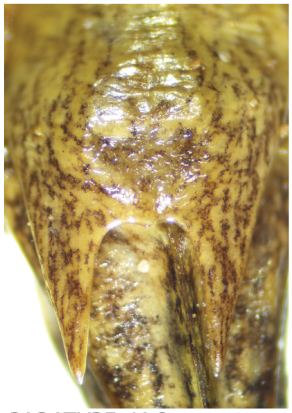
TOPOTYPE
USA. CA: Contra Costa Co.
A. diminutiva



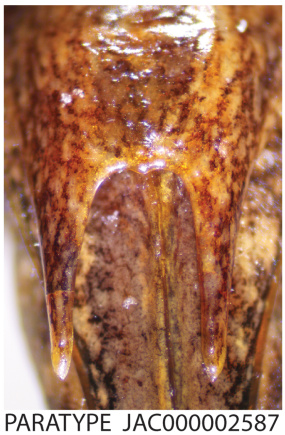
USA. CA: Santa Barbara Co.
A. constrictans



PARATYPE
USA. CA: Los Angeles Co.
A. dactyla



PARATYPE JAC000002644
USA. CA: Ventura Co.
A. oreibates



PARATYPE JAC000002587
USA. CA: Los Angeles Co.
A. acrolophitus

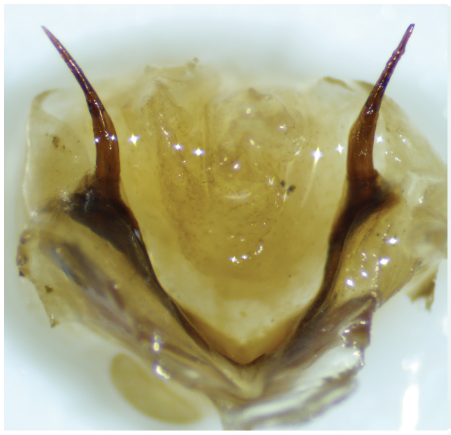


PARATOPOTYPE S21-22
USA. CA: Santa Barbara Co.
A. poecilonotum

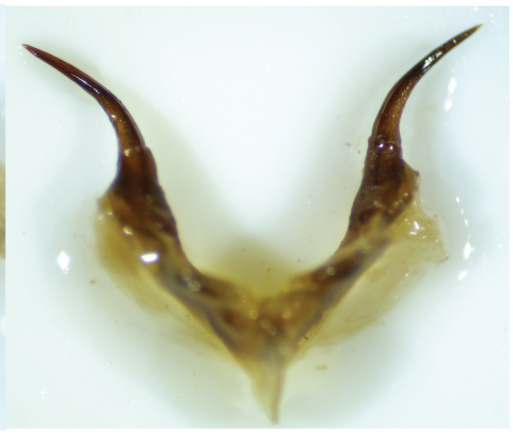
PLATE 9. Female subgenital plates of Diminutiva Group, ventral view.

At least some populations of most species occur on protected land: National Parks (e.g. *A. diminutiva* in Pinnacles National Park); National Monuments (e.g. *A. ovatus* in the Mojave National Preserve and *A. tinkhamorum* in the Santa Rosa and San Jacinto Mountains National Monument); National Forests (e.g. *A. hulodomus* in the San Bernardino National Forest and *A. poecilonotum* in the Los Padres National Forest); and State Parks (e.g. *A. nesiazo* in Torrey Pines State Natural Reserve and *A. costalis* in Point Mugu State Park). We alleviate conservation concern for the Santa Monica Mountains Shieldback *A. longipennis* (Orthopteroid Specialist Group 1996) by fleshing out the distribution and documenting the species as common in the protected areas of Topanga State Park and UCLA Stunt Ranch Reserve.

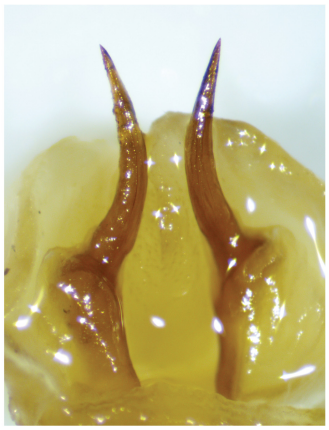
As a species of particular concern, we describe *A. amathitis* from undeveloped sand dunes such as at Ballona Wetlands in the Los Angeles Basin, although a protected population occurs inland at Kenneth Hahn State Recreation Area. High elevation populations, for example the sky island endemics *A. segnis* and *A. strobilion* in Nevada, will also be particularly vulnerable to extinction with climate change as their ranges may not be able to shift higher in elevation.



