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4910

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

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Abstract

The Nearctic shield-back katydid genus *Neduba* is revised. Species boundaries were demarcated by molecular phylogenetic analysis, morphology, quantitative analysis of calling songs, and karyotypes. Nine previously described species are redescribed: *N. carinata*, *N. castanea*, *N. convexa*, *N. diabolica*, *N. extincta*, *N. macneilli*, *N. propsti*, *N. sierranus*, and *N. steindachneri*, and twelve new species are described: *N. ambagiosa* sp. n., *N. arborea* sp. n., *N. cascadia* sp. n., *N. duplocantans* sp. n., *N. inversa* sp. n., *N. longiplutea* sp. n., *N. lucubrata* sp. n., *N. oblongata* sp. n., *N. prorocantans* sp. n., *N. radicata* sp. n., *N. radocantans* sp. n., and *N. sequoia* sp. n. We chose a lectotype for *N. steindachneri* and transferred *N. picturata* from a junior synonym of *N. diabolica* to a junior synonym of *N. steindachneri*. Diversification in this relict group reflects cycles of allopatric isolation and secondary contact amidst the tumultuous, evolving geography of western North America. The taxonomy and phylogenies presented in this revision lay the groundwork for studies of speciation, biogeography, hybrid zones, and behavioral evolution. Given that one *Neduba* species is already extinct from human environmental disturbance, we suggest conservation priorities for the genus.

Key words: bioacoustics, biogeography, cryptic species, ring species, chromosome evolution, mitochondrial capture, California floristic province

Introduction

Shield-back katydids (Orthoptera: Tettigoniidae: Tettigoniinae) of the genus *Neduba* belong to the Nearctic members of the katydid tribe Nedubini (Cole & Chiang 2016; Rentz & Colles 1990) along with *Aglaothorax* and *Phymonotus* (Lightfoot *et al.* 2011). *Neduba* are a common but understudied component of the rich orthopteran fauna of the Pacific Coast of North America. A diversity of cryptic color patterns, conservative morphology, and complex high-frequency calling songs together conspired against a thorough systematic understanding thus far. The present revision clarifies 150 years of taxonomic confusion, reveals over twice the number of species than were previously described, illustrates the strong affinity of taxa with the geography of the Pacific Coast of North America, details their complex acoustic behavior, and offers hypotheses that explain the evolution of their calling songs.

Biology. *Neduba* are large, flightless inhabitants of the understory and leaf litter of western North American chaparral, oak woodlands, and conifer forests (Rentz & Birchim 1968). During the day individuals remain motionless in bark crevices (Rehn & Hebard 1909), in leaf litter, in tangles of vegetation, or in pack rat nests (J.A. Cole (JAC) and D.B. Weissman (DBW), pers. obs.). The katydids move little, even when disturbed, and are reluctant to jump. Individuals from the same population can vary greatly from one another in color pattern, for example a morph with a mottled dorsum (Fig. 1A) and a morph with a middorsal stripe (Fig. 1B). Color patterns are also shared among multiple species (Fig. 1C–D) and species Groups, such as a countershaded morph with strong postocular bands (Fig. 1E–F). Color pattern diversity and the fact that color patterns are shared among species minimizes its utility in species identification.

Feeding, singing, courtship, mating, and oviposition take place at night. *Neduba* are omnivores, feeding primarily on the foliage of common plants in their habitats. Most species are associated with oak and conifer forests, and like the related *Phymonotus* some may feed on conifers (Lightfoot *et al.* 2011), a food preference that is rare among Orthoptera (Hojun Song pers. comm.) and that stems from nedubine ancestors that inhabited the ancient coniferous forests of western North America (Cole & Chiang 2016). *Neduba* may scavenge on dead insects but, at least in captivity, show no predaceous tendencies and do not behave aggressively towards each other, in contrast to other North American shield-back katydids like *Capnobotes* that may be predaceous, aggressive, and cannibalistic (Rentz & Birchim 1968; Tinkham 1944).

The common name of shield-back katydid describes aptly the enlarged male pronotum in *Neduba* (Figs. 1, 2F) that largely or entirely conceals the small oval front wings (tegmina; Fig. 2F). The male tegmina are used only for sound production and females are completely apterous. Male *Neduba* produce continued high frequency calling songs of appreciable complexity (Fig. 2) that may be heard at night throughout summer and fall in suitable habitats. The enlarged pronotum, together with the dorsum of abdominal segments I–III act as an acoustic horn to amplify the calling songs produced by males (Morris *et al.* 1975). Females are mute and move towards calling males to form pairs (phonotaxis; Fig. 2G). Calling typically begins at dusk and continues throughout the night as long as temperatures do not dip too low, although a few species that inhabit northern latitudes or high elevations are adapted for activity at low temperatures (see Results). Males spend a great deal of time singing: duty cycles are frequently over 50% and may be as high as 90% (see Results). *Neduba* songs are broadband signals with peak frequencies centered high on the audible spectrum (range 11–17 kHz) and with sound energy extending well into the ultrasonic (Fig. 2C, limit of human hearing at white dashed line). Song structure complexity arises from alternating major and minor pulse trains (Fig. 2A, B; Cole 2010; Morris *et al.* 1975) that are produced during closing and opening of the tegmina, respectively. All Sierranus Group species and *N. oblongata* sp. n. in the Carinata Group have elaborated this pattern, producing multiple minor pulse trains that are produced by partial closing and opening wingstrokes (Fig. 2D–E).

Systematic History. Reliance on habitus and color pattern characters have produced a confusing systematic history concerning *Neduba* and *Aglaothorax*. The first described species were *Neduba carinata* from California (Walker 1869) and *Arytropteris steindachneri* from “Fox Island, Pouget Sound” (Herman 1874). Samuel H. Scudder moved *steindachneri* to *Tropizaspis* (Scudder 1894) and described four new species under that genus: *castanea*, *diabolica*, *ovata*, and *picturata* (Scudder 1899). Caudell (1907) rearranged the nomenclature considerably in his revision of the North American Decticinae. He synonymized *steindachneri* under *carinata* and the *nomen nudum* *Tropizaspis* under *Neduba*. In that work Caudell also described *Neduba morsei* and recognized two varieties of *carinata*: Scudder’s *picturata* and a new variety *convexa*. Based on the type species *ovata*, Caudell erected *Aglaothorax* for the species with broad, ovate pronota and short hind femora, in which he placed *castanea* and *diabolica*, the latter of which paradoxically lacks both of those character states. The remaining species he retained in *Neduba* but cautioned that due to intermediate morphologies this split was imperfect. Rehn and Hebard (1909) described *Aglaothorax*

thorax sierranus. Tinkham (1944) haphazardly and erroneously applied five species names to scattered populations of *Neduba*, but correctly placed *diabolica* and *sierranus* in *Neduba* rather than in *Aglaothorax* based on songs and morphology.



A. *Neduba cascadia* sp. n. PARATOPOTYPE
OR: Jackson Co.



B. *Neduba cascadia* sp. n. PARATOPOTYPE
OR: Jackson Co.



C. *Neduba sierranus*
CA: Madera Co.



D. *Neduba radocantans* sp. n. PARATYPE
CA: El Dorado Co.



E. *Neduba ambagiosa* sp. n. PARATOPOTYPE
CA: Lake Co.



F. *Neduba inversa* sp. n. PARATYPE
CA: Fresno Co.

FIGURE 1. Color pattern variation in *Neduba*. Multiple color patterns are found within species (A and B), and color patterns may be shared among different species (C and D) and species Groups (E and F).

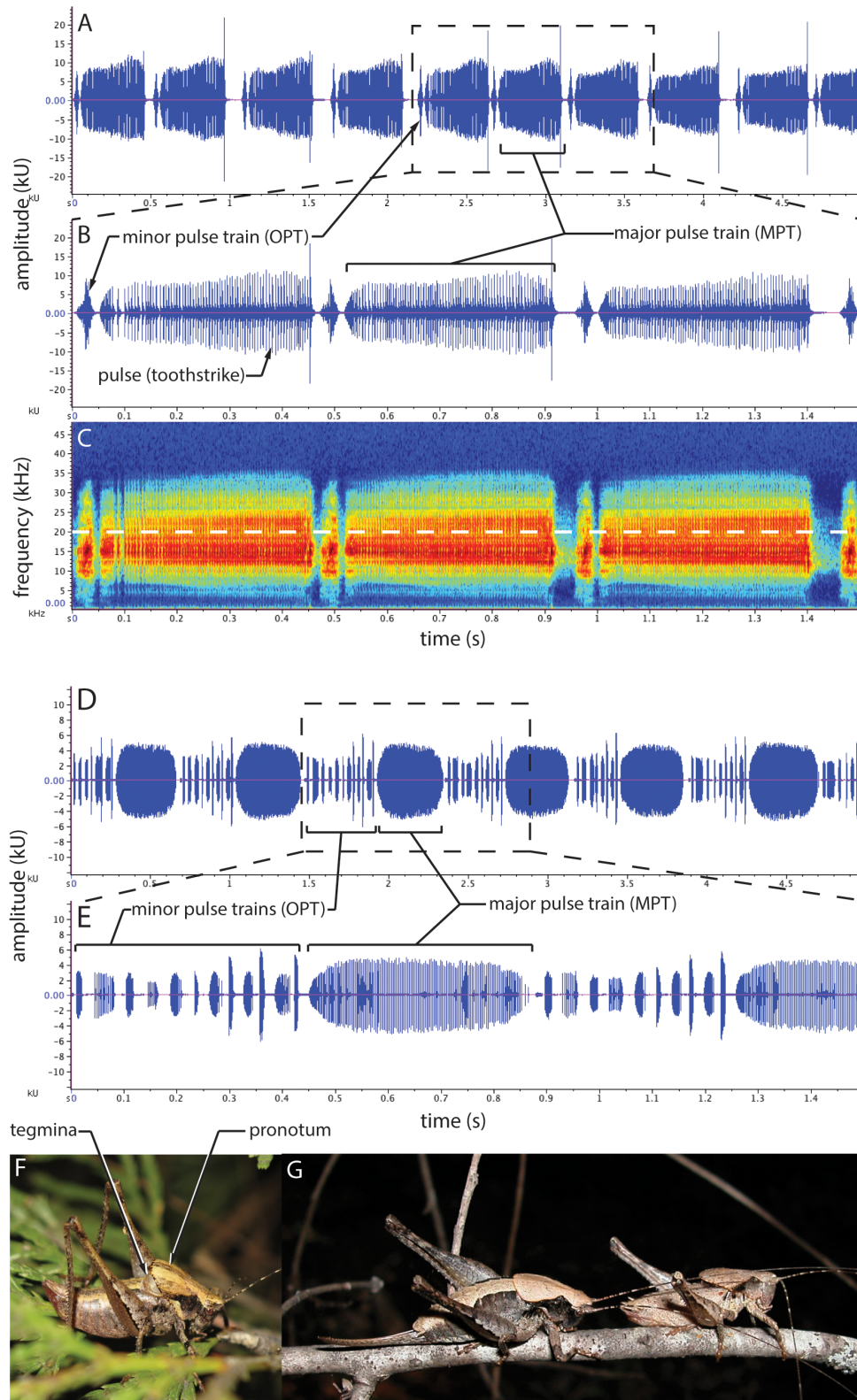


FIGURE 2. *Neduba* typical male calling song structure exemplified by *N. convexa*, recording JCR130808_01, 23.3°C (A-C), and song structure with multiple minor pulse trains exemplified by *N. sierranus* recording JCR120805_00, 21.7°C (D-E). A. 5 s oscillogram window showing 9 full wingstroke cycles (and a partial 10th major pulse train); B. 1.5 s oscillogram window showing individual pulses within major pulse trains; C. spectrogram of B with dashed line at limit of human hearing at 20 kHz; D. 5 s oscillogram window showing 6 full wingstroke cycles (and a partial series of minor pulse trains); E. 1.5 s oscillogram window of D showing individual pulses within major pulse trains; F. Male *N. sierranus* singing, Madera Co., CA. Note elevated pronotum exposing tegmina beneath; G. Phonotaxis in *N. ambagiosa* sp. n., Lake Co., CA.

The most comprehensive treatment of *Neduba* to date is that of Rentz and Birchim (1968). Based on examination of the internal genitalia of topotypes and on qualitative features of songs, they rearranged species between *Neduba* and *Aglaothorax*. The latter name was relegated to a subgenus of the former based on the aforementioned intergradation. They moved the small *morsei* to *Neduba* (*Aglaothorax*) and described *macneilli*, placing it under *Neduba* (*Neduba*) along with *castanea*, *convexa*, *diabolica*, *sierranus*, and *steindachneri*. The last species was resurrected from synonymy based on the geographic distance between its type locality and those of all other known taxa, but without examination of specimens. The descriptions of *extincta* (Rentz 1977) and *propsti* (Rentz & Weissman 1981) brought the total number of *Neduba* (*Neduba*) species up to 9 (eight extant species). Vickery & Kevan (1985) treated *N. steindachneri*, the sole species found in Canada. Gorochov (1988) reviewed the Nedubini as part of a worldwide treatise on Orthoptera evolution. *Neduba* and *Aglaothorax* were reinstated to genus rank after considering the worldwide shield-back katydid fauna (Rentz 1988). Finally, generic rank for the three Nearctic nedubine taxa was supported by bioacoustical (Cole 2010), morphological (Lightfoot *et al.* 2011), and molecular phylogenetic (Cole & Chiang 2016) investigations.

Together with *Aglaothorax* and *Phymonotus* (Lightfoot *et al.* 2011), the Nearctic Nedubini form a distinctive morphological unit that is monophyletic (Cole & Chiang 2016) due to (1) the modification of the male paraprocts into clasping organs (pseudocerci; Rentz & Birchim 1968) instead of the reduced, conical cerci (Rentz & Colless 1990) and (2) the ambidextrous condition of the tegmina (Cole & Chiang 2016; Morris *et al.* 1975; Pemberton 1911). Female nedubines are the only North American shield-back katydids with serrated ovipositors, which suggests that the oviposition substrates may include wood or other plant tissue in addition to soil, which is typical for Tettigoniinae. Although the Nedubini remain in the subfamily Tettigoniinae, which includes the worldwide shield-back katydid fauna, this subfamily is polyphyletic (Cole & Chiang 2016; Mugleston *et al.* 2013). The Nearctic Nedubini are the most basal extant clade of katydids worldwide and neither share recent common ancestors with “nedubines” from South America and Australia nor with the Holarctic shield-back fauna (Cole & Chiang 2016); thus, the shield-back body plan has evolved multiple times. We agree with Rentz (1988) and Lightfoot *et al.* (2011) that *Neduba*, *Aglaothorax*, and *Phymonotus* are of genus rank, given the date of cladogenesis of the three Nearctic nedubine lineages (~36 Ma) and given that the morphologically distinct *Phymonotus* is sister to *Aglaothorax* (Cole & Chiang 2016). Systematics of subfamilies and tribes must await phylogenetic analyses with more thorough taxon sampling than have been accomplished to date.

Philosophy and Characters Studied. Systematics that increases causal understanding of biological diversity is congruent with the overall goal of science (Fitzhugh 2013). To this end, our species hypotheses are informed by biological processes that may have generated diversity in the past and that may currently maintain it. Geography is immediately implicated as an isolating mechanism as *Neduba* generally occur in allopatric or parapatric populations that replace one another in different biogeographical regions (see Results). Whereas most species concepts perform poorly when faced with allopatric taxa (Coyne & Orr 2004), the phylogenetic or genealogical species concept (Baum & Donoghue 1995; Shaw 2001) may identify independently evolving lineages. Over the course of speciation geography may not remain constant (Butlin 2008; Fitzpatrick *et al.* 2009); thus, while we acknowledge the apparently large contribution of geography to *Neduba* diversification, we favor characters that are involved in the evolution of reproductive isolation in accordance with the biological species concept, which defines species as “...groups of interbreeding natural populations that are reproductively isolated from other such groups” (Mayr 1995). The evolution of reproductive isolation takes time, and our results suggest that several *Neduba* species are in early stages of divergence and that others are composed of formerly diverging populations that have homogenized. The version of the biological species concept employed here (Coyne & Orr 2004) allows a modicum of gene flow between taxa, which is expected in incipient species and for which there is evidence in *Neduba* (see Results).

Our systematic methodology began with the inference of phylogenetic hypotheses from multiple nuclear and mitochondrial loci. The resulting clades were then evaluated for potential reproductive isolation by observing differentially shared characters in male calling song, morphology, and karyotypes. The goal of systematics is systematization, not classification (Fitzhugh 2013), and to that end we propose species hypotheses consistent with total evidence: genetically distinct entities that are reproductively isolated by mating signals, chromosome rearrangements, and geography. Valid, behaviorally isolated biological species may be morphologically cryptic (Bickford *et al.* 2006; Wells & Henry 1998), a familiar concept to orthopterists who study bioacoustics (Walker 1964). We sought correlated characters that allow morphological diagnoses of our biological species and conclude that the majority of *Neduba* species are morphologically diagnosable, but the informative morphological characters are often quantitative and subject to continuous variation, and thus best used in conjunction with calling songs and genetics.

Methods

Collection and Preservation. *Neduba* are locally common insects that are incidentally collected by general entomologists. Many conventional and mass collecting techniques are not effective: only occasionally do individuals wander to collecting lights and beating vegetation is nonproductive. An entomologist interested in amassing a collection of these katydids must resort to specialized methods. Triangulating the source of calling songs at night is an efficient way to collect males but takes practice. Besides being challenging to localize, not everyone can hear the high frequency range of their songs, and the ability to hear the songs diminishes with age of the observer. Bat detectors may be employed to locate males that are not audible. Oatmeal trails laid down at night can be an effective way to attract individuals, especially females. Searching bark, logs, and leaf litter during the day may turn up small numbers of adults.

Gathering nymphs early in the season and raising them to maturity is a way of obtaining large samples. *Neduba* are easy to maintain in captivity, readily accept the orthopteran food mixture (Rentz 1996), are non-aggressive and thus may be group-housed, and are long-lived. None of us have successfully reared *Neduba* through an entire generation from eggs, a problem that until solved precludes detailed laboratory genetics and limits behavioral studies. Given their habitats, *Neduba* may require simulated winter conditions to break diapause (see Rentz 1973).

Quality specimen preservation requires taxidermy and/or freeze-drying to prevent shriveling of the body and loss of pigment colors. To taxidermize specimens we either (1) inserted forceps dorsally through the cervical membrane between the head and pronotum and removed the gut contents through the opening, and then inserted loosely balled cotton through the same opening, or (2) made an incision along an abdominal pleuron, removed the gut, and inserted cotton to reform the shape of the abdomen. Color preservation, especially for green tones, is improved by drying taxidermized specimens in a conventional, frost-free freezer. Freeze-drying is also effective for entire (i.e. non-gutted) specimens.

Molecular Phylogenetic Analysis. *DNA extraction, amplification, and sequencing.* Middle or hind legs, or in a few cases whole specimens, were directly frozen at -20°C or preserved in 95–100% ethanol. DNA was extracted using an ethanol precipitation method equivalent to the Puregene Extraction Kit (Gentra Systems, Inc.) or a commercially available extraction kit (DNEasy Blood and Tissue Kit, Qiagen, Inc., Valencia, CA, USA) according to the manufacturer's protocol for animal tissues. The polymerase chain reaction (PCR) was used to amplify five genes: the entire ribosomal *internal transcribed spacer 2* (ITS2, variable length), a 1030 bp fragment of *28S ribosomal RNA* (28S), a 384 bp fragment of *wingless* (*wg*), an 828 bp fragment of *cytochrome oxidase I* (COI), and a fragment of *cytochrome oxidase II* (COII) with 501 bp overlap after alignment. The first two regions are linked on the nuclear ribosomal cistrons and are collectively referred to as rDNA, while the last two loci are linked on the mitochondrial genome and are referred to as mtDNA henceforth. *wg* is a slow evolving gene (Campbell *et al.* 2000) that we included in our concatenated analysis. Primer sequences and PCR conditions are listed in Table 1. PCR reactions were performed in either 10 or 25 μ L volumes on a GeneAmp 9700 (Applied Biosystems) or MyCycler (BioRad) thermocycler using a Taq master mix (HotStar Plus Taq Master Mix, Qiagen Inc., Valencia, CA, USA) according to the cycling conditions in Table 1. Direct sequencing of PCR products followed enzymatic cleanup (ExoSAP-*it*, Affymetrix, Santa Clara, CA, USA).

Sequence alignment. Trace files were imported into Geneious v. 6.1.8 (created by Biomatters, available from <http://www.geneious.com/>) for contig assembly and editing. Protein coding COI, COII and *wg* genes were unambiguously aligned by amino acid sequence in Geneious. 28S was aligned using the *x-ins-i* algorithm (Katoh & Toh 2008) in MAFFT (Katoh *et al.* 2002; Katoh & Standley 2013). ITS2 alignment was aided by estimating secondary structures. The precise start and end points of each ITS2 sequence were annotated using a hidden Markov model (Eddy 1998) implemented through the ITS2 database (Koetschan *et al.* 2010). Secondary structures were estimated for batches of sequences using the TurboFold algorithm (Harmanci *et al.* 2010) as implemented in RNAstructure v. 5.3 (Reutters & Mathews 2010) set to default parameters. The resulting secondary structures were used to produce a simultaneous sequence and structure alignment in RNAsalsa (Stocsits *et al.* 2009).

Phylogenetic analysis. Phylogenetic analyses were run on the supercomputer resources available at the CIPRES Science Gateway (Miller *et al.* 2010). Models of sequence evolution and partitioning schemes were evaluated simultaneously for the combined dataset using Partition Finder v. 2 (Lanfear *et al.* 2016) using a greedy search algorithm (Lanfear *et al.* 2012) and PhyML (Guindon *et al.* 2010). Bayesian phylogenetic analysis was performed in MrBayes v. 3.2.6 (Huelsenbeck & Ronquist 2001; Ronquist *et al.* 2012; Ronquist & Huelsenbeck 2003). Branch lengths were unconstrained and all topologies were considered equally likely. Gaps in ITS2 secondary structure in-

TABLE 1. Primers and PCR conditions. Primers marked with asterisks (*) were used in nested PCR reactions.

Locus	Primer name	Primer sequence	Annealing conditions	Extension time (s)	Cycles	Reference
ITS2	3S	GGTACCGGTGGATCACTGGGCTCGTGG	53°C 15 s	60	30	(Slaney & Blair 2000)
	BD2	TATGCTTAAATTCAGCGGGT				(Slaney & Blair 2000)
28S	NLF184-21	ACCCGCTGAAYYTTAAGCAIAT	54°C 30 s	60	30	(Van der Auwera <i>et al.</i> 1994)
	LS1041R	TACGGACRTCCATCAGGGTTTCCCCTGACTTC				(Wild & Maddison 2008)
wg	LEPWG1	GARTGYAARTGYCAYGGYATGTCTGG	59°C 15 s	60 s	40	(Brower & DeSalle 1998)
	modLEPWG2	ACTICGCARCACCARTGGAATGTRCA				
	WG550Fkt	ATGCGTCAGGARITGYAARTGY	46°C 30 s	45 s	30	(Mugleston <i>et al.</i> 2013)
	WgAbRz	CACTTNACYTCRCAR CACCARTG				(Wild & Maddison 2008)
COI	*WgITET	GAGTGTAAGTGTCAATGGTATGTCTGG	50°C 30 s	45 s	30	(Cole & Chiang 2016)
	*WgAbRNed	ACTGGCAGCACCARTGGAA				This study.
	COI-J-2195	TTGATTTTTTGGTCAIACCAGAAAGT	50°C 60 s	60 s	35	(Simon <i>et al.</i> 1994)
	TL2-N-3014	TCCAATGCACTAATCTGCCATATTA				(Simon <i>et al.</i> 1994)
	Jerry	CAACAYTTAATTTTGAATTTTTTGG	50–52°C 60 s	60–75 s	30–35	(Simon <i>et al.</i> 1994)
	Pat	ATCCATTACATATAATCTGCCATA				(Simon <i>et al.</i> 1994)
	C2-J-3279	GGACAAACAATTGAGTTAATTGGAAC	45–47°C 60 s	60 s	30	(Simon <i>et al.</i> 1994)
	TD-N-3862	TTTAGAATTGACATTTCTAATGTTAT				(Simon <i>et al.</i> 1994)
	COII Flue	TCTAATAITGGCAGATTAGTGC	46–50°C 30–60 s	75 s		(Svenson & Whiting 2004)
	COII Rlys	GAGACCAAGTACTTTGCTTTTCAGTCATC				(Svenson & Whiting 2004)
*COII 2a	ATAGAKCWTCYCCHTTAATAGAACA	46–51°C 30–60 s	75 s		(Mugleston <i>et al.</i> 2013)	
*CPOO 9b	GTACTIONGCTTTTCAGTCAICTWATG				(Mugleston <i>et al.</i> 2013)	

formation were modeled as binary restriction data (1 = nucleotide, 0 = gap) with variable coding. Four runs of four chains each were continued for 5×10^7 generations, after which convergence was inferred from a standard deviation of split frequencies of < 0.02 . Consensus trees were calculated from the posterior probability distributions after burnin fractions of 0.25 were discarded.

Morphology. Specimens were examined in the collections of the California Academy of Sciences (CAS), the Natural History Museum of Los Angeles County (LACM), the Bohart Museum of Entomology (BMED) at UC Davis, California State University Northridge (CSUN), the personal collection of the senior author (JAC), and the California State Collection of Arthropods (CSCA) in Sacramento, CA. Localities on museum specimen labels were georeferenced using the batch client at GeoLocate (<http://www.museum.tulane.edu/geolocate/>). Distribution maps were generated from georeferenced data using ArcMap v. 10.5.1 (www.esri.com). The authors collected the bulk of the material examined in this revision. Holotypes are deposited at CAS.

A system of codes appears on our labels and are referred to throughout this manuscript to organize specimen data. Many codes take the form two-digit year—(hyphen) event numbered in sequence for that year:

S = DBW stop, i.e. collecting event, e.g. S82-37, the 37th collecting event in 1982

R = DBW recording number

JCS = scanning electron microscope (SEM) preparation

T = DBW testes preparation for karyotyping

JCT = JAC testes preparation for karyotyping

Other codes include:

A (adult) = eclosion date of adult reared from nymph

D = number associating DBW voucher specimen with tissue, usually right middle leg

DNA = number associating JAC voucher specimen with tissue

JAC = specimen barcode, 9-digit number

JCR = JAC recording date_(underscore) number, e.g. 160729_03, the 3rd recording on 29-VII-2016.