JAC000003107
USA. Los Angeles Co.

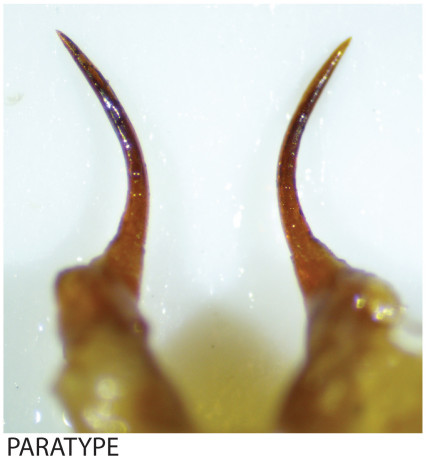


longicaudus PARATYPE
USA. CA: Kern Co.



PARATYPE
USA. CA: Inyo Co.
A. giganteus

A. ovatus



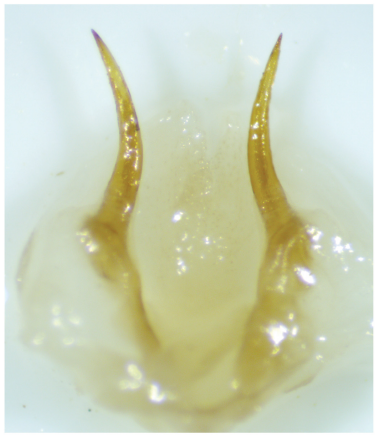
PARATYPE
USA. CA: San Bernardino Co.
A. tinkhamorum



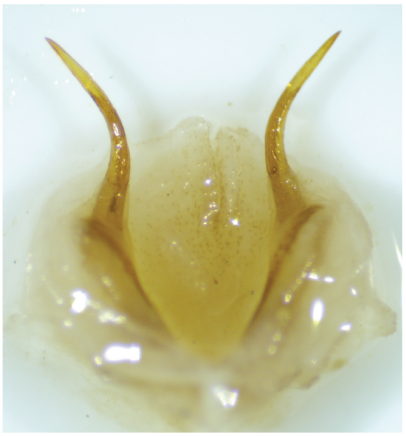
S82-78
USA. NV: Lincoln Co.
A. segnis



TOPOTYPE JAC000006527
USA. NV: Clark Co.
A. armiger



PARATYPE S86-103, T86-117
USA. NV: Nye Co.
A. strobilion

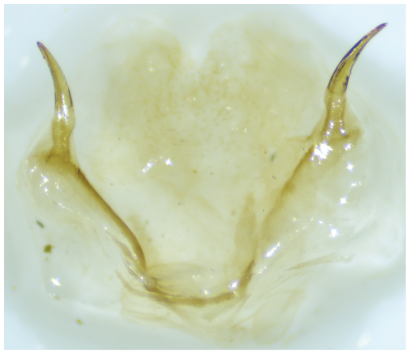


PARATYPE JAC000003019
USA. CA: Inyo Co.
A. khioneos

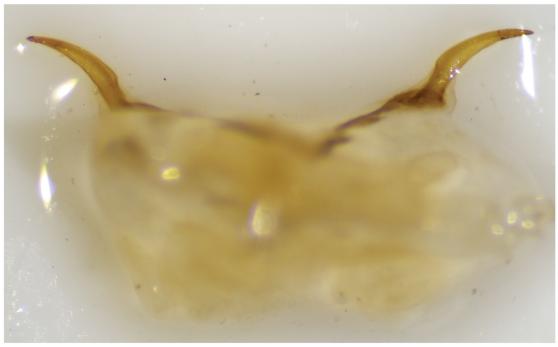


PARATYPE
USA. CA: San Bernardino Co.
A. gurneyi

PLATE 10. Male titillators of Ovatus Group.

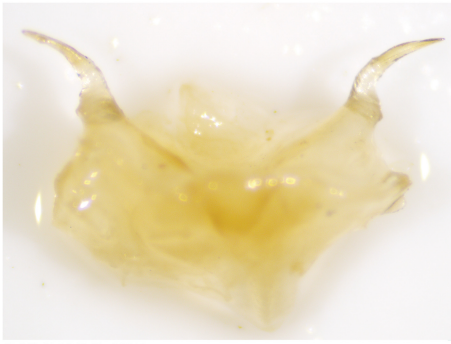


JAC000002931
USA. CA: Los Angeles Co.

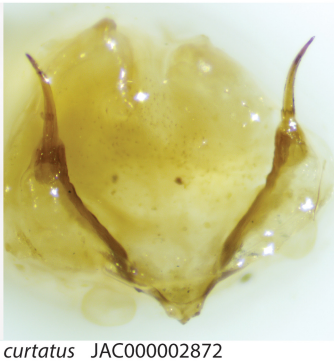


JAC000002942
USA. CA: Los Angeles Co.

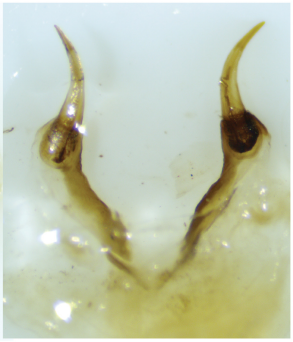
A. morsei



PARATOPOTYPE
USA. CA: Ventura Co.

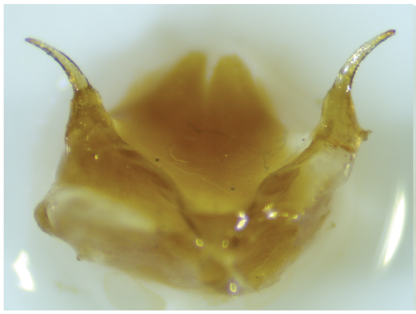


curtatus JAC000002872
USA. CA: Los Angeles Co.

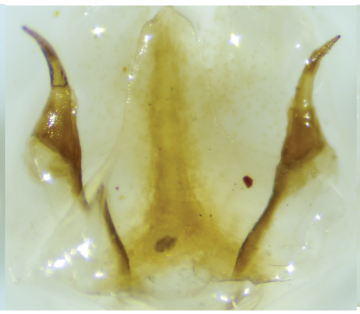


tectinota TOPOTYPE
USA. CA: Los Angeles Co.

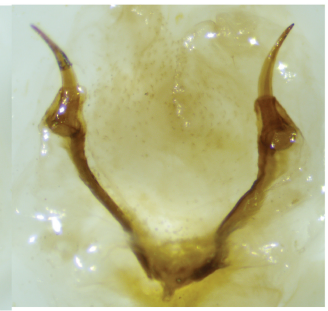
A. costalis



TOPOTYPE
USA. CA: Los Angeles Co.

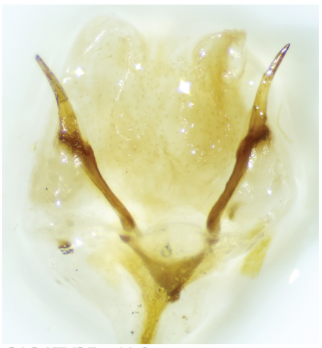


JAC000002722
USA. CA: Los Angeles Co.

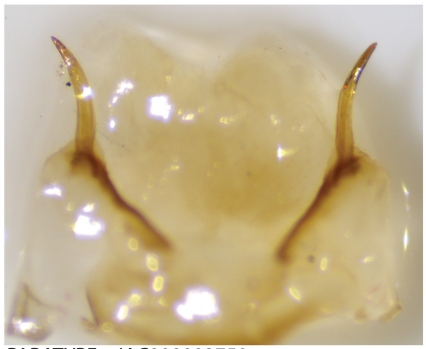


JAC000002734
USA. CA: Los Angeles Co.

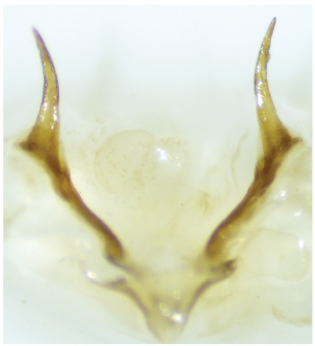
A. longipennis



PARATYPE JAC000002741
USA. CA: Los Angeles Co.



PARATYPE JAC000002758
USA. CA: Los Angeles Co.



PARATYPE JAC000002767
USA. CA: Los Angeles Co.