SING = DNA extraction, numbered sequentially

Morphological measurements were made with Vernier calipers and are a subset of the measurements established for *Phymonotus* (Lightfoot *et al.* 2011) as relevant for *Nedubini*. All measurements are expressed in mm. Photographs of habitus and terminalia were made with a digital camera (model TG-5, Olympus Inc., Center Valley, PA, USA) set to image stacking in microscope mode.

Preserved males were relaxed for genitalia dissection by immersing the abdomen tip in boiling water for a few minutes. The subgenital plate was then reflexed and the entire genital capsule was removed with fine forceps. Soft tissue was cleared by immersion in 10% KOH for 0.5–1.0 d followed by neutralization in distilled white vinegar for 0.5 d. Genitalia for light microscopy are stored in glycerol-filled genitalia vials that accompany the specimens. Genitalia preparations were illustrated by hand with the aid of a camera lucida attached to a stereo zoom microscope set to 10×zoom.

Genitalia for SEM preparations were chemically dried by immersion in 70% ethanol for 1 d, 95% ethanol for 1 d, and then two changes of hexamethyldisilazane (HMDS) for 20 min each. Chemically dried specimens were adhered onto pennies with carbon stickers and sputter-coated with a 60% Au/40% Pd mixture. Imaging was performed on a scanning electron microscope (model Phenom X, Thermo-Fisher Scientific, Waltham, MA, USA) set to 10 kV beam strength. An additional carbon sticker adhered the penny with the sample onto an SEM stub so that the stub could be reused.

Surprisingly, study of the stridulatory file, which is commonly employed in the systematics of ensiferan Orthoptera (e.g. Walker & Funk 2014; Weissman & Gray 2019), has been neglected in *Neduba* and turns out to be an important diagnostic character for species Groups and species (see Results). Stridulatory files were studied on excised tegmina. The tegmina of *Neduba* are ambidextrous (Cole & Chiang 2016; Pemberton 1911) but do not switch position while singing (Morris *et al.* 1975); thus the dorsal tegmen, which will have the functional stridulatory file if there is any asymmetry in tegminal development, was excised and mounted upside down on a microscope slide. Excision was more easily accomplished when the specimens were fresh. Dried specimens were relaxed as described

above. File teeth were counted under a compound microscope (Zeiss, White Plains, NY, USA) at 500× magnification. The length of the file was measured in mm (across the curve) with an ocular micrometer as a straight line between the ends of the file. File length and tooth number were not significantly different across our specimen series; instead, the standardized measurement of tooth density, the ratio of the tooth count divided by file length, differs significantly between *Neduba* species and facilitates diagnosis.

Color patterns vary widely within and between species (Fig. 1). We offer images of living katydids as examples of common color patterns (Plates 1–3) but do not describe color patterns for each species for the following reasons: (1) preservation of color patterns is unreliable in museum specimens unless properly prepared (see Collection and Preservation above), (2) a single species may have multiple color patterns with slight variations, and (3) reliance on color pattern has in part led to the confusing taxonomy of *Neduba* (e.g. Caudell 1907; Tinkham 1944), and we emphasize characters that have diagnostic utility.

Song Recording and Analysis. The acoustic pair-formation mechanism employed by *Neduba* katydids permits inferences to be made about reproductive compatibility between populations and therefore about species status. Rates of sound production serve as species-specific mate recognition features in many acoustic animals (e.g. Gerhardt 2013; Gerhardt & Huber 2002; Gray *et al.* 2016; Rodriguez *et al.* 2006) including the related nedubine genus *Aglaothorax* (Cole 2016). Therefore, among the seven song characters we analyzed, rates of pulse train production ranked highly among potential mate recognition cues. Calling songs are only half of the pair formation equation; future research may test species boundaries inferred from calling song differences with female preference experiments (e.g. Cole 2016; Ritchie 1991; Rodriguez *et al.* 2006; Schul 1998; Shaw & Herlihy 1999). DBW recordings were made with a condenser microphone (model ME40 microphone and model K34 power module, Sennheiser Electronic Corp., Old Lyme, CT, USA) and reel-to-reel tape recorder (model 4000 Report LC, Uher, Munich, Germany) indoors where temperature was maintained at or near 25°C (24.3 ± 1.7°C). JAC digitized DBW analog recordings at a sampling rate of 44.1 kHz through a firewire interface (Cakewalk FA-66, Roland Corp., Los Angeles, CA, USA) into a MacBook Pro computer running Logic Pro v. 10.3.3 (Apple Inc.). JAC field recordings were made with a linear PCM recorder (model PCM-D50, Sony Corp., New York, NY, USA) with integral condenser microphones. This device recorded 16-bit audio at a sampling rate of 96 kHz. A low cut-off frequency of 75 Hz was set to reduce wind and other ambient noise. Together, the microphones and sampling parameters recorded a frequency range that extended to 40 kHz. High-frequency laboratory recordings were made by JAC in a semi-anechoic chamber at the University of Kansas in which temperature was maintained near 25°C (24.5 ± 0.7°C). High frequency equipment consisted of a 1/2 inch electret condenser microphone (model M51, Linear-X, Tualatin, OR, USA) and a PC computer running BatSound v. 3.3 (Pettersson Elektronik AB, Uppsala, Sweden) sampling at 150 kHz for 1 min. The high frequency laboratory recording apparatus captured frequencies up to 75 kHz, with a flat response from 10 Hz to 40 kHz.

A high pass filter set to 24 dB roll-off and a cutoff frequency from 1 to 6 kHz reduced tape transport and other noise, the higher cutoffs used for correspondingly greater intrusion of noise levels into higher frequencies of the recording. Cutoff frequencies did not affect the frequency range of *Neduba* calling songs, the minimum of which for all species seldom extended to 4 kHz. The complexity of *Neduba* calling song waveforms confounded automatic analysis of the temporal song features. Specifically, automatic waveform detection methods produced a dataset of high precision but low accuracy that underestimated pulse train lengths as automatic detection did not reliably find the start and end points of pulse trains. Manual measurement of song components was therefore undertaken using Audacity v. 2.1.0 (available from www.audacityteam.org). Six successive wingstroke cycles were randomly chosen and measured with the cursor to the nearest ms. Peak frequencies were measured from a portion of a randomly selected wingstroke cycle using a 256 Hz Fast Fourier transform algorithm and a Hanning window in Audacity. Oscillograms and spectrograms figured in this revision were generated with Raven Lite v. 2.0 (Cornell Laboratory of Ornithology, available from ravensoundsoftware.com). Recordings will be deposited in Macaulay Library–Cornell Lab of Ornithology and on Singing Insects of North America (<https://orthsoc.org/sina/>). Terms used to describe song characters are as follows, and the fundamental characters are shown graphically in Fig. 2:

PT = pulse train

MPT = major pulse train (always made by tegmina closing)

OPT = minor pulse train (usually made by tegmina opening, exceptions are species with multiple OPT in Sierranus Group (Fig. 2D–E) and *N. oblongata* sp. n. in the Carinata Group)

MPTL = major pulse train length, standardized by regression to 25°C

PTP = pulse train period (measured either from beginning to beginning or from end to end of MPT, depending on which measurement was more clearly identifiable on the oscillograms)

PTR = pulse train rate/s, standardized by regression to 25°C (= 1/(PTP × 1000))

PTdc = pulse train duty cycle (= MPTL/PTP)

PTF = frequency at maximum amplitude of major pulse train

PTN = pulse train number (counted for multiple OPT generated by partial wing closing and opening)

Statistical song analysis was performed in R v. 3.2.3 (available from www.r-project.org). Temperature dependent song parameters (PR, MPTL) were tested for significance between putative taxa using ANCOVA, with taxon as the factor and temperature as the covariate. A significant temperature × taxon interaction indicated different regression slopes. Population was also included in some ANCOVA models as a factor to test for interpopulation differences within taxa. Temperature-independent characters (PTdc, PTN) were tested with ANOVA.

Karyotypes. Chromosome rearrangements are frequently associated with species boundaries in animals ranging from grasshoppers (Weissman & Rentz 1980) to beetles (Maddison 2008) to velvet worms (Onychophora; Rockman & Rowell 2002) to rodents (Cross 1931). Diverse karyotypes are found in *Neduba* katydid. Apart from differences in autosome number and centromere locations, multiple sex chromosome systems have evolved: all males possess at least one X chromosome and in some species males have an additional X chromosome and/or a Y chromosome (Ueshima & Rentz 1979). We regard chromosomal differences between *Neduba* taxa as evidence for specific distinction, and we invite testing of our species hypotheses with population genetic analysis or crossing experiments.

Testes were removed from living males through an incision along the midline of the abdominal dorsum. Scissors were inserted underneath the tergite in front of the supra-anal plate and continued anteriorly. Excised testes were immediately stored in a freshly prepared 1:3 mixture of glacial acetic acid and 100% ethanol. Testes were prepared for light microscopy by squashing on microscope slides and staining according to the standard Schiff-Giemsa method. Karyotypes are reported in the descriptions as diploid counts followed by counts that are arranged by centromere location, where m = metacentric and t = telocentric. For example, a common *Neduba* karyotype is $2n\sigma = 26 (2m + 22t + XtYt)$, which denotes a diploid chromosome count of 26 that is composed of 2 metacentric autosomes, 22 telocentric autosomes, and a pair of telocentric sex chromosomes: one X and one Y. Where appropriate, the autosomes are noted to be large, medium, or small in size.

Results

Phylogenetic Analysis. GenBank accessions and voucher specimen information are reported in Supplementary Table 1. PartitionFinder results are summarized in Table 2. Bayesian analysis of the concatenated genetic data separated two major *Neduba* clades (posterior probability = 1) that are subdivided into six Species Groups (all posterior probabilities = 1): Carinata, Propsti, Castanea, Lucubrata, Sierranus, and Sequoia (Fig. 3). The Carinata Group consists of eight lineages, four of which are currently recognized species (*N. carinata*, *N. convexa*, *N. diabolica*, and *N. steindachneri*). The Carinata Group is comprised of two clades (posterior probability = 1): the Carinata Clade and the Convexa Clade. Although Convexa Clade lineages clearly cluster, the interrelationships of those lineages are poorly resolved. The Propsti and Lucubrata Groups contain one lineage each. The Castanea Group consists of reciprocally monophyletic lineages corresponding to *N. castanea* and *N. macneilli*. The Sierranus Group consists of four lineages, with a deep split across *N. sierranus* rendering that species paraphyletic. The Sequoia Group consists of four lineages that are not resolved by concatenated genetic data.

TABLE 2. Partitioning scheme for phylogenetic analysis as selected with PartitionFinder.

Partition	Gene fragment(s) and codon positions	model
1	wg 1st, wg 2nd, 28S	HKY + I
2	wg 3rd	HKY + Γ
3	COI 1st, COI 2nd, COII 1st, COII 2nd	HKY + I + Γ
4	COI 3rd, COII 3rd	GTR + Γ
5	ITS2	HKY + Γ

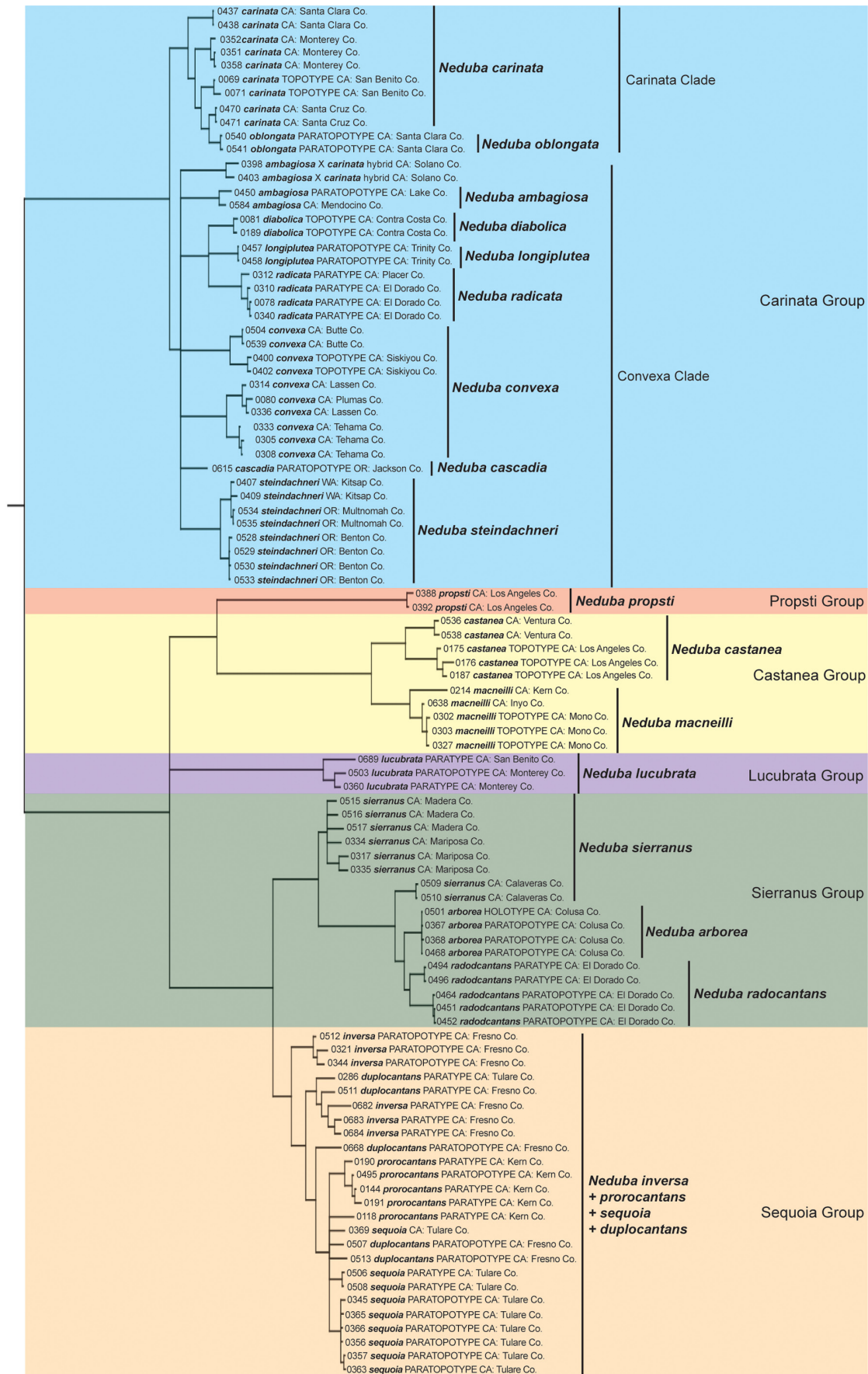


FIGURE 3. Bayesian consensus tree showing species Groups (color coded) and species hypotheses. Nodes with <85% posterior probability are collapsed.

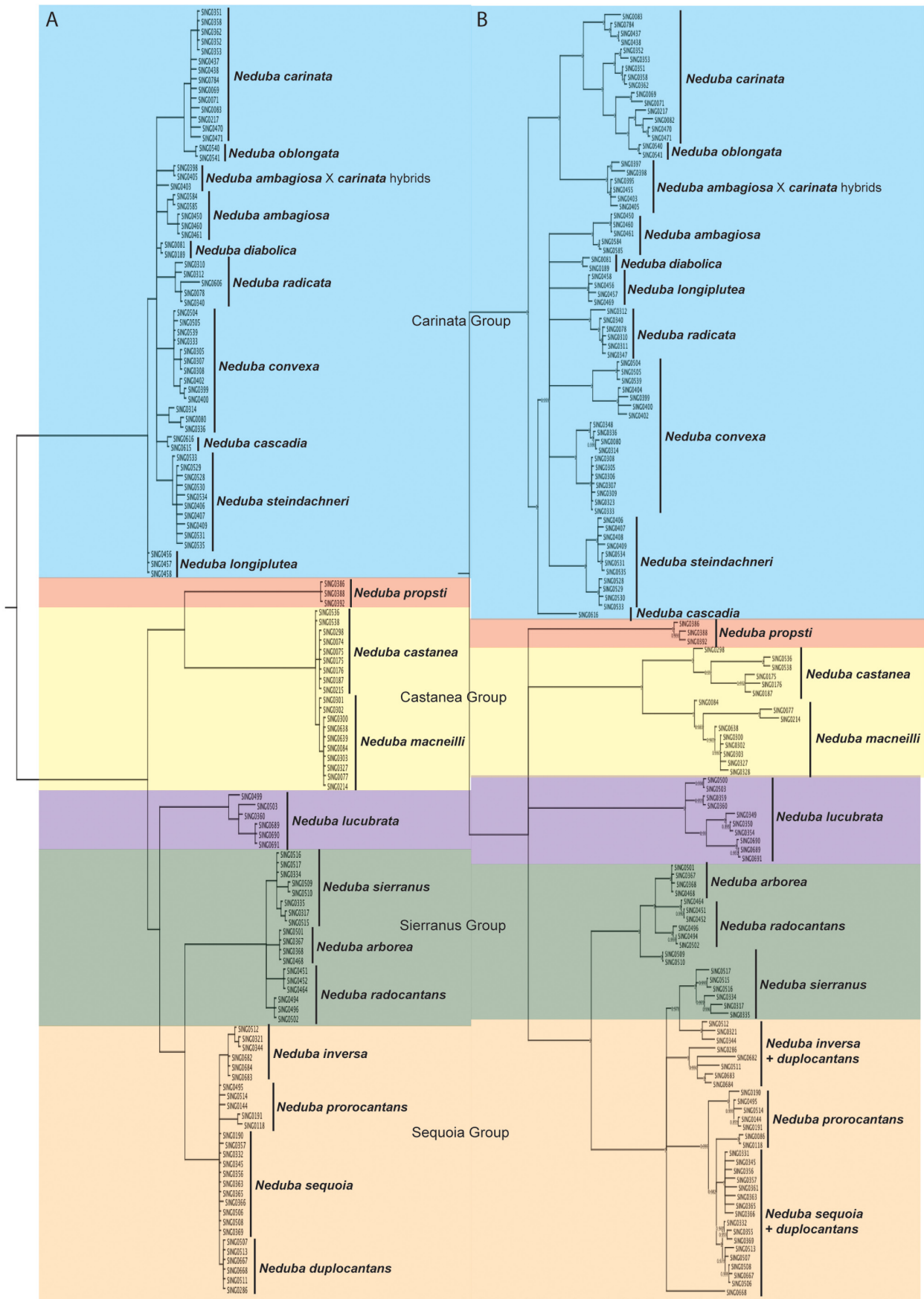


FIGURE 4. Comparison of A. rDNA, and B. mtDNA trees. Nodes with <85% posterior probability are collapsed. Species Groups are color coded.

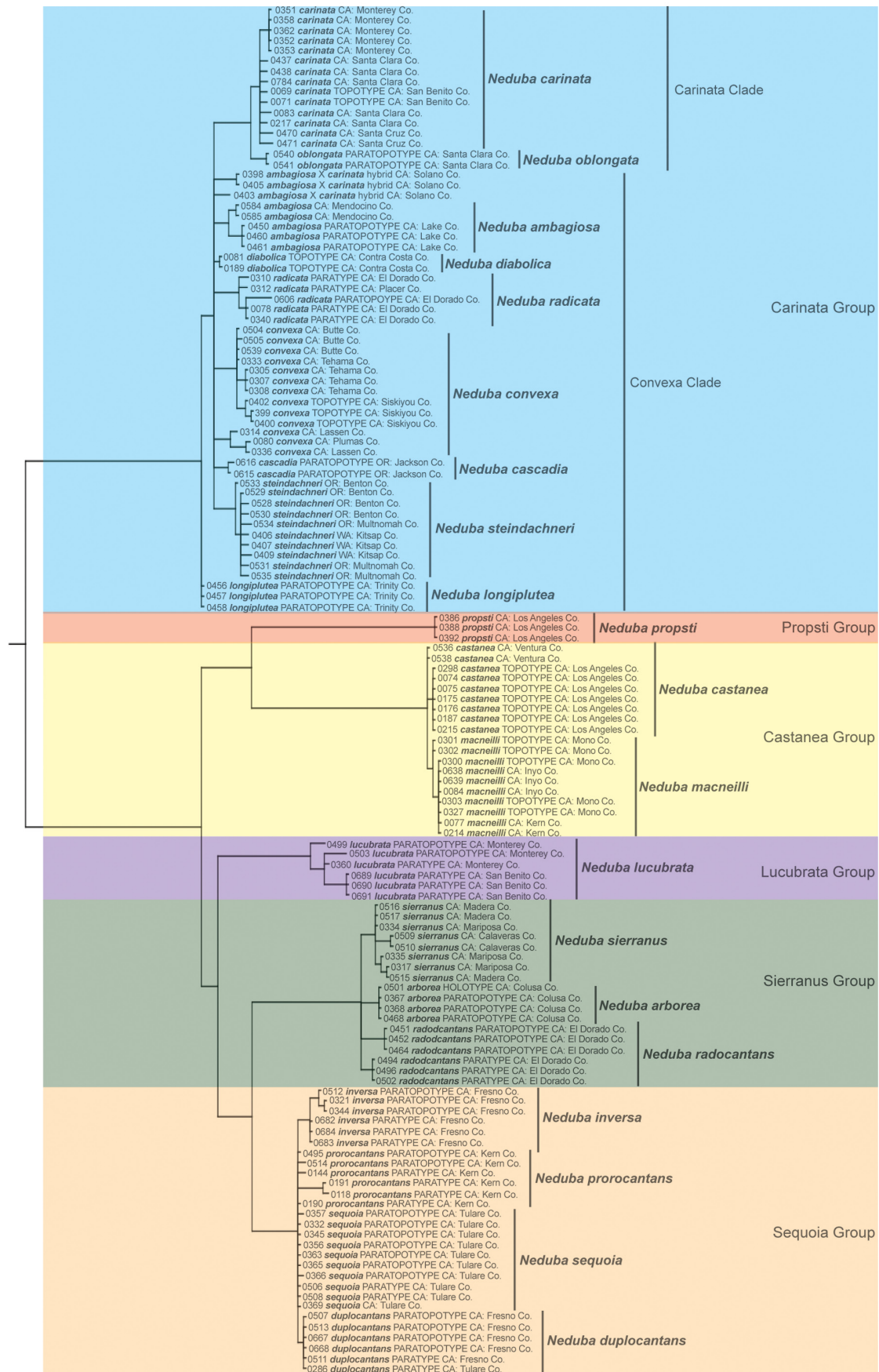


FIGURE 5. rDNA Bayesian consensus tree. Nodes with <85% posterior probability are collapsed. Species Groups are color coded, and species hypotheses are indicated.

Hypotheses resulting from rDNA and mtDNA were incongruent (Fig. 4): the mtDNA consensus tree nested *N. oblongata* within *N. carinata*, and *N. sierranus* collapsed into the poorly resolved Sequoia Group. In both cases, incongruence was due to mtDNA grouping species with adjacent geographic ranges (for a similar pattern in *Aglaothorax* see Cole 2016).

The rDNA consensus tree (Fig. 5) delineates species hypotheses in congruence with morphological, geographical, and bioacoustical character sets. rDNA resolved the lineages of the Sequoia Group, which were obscured in the concatenated dataset by mtDNA introgression.

Morphology

Genus *Neduba* Walker, 1869

Type species. *Neduba carinata* Walker, 1869

Generic characters. The following description of the genus is based on topotypic *N. carinata* (specimens ♂ JAC000001970 and ♀ JAC000001991 with variation from topotype series). While this description applies directly to the Carinata Group, because general morphology is conserved throughout the genus, this description is not repeated for other species Groups or species. Rather, deviations from this description are indicated under the appropriate descriptions (see Diagnosis, *Neduba* species identification and species accounts below for figures).

Head. Labrum circular to teardrop-shaped, flat with median ridge. Clypeus trapezoidal, junction of clypeus and frontal costa with central depression. Frons flat to slightly convex to the level of the circumantennal sulci; a projection extends dorsally to a rounded point at the midpoint of antennal sockets, median ocellus indicated by pale coloration at base of mid-dorsal projection of frons. Gena ovoid, slightly convex, with dorsoventral long axis. Vertex broad dorsally, base subequal to or slightly narrower in width to one antennal scape, median and lateral carinae faintly indicated, sometimes with faint depression or groove in vicinity of median carina. Fastigium projects beyond scapes to a narrow truncate apex, rounds smoothly onto front of head, then narrows ventrally between antennal sockets to join tightly with dorsal projection of frons. Junction of vertex and occiput obsolete, occiput evenly convex. Eye subspherical, slightly elongate along a dorsoventral axis and to posterior. Antennae approximately 1.5 times body length, with faint to strong alternating dark and pale annulations that may not coincide with antennomere articulations.

Thorax. Pronotum of male greatly expanded posterolaterally into a shield-like sclerite that completely covers the tegmina and the first two abdominal terga, disk of pronotum bordered by a broadly rounded cord-like margin. Median carina moderately developed, sometimes obsolete in center of pronotal disk. Lateral carinae strongly indicated, constricted on prozona in the anterior 1/6 of pronotal length where a transverse sulcus may be present that approaches or crosses the median carina. At junction of prozona and metazona, faintly indicated partial oblique transverse grooves or ovoid depressions extending posteromedially from lateral carinae toward but not meeting median carina. Pit on both sides of median carina just anterior to transverse carinae often connected to small sinuate anterolaterally trending grooves. Prozona occupies 0.44 of pronotal dorsum (median, $n_{\text{♂}} = 261$). Prozona flat, gradually sloping laterally from median carina towards lateral carinae. Metazona weakly to moderately convex, rugose. Lateral lobes of pronotum longer than deep, trapezoidal below prozona, abruptly narrowed posterodorsally from transverse carina at prozona-metazona junction to meet lateral carina at an acute angle. Auditory spiracle elongate oval, fringed with fine setae, the upper 1/3 to 1/2 hidden by lateral lobe. Prosternum armed with two acute spines. Mesosternal and metasternal lobes produced, wedge-like. Female thorax similar to male except pronotum less well developed, not as expanded laterally or posteriorly, usually not covering entire tergite I, prozona and metazona subequal in length (median = 0.51 of pronotal dorsum, $n_{\text{♀}} = 75$).