A. amathitis

PLATE 11. Male titillators of Morsei Group (in part).



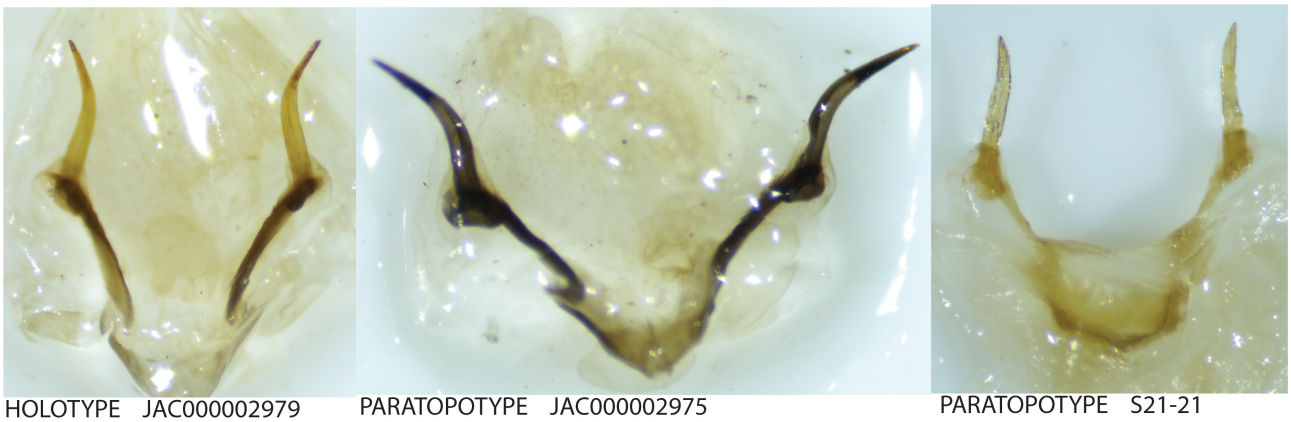
S82-40
USA. CA: Santa Barbara Co.

PARATOPOTYPE
USA. CA: Ventura Co.

PARATYPE S82-65, R82-252
USA. CA: San Bernardino Co.

A. islandica

A. hulodomus



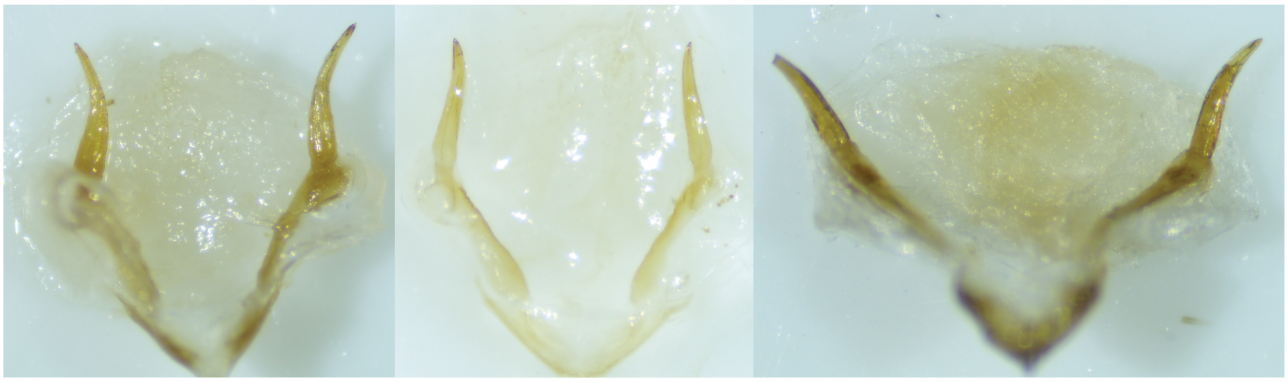
HOLOTYPE JAC000002979
USA. CA: Los Angeles Co.

PARATOPOTYPE JAC000002975
USA. CA: Los Angeles Co.

PARATOPOTYPE S21-21
USA. CA: San Diego Co.

A. conistylus

A. nesiazo



PARATOPOTYPE S89-21, R89-31
México. Baja California
A. bufonoides

PARATOPOTYPE S88-84, R88-122
México. Baja California
A. kelainops

PARATOPOTYPE S88-85, R88-145
México. Baja California
A. sphenosternum

PLATE 12. Male titillators of Morsei Group (in part).