Legs. Front coxae with stout anterior spine that projects distally to trochanter, other coxae unarmed. Dorsal surface of front and middle femora with scattered small spines, ventral margin bordered with strong inner and outer carinae that line a wide ventral groove. Front tibiae with tympana partially exposed dorsally by similar lunular slits on both cephalic and lateral margins. Front tibiae with one spine on dorsal margin immediately distal to tympana, 2 spines at apex of tibiae, and 6–8 spines along inner and outer carinae. Middle tibiae rectangular in cross section with spines along all four margins, variable in number but more numerous on ventral carinae (6–8) than dorsal angles

(3–4). Hind femora elongated, extending beyond apex of abdomen, with numerous small spines on basal half of dorsal surface. Hind tibiae rectangular in cross section, apical spurs approximately 1/2 length of basitarsus.

Wings. Male tegmina brachypterous, ovoid, ambidextrous: functional stridulatory files and scrapers on both tegmina, either left or right tegmen may lie uppermost with frequency ~0.5 (Cole & Chiang 2016). Wings absent. Female tegmina and wings absent.

Abdomen. Fusiform in life, gradually tapering to posterior, distorts and shrivels in dried, non-taxidermized specimens. Tergites with median carinae that begin in approximately anterior 1/3 and elevate towards posterior, may become knob or spine-like at posterior margin. Posterior tergite margins crenulate, the crenulations frequently accompanied by dark maculations.

Male terminalia. Epiproct (supra-anal plate) quadrate (type) to pentagonal, medial and lateral margins obtusely angulate, center with transverse depression. Cerci reduced, subequal in length to tergites VIII + IX, covered with dense fine pile. Paraprocts (pseudocerci) short, extending little beyond supra-anal plate, oblong, swollen, a carina surrounding entirety of lateral margins. Titillators with long, curved, horn-like arms and plate-like ventral sclerites, dorsal sclerites absent. Male subgenital plate scoop-like with strong median carina and parallel lateral carinae that terminate in articulate styli.

Female terminalia. Epiproct tongue-like with low median carina. Cerci similar to male. Ovipositor approximately 3/4 as long as hind femur (median = 0.731, $n_{\text{♀}} = 75$), gently upcurved, serrate with blunt teeth on dorsal and ventral margins over apical 1/3 of length. Subgenital plate pentagonal, flat, without (type) or with a median groove, depending on species.

Etymology. Unknown. We speculate the name may be a combination of the Latin roots *nedum* (much more) and *bas* (base, pedestal, foundation, chord of an arc). This name describes the large, flat dorsal aspect of the shield-like pronotum, or alternatively the great arc formed by the posterior margin of the pronotum.

Diagnosis. Body fusiform in both sexes (Fig. 6A, G; compared with more robust body of *Aglaothorax* (Fig. 6B, H) and the cylindrical male body of *Phymonotus* (Fig. 6C)). Hind legs elongate, with apices of hind femora extending distinctly beyond the tip of the abdomen (Fig. 6A, G; short hind femora in *Aglaothorax* extend little beyond the tip of the abdomen (Fig. 6B, H), and in *Phymonotus* are subequal to or shorter than the abdomen (Fig. 6C, I)). *N. castanea* is an exception with a robust body and short hind femora as in *Aglaothorax*. No green forms (as in *A. ovata* (Fig. 6B, H)). Dorsum of male pronotum flat to slightly convex (Fig. 6A; convex and dome-like in *Phymonotus*, (Fig. 6C)). Supra-anal plate of male quadrate or pentagonal, often with acute corners (Fig. 6D; rounded and tongue-like in *Aglaothorax* (Fig. 6E) and hourglass shaped in *Phymonotus* (Fig. 6F)). Paraprocts oblong, swollen and lacking an internal tooth (Fig. 6D; forceps-like and with an internal tooth in *Aglaothorax* (Fig. 6E) and *Phymonotus* (Fig. 6F)). Cerci reduced and conical as in other nedubine genera (Fig. 6D–F). Female subgenital plate triangular to oval, without processes but sometimes notched (Fig. 6J; with paired posterior processes in *Aglaothorax* (Fig. 6K) and shallowly notched in *Phymonotus* (Fig. 6L)).

For additional morphological comparison of the nedubine genera see Table 1 in Lightfoot *et al.* (2011). We amend the character state of the female subgenital plate for *Neduba*: some *Neduba* females have an apical indentation on the subgenital plate.

***Neduba* species identification.** It is difficult to identify *Neduba* species with morphological characters. We sought morphological synapomorphies for all species and conclude that most are morphologically diagnosable; however, the characters involved are often hidden (e.g. internal male genitalia) or require special preparation (e.g. stridulatory files of the tegmina). Furthermore, characters are often continuous measurement variables, in which individual variation may deviate from statistical distributions. Species hypotheses in the Sierranus and Sequoia Groups are clear based on molecular genetic, bioacoustical, and cytogenetic data; however, there are few correlated morphological features, rendering the species of the Sierranus and Sequoia Groups morphologically cryptic. Morphological separation of Sierranus and Sequoia Group species may be attempted through comparison of the measurements of various body parts as included in the key. We suggest the following strategies for *Neduba* identification:

1. With specimens in hand, use the dichotomous key (below). The key includes morphological characters for both males and females when available. Bioacoustical characters and distributions are also provided in the key.
2. Use geography to eliminate possibilities. *Neduba* are flightless and therefore strongly philopatric. Sympatric *Neduba* usually belong to different species Groups that are more clearly diagnosable than species.

3. Calling songs of males are diagnostic of many species. Compare calling song recordings with those on Singing Insects of North America (<https://orthsoc.org/sina/>). Be aware that calling songs are affected by temperature. Rate-based character data in the key are for 25°C. Also be aware that specialized equipment is required to record the high frequencies found in *Neduba* calling songs.

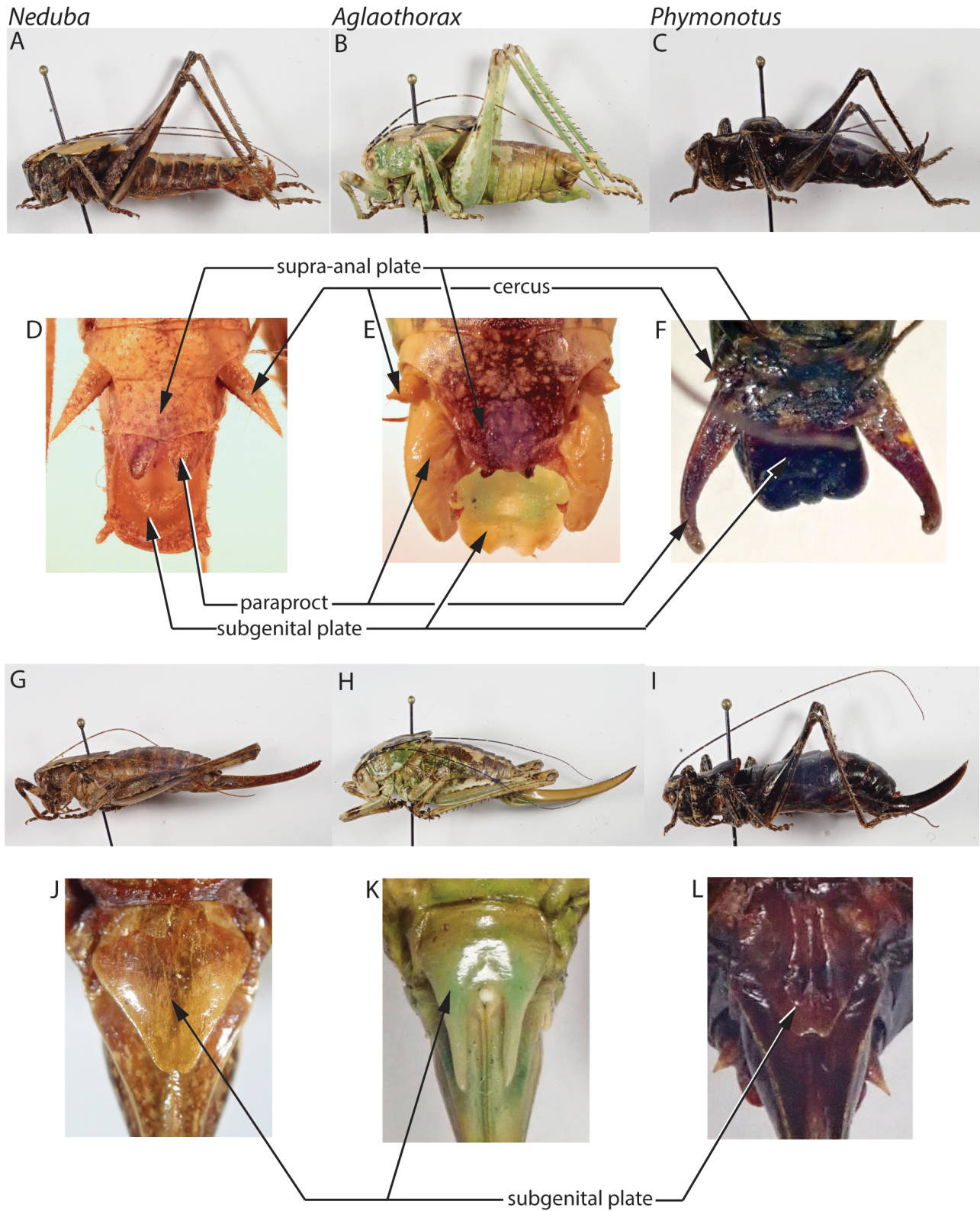


FIGURE 6. Characters of genera of Nedubini. Left lateral habitus of adult male: A. *Neduba*; B. *Aglaothorax*; C. *Phymonotus*. Dorsal view of adult male terminalia: D. *Aglaothorax*; E. *Neduba*; F. *Phymonotus*. Left lateral habitus of adult female G. *Neduba*; H. *Aglaothorax*; I. *Phymonotus*. Ventral view of adult female terminalia: J. *Neduba*; K. *Aglaothorax*; L. *Phymonotus*.

4. Avoid using color pattern. Color patterns are more variable within species than between (Fig. 1): *Neduba* coloration is a defensive strategy that relies on color pattern diversity (see Discussion), and color patterns in museum specimens are often faded or distorted from improper preservation.

Key to *Neduba* species based on morphological and bioacoustical characters and geography

- 1a.
- Both sexes: dorsal margin of fore tibia with apical spines on both anterior and posterior margins (Fig. 7.1a.1).
 - Males: subgenital plate lateral carinae parallel or gradually converging to posterior, with articulate styli (Figs. 10–18). Ventral sclerite of titillators of male genitalia strip- or plate-like (Fig. 7.1a.2). Titillator arms curved in a semicircle, smoothly curving dorsally along their length (Fig. 7.1a.2, Plate 9). Carinata Group 2
- 1b.
- Both sexes: dorsal margin of fore tibia with apical spine on posterior margin only (Fig. 7.1b.1).
 - Males: ventral sclerite tiny and forked (Fig. 7.1b.2). Titillator arms long, thick and straight over the majority of their length, the tips abruptly narrowed and upturned (Fig. 7.1b.2). Pronotum variable, may not be as dilated as above 10
- 2a.
- Males: stridulatory file tooth density (i.e. tooth count/file length) 36–56 teeth/mm. Calling song of the “chu-chu” type with continuous, rapidly produced pulse trains (PTR 6–16 s⁻¹ at 25°C. Plate 4A–B, D).
 - Females: subgenital plate flat, pentagonal, medial groove absent, lateral margins straight to slightly emarginate, apex pointed (Fig. 7.2a).
 - Distribution: Coast Ranges south of the San Francisco Bay Area, California. 3
- 2b.
- Males: stridulatory file tooth density 27–41 teeth/mm. Song of the “zwee-zwee” type with continuous, slowly produced pulse trains at a rate of 4 s⁻¹ or below at 25°C (Plate 4C, E–I).
 - Females: subgenital plate with curved or sinuate apical margins, medial groove present (Fig. 7.2b, *N. cascadia* is an exception, Plate 11).
 - Distribution: widespread in the Pacific Northwest north of the San Francisco Bay Area 5
- 3a.
- Males: apex of ventral sclerite convex rounded to subconical, lateral process short and directed 30° anterior to plane of shaft, which broadens and curves laterally from base to apex. Tubercles small and numerous on apex (Fig. 7.3a.1). Song PTdc 54–66% (Plate 4D).
 - Females: subgenital plate with medial groove (Fig. 13, Plate 11).
 - Distribution: known only from Mount Diablo, Contra Costa County, California *diabolica*
- 3b.
- Males: ventral sclerite with a low, rounded apex and a straight shaft (Fig. 7.3b.1; curved in *N. carinata* populations from the Santa Cruz Mountains, California, e.g. Fig. 10), some tubercles on apex large.
 - Females: subgenital plate flat, without medial groove (Fig. 7.2a) 4
- 4a.
- Males: stridulatory file tooth density 39–56 teeth/mm. Ventral sclerite lateral process usually short (Fig. 7.3b.1; long in the Santa Cruz Mountains vicinity). Calling song PTR uniform, 6–16 s⁻¹ at 25°C, PTdc 47–59% (Plate 4A).
 - Females: indistinguishable from *N. oblongata* (Fig. 7.2a).
 - Distribution: widespread in the South Coast Ranges, California *carinata*
- 4b.
- Males: stridulatory file tooth density 36–41 teeth/mm. Ventral sclerite lateral process minute (Fig. 7.4b). Male calling song PTR bimodal, switching between 6–8 s⁻¹ and 9–13 s⁻¹ at 25°C (Plate 4B).
 - Females: indistinguishable from *N. carinata* (Fig. 7.2a).
 - Distribution: known only from Mount Hamilton, Santa Clara County, California *oblongata*
- 5a.
- Males: ventral sclerite with a lateral process of appreciable length that is densely covered with tubercles that are often arranged in rows (Figs. 7.5a, 12, 14, 16).
 - Females: subgenital plate length/width ratio variable, distal margins always curved or sinuate (Fig. 7.2b) with a medial groove, apex may be bifurcate. 6