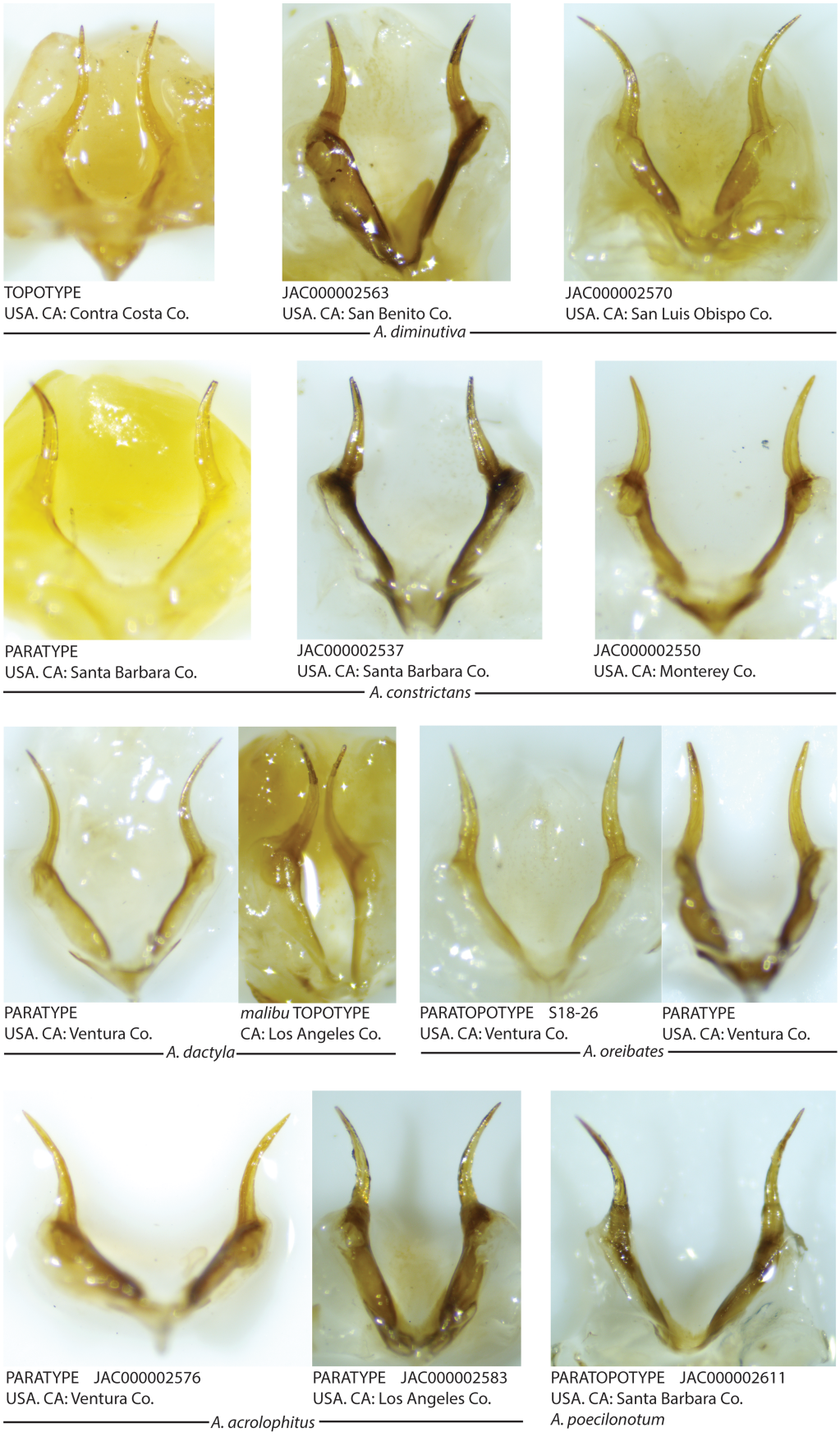


PLATE 13. Male titillators of Diminutiva Group.

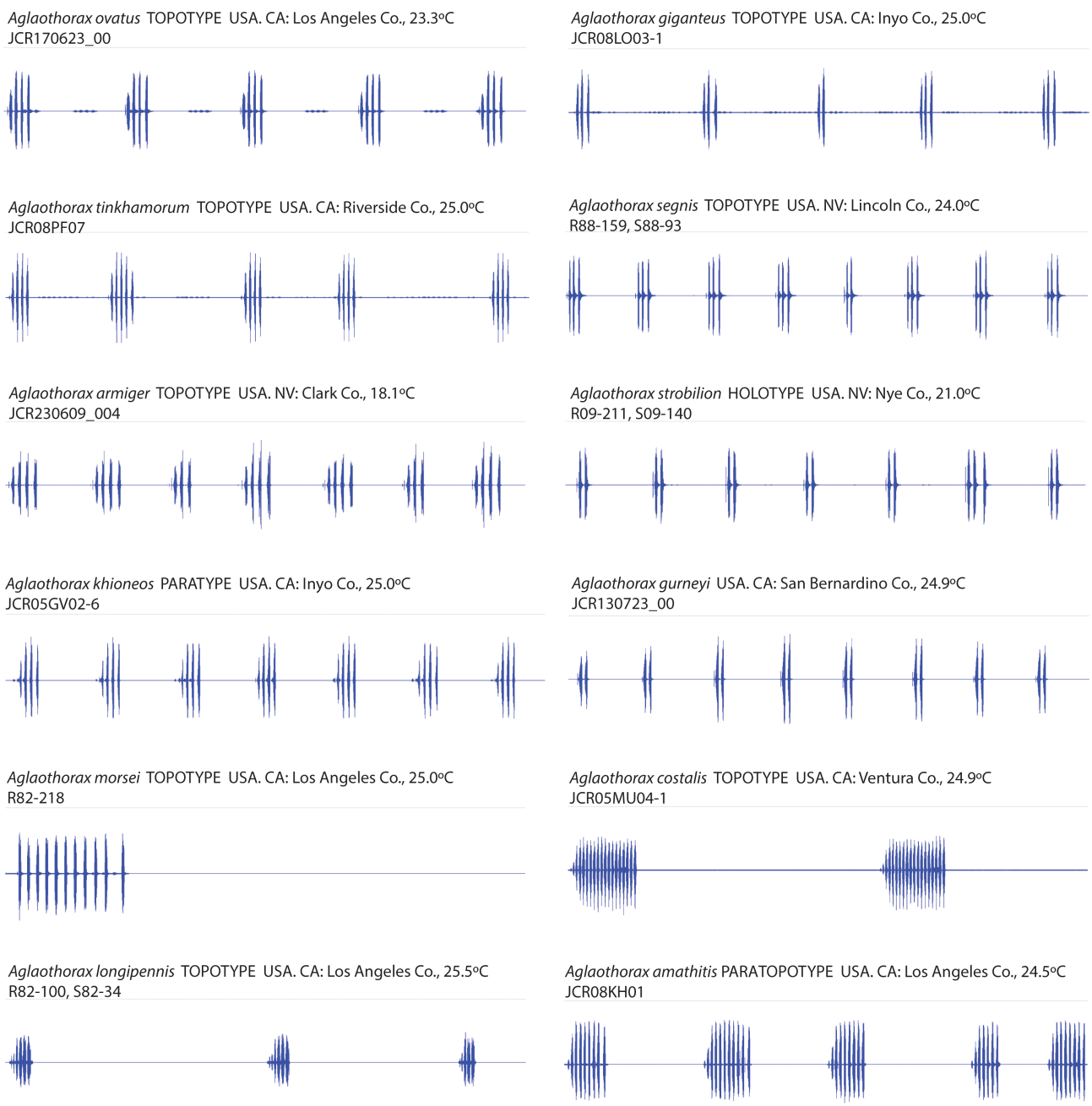


PLATE 14. Male calling songs of Ovatus and Morsei Groups, 10 s oscillogram windows.



PLATE 15. Male calling songs of Morsei and Diminutiva Groups, 10 s oscillogram windows.

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Sophia Garnica, Valorie Gonzalez, Jessica Mu, and Caressa Wong helped in the molecular lab. Suzanne Goode granted collecting permits for California State Parks. The USDA approved import permits and containment facility permits for Baja California specimens.

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SUPPLEMENTARY MATERIALS. The following supporting information can be downloaded at the DOI landing page of this paper.

SUPP TABLE 1. *Aglaothorax* Molecular Vouchers.