- 5b.
- Males: ventral sclerite with a lateral process short or lacking (like Fig. 7.3b.1, Figs. 15, 17-18). Tubercles generally confined to apex and do not lie in rows.
 - Females: subgenital plate as wide as long or wider than long, distal margins and medial groove variable (Figs. 15, 17-18) . . . 8
- 6a.
- Males: ventral sclerite with lateral process as long or longer than short, thick shaft (Figs. 7.6a1, 14).
 - Females: subgenital plate longer than wide, apex bifurcate (Figs. 7.6a2, 14), otherwise indistinguishable from *N. convexa*.
 - Distribution: Trinity Alps of California (Fig. 9) *longiplutea* **sp. n.**
- 6b.
- Males: ventral sclerite with lateral process not as long as above, shorter than length of shaft and apex combined (Fig. 7.5a).
 - Females: subgenital plate variable 7
- 7a.
- Males: ventral sclerite with lateral process of moderate length (Fig. 7.5a), apex flat and not differentiated from lateral process (Plate 7C) or low, rounded, and slightly separated from lateral process (Plate 7A–B).
 - Females: subgenital plate longer than wide, distal margins curved to sinuate, apex entire (Fig. 7.2b) or bifurcate, when bifurcate may not be separable from *N. longiplutea*.
 - Distribution: Sierra Nevada, Cascades, and northern Central Valley, California *convexa*
- 7b.
- Males: ventral sclerite apex convex, often of pyramidal, lateral process short and directed laterally in plane of shaft (0° angle) to anteriorly at up to a 45° angle from plane of shaft (Fig. 7.7b.1).
 - Females: subgenital plate length subequal to width, distal margins curved, apex narrow and pointed (Fig. 7.7b.2).
 - Distribution: found in northern Coast Ranges of California *ambagiosa* **sp. n.**
- 8a.
- Males: ventral sclerite lightly sclerotized (Fig. 7.8a.1), shaft is short, straight, thick, and tapers from base to apex, apex arcuate, lending the sclerite a mushroom-like appearance. Lateral process short, blunt, and recurved. Tubercles are large, few in number, and restricted to the dorsal surface. Stridulatory file tooth density low, 27–36 teeth/mm.
 - Females: subgenital plate length subequal to width, distal margins smoothly curved, medial groove absent (Fig. 7.8a.2).
 - Distribution: Central Oregon Cascade Ranges north to coastal British Columbia *steindachneri*
- 8b.
- Males: ventral sclerite fully sclerotized, not mushroom-like and otherwise not as above.
 - Females: subgenital plate with medial groove 9
- 9a.
- Males: ventral sclerite shaft gently curved and gradually tapering from the broad base to the apex (Fig. 7.9a.1). Lateral process is short and directed 45° to the anterior from the plane of the shaft. Apex covered with numerous small tubercles. Song PTR 2.7–4.0 s⁻¹ at 25°C (Plate 4F).
 - Females: ventral sclerite wider than long, medial groove deep, apex bifurcate (Fig. 7.9a.2).
 - Distribution: high elevations of northern Sierra Nevada, California *radicata* **sp. n.**
- 9b.
- Males: shaft of ventral sclerite thick and straight (Fig. 7.9b.1), apex blunt with scattered large tubercles. Lateral process blends into shaft at an obtuse angle. Male song PTR 1.6–2.0 s⁻¹ at 25°C (Plate 4H).
 - Females: subgenital plate length subequal to width, apical margins straight, apex broadly rounded (Fig. 7.9b.2).
 - Distribution: southern Cascade and Siskiyou mountain ranges of Oregon *cascadia* **sp. n.**
- 10a.
- Both sexes: prosternum unarmed (Fig. 7.10a). Body robust, hind femora short, scarcely longer than abdomen. (Plate 2B–D).
 - Males: pronotum greatly enlarged. Subgenital plate with lateral carinae converging, styli developed or absent. Stridulatory file tooth density 19–27 teeth/mm. Castanea Group. 11
- 10b.
- Both sexes: prosternum armed with a pair of spines (Fig. 7.10b). Body slender, hind femora clearly exceed abdominal apex.
 - Male: stridulatory file tooth density always greater, other characters variable 12
- 11a.
- Males: morphologically and bioacoustically indistinguishable from *N. macneilli*.
 - Females: subgenital plate rounded, highly convex (Fig. 7.11a).
 - Distribution: North slope of Transverse Ranges of southern California *castanea*

11b.		
•	Males: morphologically and bioacoustically indistinguishable from <i>N. castanea</i> .	
•	Females: subgenital plate triangular, apex pointed (Fig. 7.11b).	
•	Distribution: east slopes of the Sierra Nevada, California	<i>macneilli</i>
12a.		
•	Males: tegmina darkened at apex (Fig. 7.12a)	13
12b.		
•	Males: tegmina entirely immaculate ivory or white (Fig. 7.12b). Sierranus and Sequoia Groups	14
13a.		
•	Both sexes: large body size, male hind femora 20–24 mm, female hind femora 24–26 mm.	
•	Males: subgenital plate lateral margins parallel (Fig. 7.13a.1). Song is a continuous series of PT (Plate 4J).	
•	Females: subgenital plate 1.5 times longer than wide, highly convex, distal margins converge to a blunt apex (Fig. 7.13a.2).	
•	Distribution: Santa Catalina Island, Los Angeles County, California. Propsti Group	<i>propsti</i>
13b.		
•	Both sexes: small body size, male hind femora 16–21 mm, female hind femora 21–23 mm.	
•	Males: subgenital plate lateral margins converging to apex (Fig. 7.13b.1). Song is a chirp with long periods of silence between PT bouts (Plate 5C).	
•	Females: subgenital plate length subequal to width, distal margins converge to a broad, rounded apex, convex centrally with flattened margins (Fig. 7.13b.2).	
•	Distribution: South Coast Ranges, California. Lucubrata Group	<i>lucubrata</i> sp. n.
14a.		
•	Male	15
14b.		
•	Female (<i>N. extincta</i> female unknown)	22
15a.		
•	Stridulatory file tooth density < 53 teeth/mm.	16
15b.		
•	Stridulatory file tooth density ≥ 55 teeth/mm.	18
16a.		
•	Large species, pronotum length 9.9 mm, stridulatory file tooth density 52.2 teeth/mm (measurements from single known specimen).	
•	Distribution: extinct species known only from the Antioch Sand Dunes, Contra Costa Co., California.	<i>extincta</i>
16b.		
•	Without above combination of characters: either pronotum length < 9.5 mm or if greater, tooth density < 52 teeth/mm.	
•	Distribution: Extant species distributed in mountains of central and northern California.	17
17a.		
•	Pronotum not strongly constricted on prozona, ratio of metazona width to prozona constriction width 2.0–2.1 (Fig. 7.17a). Calling song with alternating MPT and OPT, PTR 1.9–2.4 s ⁻¹ (Plate 5H), PTdc above 50% (52–72%).	
•	Distribution: southern Sierra Nevada and Tehachapi Mountains.	<i>prorocantans</i> sp. n.
17b.		
•	Prozona strongly constricted, ratio of metazona width to prozona constriction width 2.4–2.6 (Fig. 7.17b). Calling song also with alternating MPT and OPT but PTR rapid, > 4.5 s ⁻¹ at 25°C (Plate 5J), PTdc < 40%.	
•	Distribution: vicinity of Sequoia National Park, Sierra Nevada, California	<i>duplocantans</i> sp. n.
18a.		
•	Stridulatory file tooth density 55–62 teeth/mm	19
18b.		
•	Stridulatory file tooth density > 62 teeth/mm.	20
19a.		
•	Robust, pronotum 10.3–11.5 mm long. Prozona weakly constricted, ratio of metazona width to prozona constriction width 2–2.2. Stridulatory file tooth density 59–62 teeth/mm. Calling song with multiple OPT between MPT producing a fluttering sound, PTR 1.2 s ⁻¹ at 25°C (Plate 5F).	

- Distribution: east slope of the North Coast Ranges bordering the Sacramento Valley, California *arborea* **sp. n.**
- 19b.
- Fusiform, pronotum ≤ 10 mm in length. Pronotum constriction variable. Stridulatory file tooth density 55–59 teeth/mm. Song with alternating MPT and OPT at PTR 2–4 s⁻¹ at 25°C (Plate 5I).
- Distribution: vicinity of Sequoia National Park in the Southern Sierra Nevada, California *sequoia* **sp. n.**
- 20a.
- Prozona weakly constricted, ratio of metazona width to prozona constriction width 2.0–2.2. Calling song with multiple OPT between MPT, PTR 1.4–2.0 s⁻¹ at 25°C (Plate 5D).
- Distribution: vicinity of Yosemite National Park, California *sierranus*
- 20b.
- Pronotum strongly constricted, ratio of metazona width to prozona constriction width 2.3–2.6. Song variable 21
- 21a.
- Stridulatory file tooth density 68–73 teeth/mm. Song with high number of OPT between MPT imparting a rasping sound, PTN > 15, PTR 0.7–1.1 s⁻¹ at 25°C (Plate 5E).
- Distribution: west slopes of the Sierra Nevada bordering the Sacramento Valley. *radocantans* **sp. n.**
- 21b.
- Stridulatory file tooth density 64–68 teeth/mm. Song with lower number of OPT, PTN < 12, PTR faster at 1.0–2.6 s⁻¹. (Plate 5G).
- Distribution: central Sierra Nevada of California *inversa* **sp. n.**
- 22a.
- Ovipositor short, 8–10 mm in length. Subgenital plate length subequal to width, apex broadly rounded *prorocantans* **sp. n.**
- Ovipositor length > 12 mm. 23
- 23a.
- Large body size: pronotum length ≥ 9.5 mm 24
- 23b.
- Small body size: pronotum length ≤ 9 mm 25
- 24a.
- Robust, pronotum length ≥ 10 mm. Subgenital plate round, highly convex (Fig. 7.24a).
- Distribution: east slope of the North Coast Ranges bordering the Sacramento Valley, California *arborea* **sp. n.**
- 24b.
- Fusiform, pronotum length 9.5–10 mm. Subgenital plate wider than long, apex broadly rounded (Fig. 7.24b).
- Distribution: vicinity of Sequoia National Park in the Southern Sierra Nevada, California *sequoia* **sp. n.**
- 25a.
- Hind femora long, > 23 mm in length. Ovipositor length > 15 mm. Subgenital plate wider than long, apex broadly rounded.
- Distribution: central Sierra Nevada of California *inversa* **sp. n.**
- 25b.
- Hind femur length < 23 mm, or if > 23 mm then ovipositor < 15 mm 26
- 26a.
- Hind femur short, < 21 mm in length. Subgenital plate length subequal to width (Fig. 7.26a).
- Distribution: west slopes of the Sierra Nevada bordering the Sacramento Valley. *radocantans* **sp. n.**
- 26b.
- Hind femur > 21 mm in length. Subgenital plate distinctly longer than wide or wider than long. 27
- 27a.
- Subgenital plate longer than wide, convex (Fig. 7.27a).
- Distribution: vicinity of Yosemite National Park, Sierra Nevada, California. *sierranus*
- 27b.
- Subgenital plate wider than long, apex broadly rounded (Fig. 7.27b).
- Distribution: vicinity of Sequoia National Park, Sierra Nevada, California *duplocantans* **sp. n.**

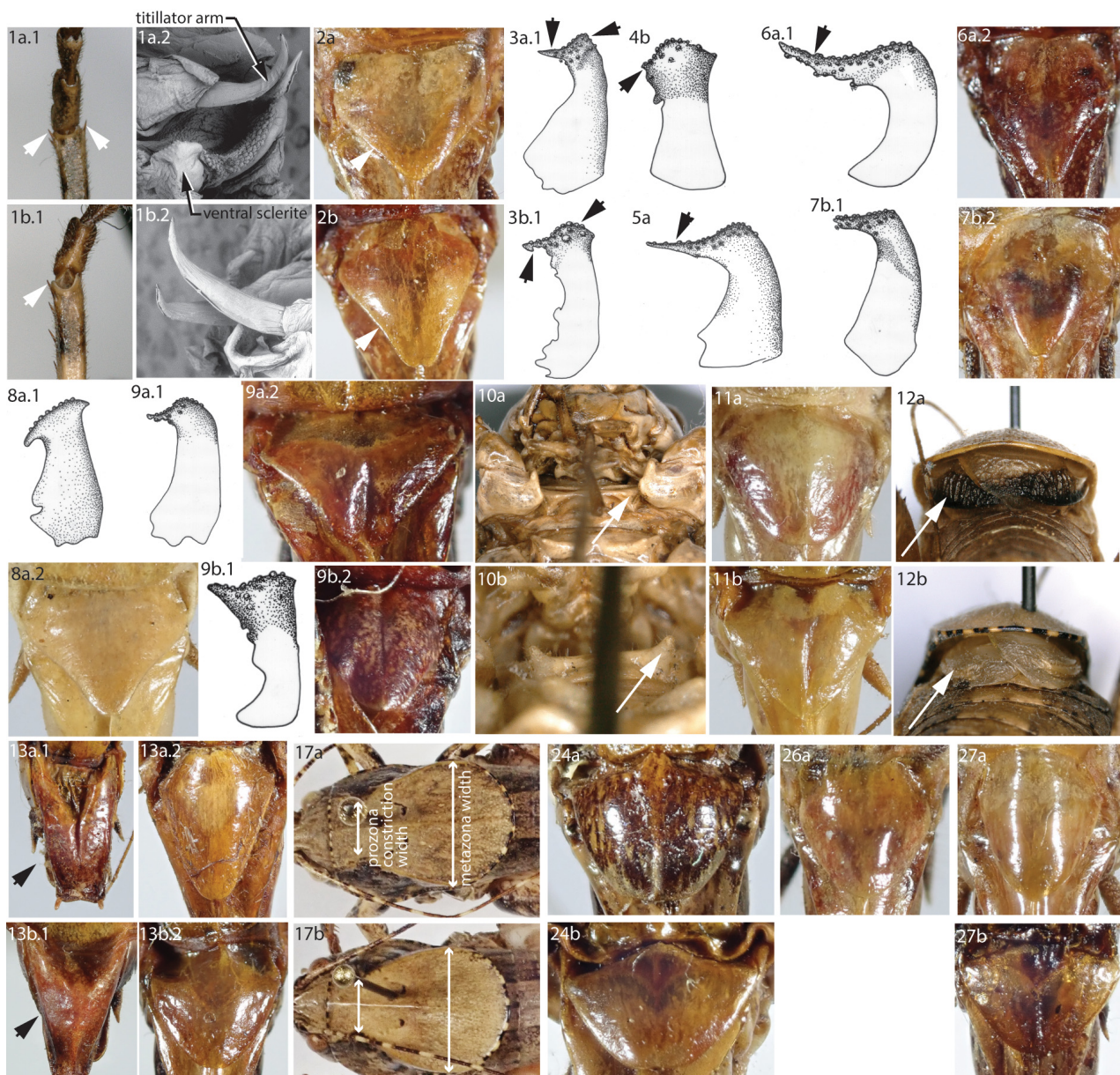


FIGURE 7. Diagnostic characters in *Neduba*. Figure component numbers correspond to couplets in the key.

Carinata Group

Carinata Group lineages are closely related genetically (Figs. 3–5), and we treat those lineages that are morphologically and/or bioacoustically diagnosable as species. The Carinata Group is diagnosed morphologically in both sexes by having a spine on both the anterior and posterior margins at the apex of the fore tibiae (see Key above, couplet 1; Fig. 7.1a.1). Male internal genitalia consist of short, evenly curved titillators (Fig. 7.1a.2, Plate 9) and strip-like ventral sclerites (Plates 6–7) that are often species-specific. Female subgenital plates are triangular to pentagonal and may also be species specific (Plate 11). The generic description (above) applies generally to the species of this Group.

Three male song types exist in this Group (Plate 4A–I). The $2n\♂ = 26$ ($2m + 22t + XtYt$) karyotype is invariable (Figs. 10–18). This group ranges farther north than other Species Groups, extending from the Coast Ranges and northern Sierra Nevada of California throughout the boreal forests of northwestern North America to British Columbia, Canada (Figs. 8–9).

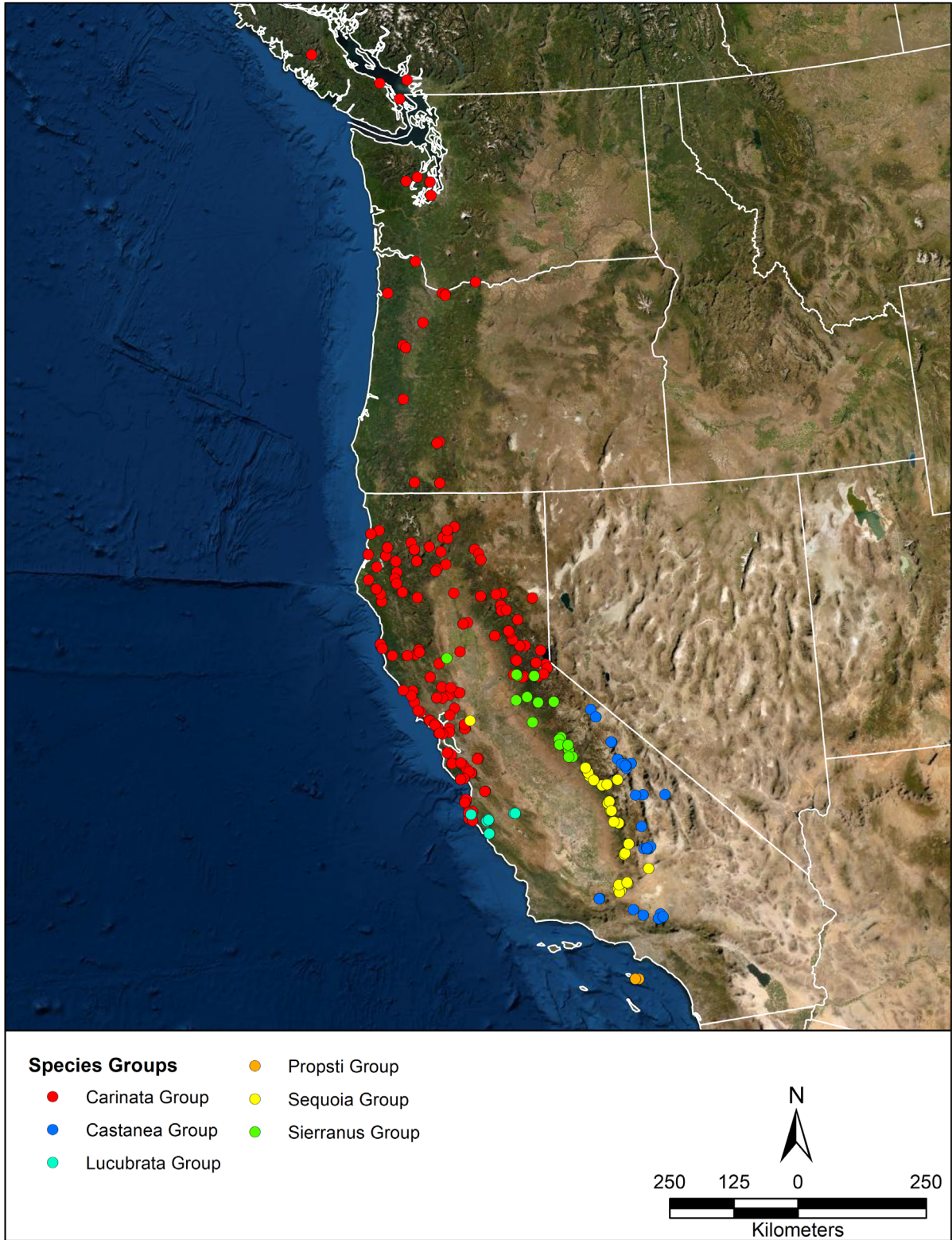


FIGURE 8. Distribution of *Neduba* species groups generated from records in this work.

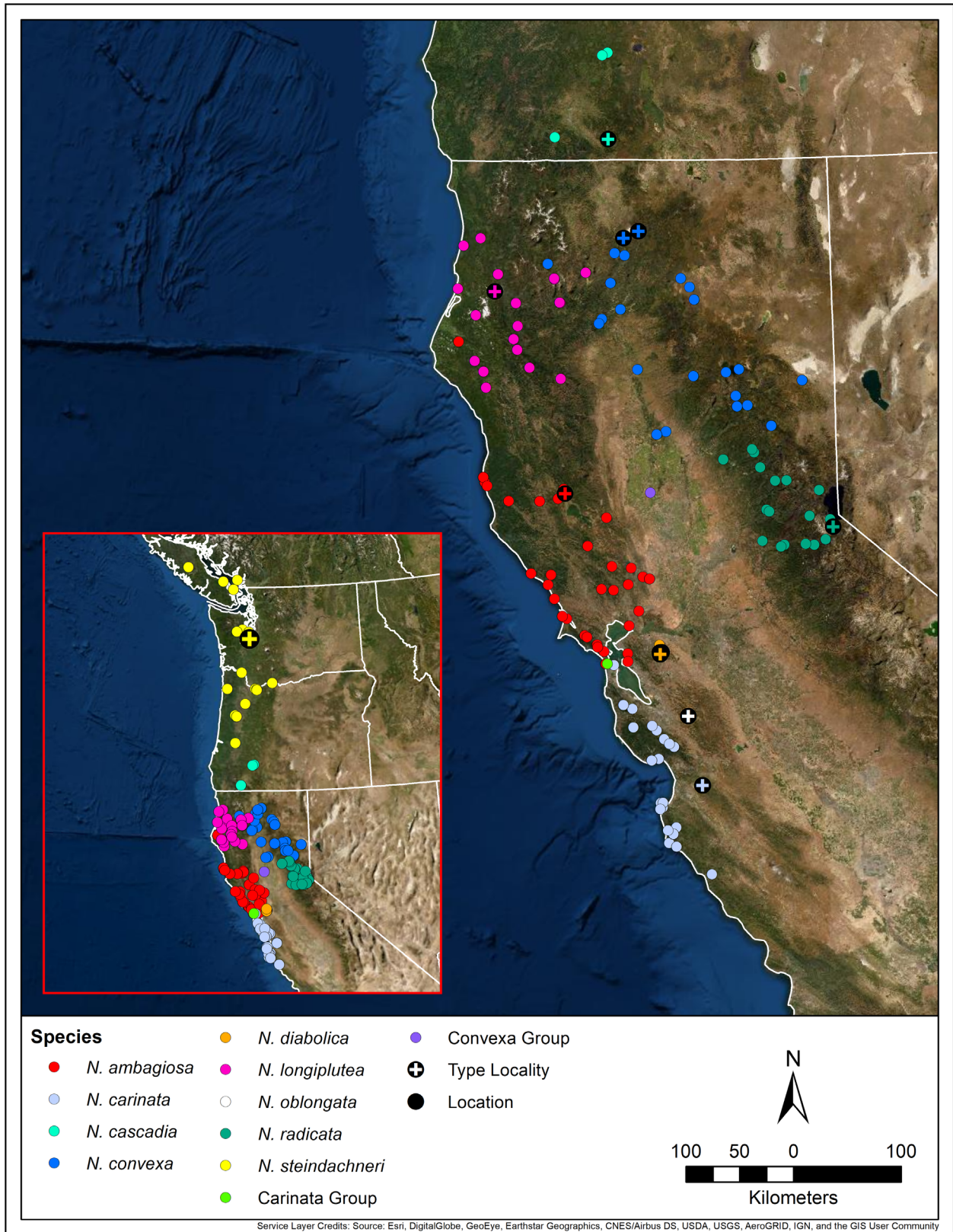


FIGURE 9. Distribution of Carinata Group species showing records in this work.

Neduba carinata Walker, 1869

Figure 9 (distribution), Fig. 10 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 1A (live habitus), Plate 4A (male calling song), Plate 6A–D (ventral sclerites), Plate 9A–C (male titillators), Plate 11A (female subgenital plate).

Common name. Carinate Shieldback.

History of recognition. As the type species of *Neduba*, establishing the identity of *N. carinata* is of central taxonomic importance. In a situation resembling that of *Gryllus assimilis* (Rehn & Hebard 1915), *N. carinata* was at times used as a “trash can” taxon (Rentz & Birchim 1968), into which multiple species were binned (e.g. Tinkham 1944). The broad type locality of “California” was narrowed to Fremont Peak, San Benito County, California, USA (Rentz & Birchim 1968). We accepted this type locality designation and determined taxonomic and geographic relationships relative to this locality. The Fremont Peak type locality is in the Gabilan Range of the South Coast Ranges of California. In over 40 years of fieldwork by orthopterists at Fremont Peak (e.g. Helfer 1987; Rentz & Birchim 1968; Strohecker *et al.* 1968), sympatric *Neduba* species have not been found at this locality; however, the correct assignment of the name *N. carinata* requires that all other possibilities are eliminated. This is a valid concern considering that an additional *Neduba* species occurs in the South Coast Ranges (see *N. lucubrata*). Images of the *N. carinata* holotype show a subgenital plate with parallel lateral carinae and long, articulate styli (Cigliano *et al.* 2020), a condition that is found in all topotypic males that we have examined. In contrast, the subgenital plate of *N. lucubrata* has lateral carinae that converge to the apex and terminate in rudimentary knob-like styli. Thus, we conclude that the name *N. carinata* indeed belongs to our topotypic series. Variety *picturata* (Scudder 1899) was synonymized under *N. diabolica* (Rentz & Birchim 1968).

Type material. F. Walker’s male holotype of *N. carinata* resides in the British Museum. Type not examined by us but images available at OSFO (Cigliano *et al.* 2020). TOPOTYPES EXAMINED (n = 25): **USA, CA, San Benito Co.**, 2♂, Fremont Peak State Park, peak area, 36.760793N, 121.502442W, 457 m, 25-VI-1982, DB Weissman, CAS; 6♂, 1♀, same data except 762 m, 25-VI-1982, DB Weissman, CAS; 14♂, 1♀, Fremont Peak State Park, Valley View Campground, 11 mi. S of San Juan Bautista on County Road G1, 36.7597N, 121.505W, 829 m, 18–19-VII-2005, JA Cole, JF Eguizabal, LACM; 1♂, same data except JAC.

Measurements. (mm, ♂n = 34, ♀n = 7) Hind femur ♂18.33–28.80, ♀21.55–26.21, pronotum total length ♂8.23–10.72, ♀8.35–10.05, prozona length ♂3.43–4.88, ♀4.02–5.20, metazona dorsal length ♂4.45–6.45, ♀3.67–4.85, pronotum constriction width ♂2.00–2.78, ♀2.35–3.00, metazona dorsal width ♂5.11–7.25, ♀5.18–6.45, head width ♂3.89–4.84, ♀4.60–5.32, ovipositor length ♀16.00–18.27.

Distribution. South Coast Ranges of California, from the southern San Francisco Bay Area south along the Santa Lucia Range to Morro Bay.

Habitat. Understory vegetation, tangles, and leaf litter in mixed woodland, riparian woodland, and coastal redwood (*Sequoia sempervirens* (Lamb. ex D. Don) Endl.) forest. Males call near the forest floor from plants such as poison oak (*Toxicodendron diversilobum* (Torr. & A. Gray)), introduced Mediterranean grasses, and peavines (*Lathyrus* sp.).

Seasonal occurrence. Adults from late June (23-VI-1957, TJ Cohn, CAS) through December (18-XII-2016, DW Weissman, CAS). Nymphs collected in May and alongside adults in late June (CAS).

Stridulatory file. (n = 24) length 2.4–3.4 mm, 115–159 teeth, tooth density 44.7 ± 3.9 (38.5–55.3) teeth/mm.

Song. (n = 52) Frequent sustained bouts of low frequency lisping. Males call incessantly at night and sometimes during the afternoon. PTR 10.9 ± 2.1 s⁻¹. The MPT and OPT are subequal in length. Males spend a lot of time singing with PTdc $73.1 \pm 9.7\%$ (calculated by combining both MPT and OPT). PTF 11.4 ± 1.7 kHz is among the lowest carrier frequencies in the genus.

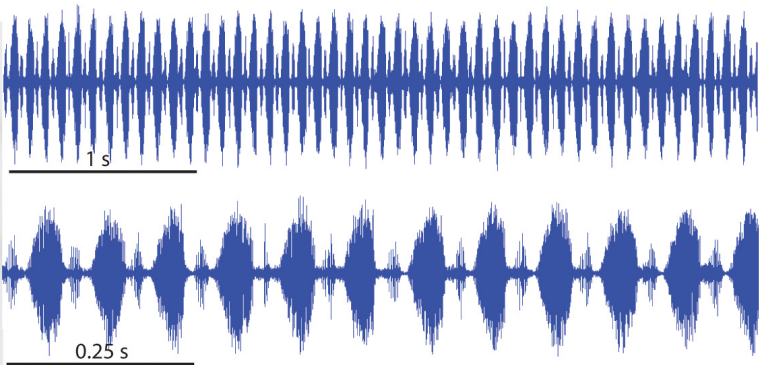
Karyotype. (n = 22) $2n♂ = 26$ (2m + 22t + XtYt). T82-6, S82-26, topotype.

Recognition. This species is separated morphologically from all other species in the Carinata Group except *N. diabolica* by the high stridulatory file tooth density (38–55 teeth/mm). The male ventral sclerite throughout most of the range has the shaft broad and straight (narrow, curved shaft in Convexa Clade), the apex broad and convex to subconical covered with tubercles of large size, and a short lateral process (often long and shelf-like in the Convexa Clade). In *N. carinata* populations found near the Convexa Clade in the South Bay Area, the ventral sclerite of the former species resembles the latter and is an unreliable diagnostic feature; songs remain diagnostic. Acoustically, the low frequency, rasping or lisping bouts of song with a fast uniform PTR (~11 s⁻¹) separate this species from all

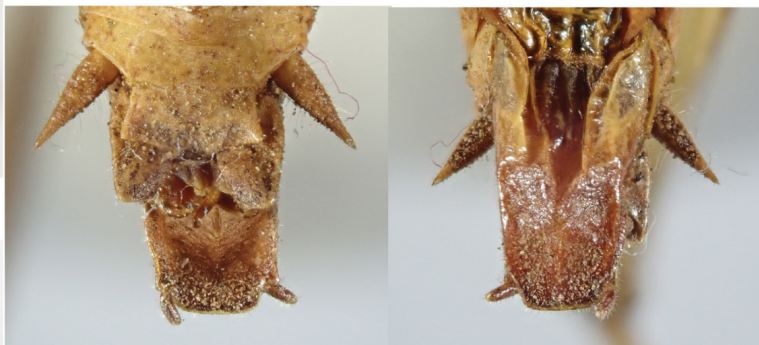
male TOPOTYPE CA: San Benito Co.
S82-25 R82-56



calling song TOPOTYPE CA: San Benito Co. 23.5°C JCR050718_00



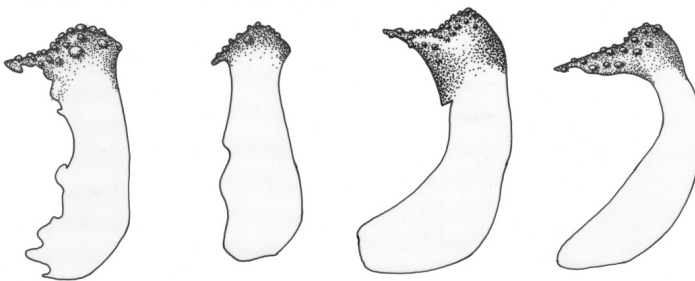
male terminalia TOPOTYPE CA: San Benito Co. JAC000001966



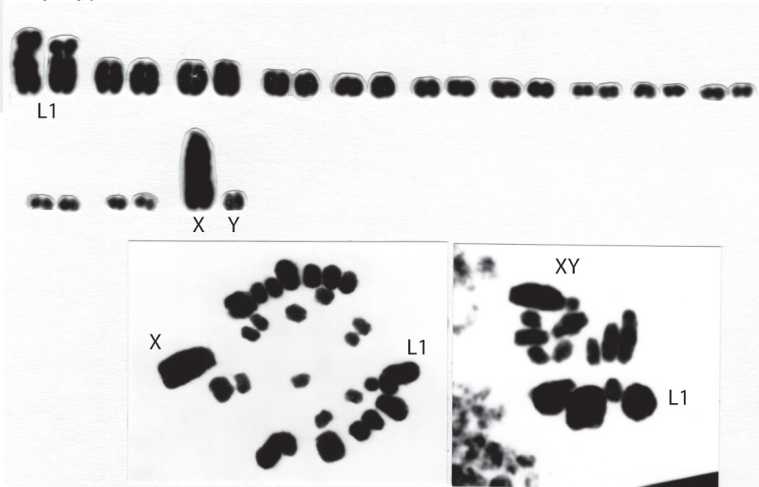
female CA: Santa Cruz Co. JAC000001984



ventral sclerites	CA:	CA: Santa	CA:
TOPOTYPE	Monterey Co.	Clara Co.	Santa Cruz Co.
S82-25 R82-71	S86-74, R86-146	S87-78, R87-82	S82-29, R82-99



karyotype TOPOTYPE CA: San Benito Co. S82-26 T82-6



female terminalia CA: Monterey Co.
JAC000001991

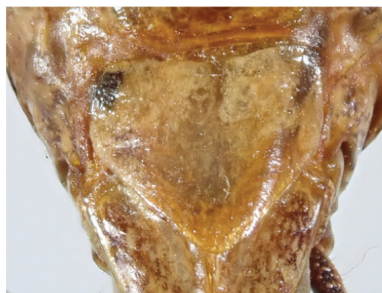


FIGURE 10. *N. carinata* male and female habitus, calling song, male and female terminalia, karyotype.

other *Neduba* except *N. diabolica*. Females have a pentagonal subgenital plate without sinuous distal margins and no medial groove, characters shared only with *N. oblongata*.

Notes. This is a common species in California Coast Range woodlands throughout summer and fall. The proximity of the range to the heavily populated San Francisco Bay Area and the low frequency calling song that many people can hear makes this one of the most commonly encountered species. Considerable variation exists in the male internal genitalia, which we attribute to historical episodes of population isolation and contact as the California coastline and Coast Ranges changed repeatedly and dramatically over the Cenozoic Era. The Santa Lucia Range and portions of the Santa Cruz Mountains have changed between islands, peninsulas, and broad mainland connections (Bartow 1991). A distinct ventral sclerite shape is found in the Santa Lucia Range (Fig. 10, Plate 6B), which may reflect separation from the Coast Ranges north of Monterey Bay by a marine embayment that lasted from 18 to 2 Ma (Hall 2002). Santa Cruz Mountains *N. carinata* have ventral sclerites with long lateral processes (Fig. 10, Plate 6D) that resemble those of several Convexa Clade taxa (Plates 6–7). The Carinata and Convexa Clades meet geographically in the San Francisco Bay Area, where mtDNA introgression (Fig. 4) suggests gene flow as the explanation for shared ventral sclerite morphology despite distinct calling song differences.

Material examined (n = 116). All USA, CA, Monterey Co., 1♂, 1.5 mi. N of Carmel, 36.58N, 121.92W, 213 m, 23-VI-1957, TJ Cohn, CAS; 1♂, 1♀, 11.2 mi. N Pfeiffer Big Sur State Park off Hwy 1, 36.411288N, 121.782732W, 5-VII-1986, DB & BI Weissman, CAS; 1♀, Asilomar, 1.3 mi. W of Pacific Grove, 36.617735N, 121.94011W, 10-VII-1957, TJ Cohn, CAS; 1♀ nymph, Big Sur River Trail, 36.280942N, 121.860028W, 21–23-V-1971, FS Bartholomew, CAS; 6♂, 1♀, Big Sur, SR1, 36.3547N, 121.8136W, 685 m, 20-VIII-2012, JA Cole, LACM; 2♂, Bottcher's Gap, Los Padres National Forest, 19 miles north of Big Sur off SR1 on Palo Colorado Road, 36.355N, 121.8138W, 652 m, 20-VIII-2012, JA Cole, LACM; 2♂, same data except 7-IX-2002, JA Cole, LACM; 1♂, 1♀, same data except JAC; 1♂, Nacimiento-Ferguson Rd., at bridge of Nacimiento R., 8.4 mi. E of SR1, 36.0135N, 121.4216W, 587 m, 19–20-VIII-2012, JA Cole, JAC sound record; 2♂, 1♀, Pacific Grove, 36.617738N, 121.916622W, 4-VII-1925, HH Keifer, CAS; 1♂, Palo Colorado Rd., 3 mi. E of SR1, 36.3864N, 121.8687W, 327 m, 20-VIII-2012, JA Cole, JAC sound record; 1♂ nymph, Pebble Beach, 36.56635N, 121.946622W, 18-V-1969, RP Allen, CSCA; 1♀ nymph, same data except 27-V-1921, EC VanDyke, CAS; 1♂, Pfeiffer Big Sur State Park, 36.248852N, 121.782732W, 60 m, 23-IX-1995, DB Weissman, CAS; 3♂, same data except 27-IX-1985, DB Weissman, CAS; 4♂, 3♀, same data except 5-VII-1986, DB & BI Weissman, CAS; **San Benito Co.**, see Type material above; **San Francisco Co.**, 1♂, San Francisco, 37.77493N, 122.419416W, 24-X-1909, FX Williams, CAS; **San Mateo Co.**, 2♂, Jasper Ridge, 37.407995N, 122.22691W, 12-VII-1982, DB Weissman, CAS; 1♂, Kings Mount, 37.44083N, 122.32333W, 14-X-1946, ES Ross, CAS; 1♂, 1♀, same data except 17-VIII-1946, ES Ross, CAS; 1♂, Portola State Park, 37.2527N, 122.21854W, 8-VIII-1962, RP Allen, CSCA; **Santa Clara Co.**, 1♀, Los Gatos, 12-XII-1965, J Harville, CAS; 2♂, Los Gatos, 15431 Francis Oaks Way, 37.22661N, 121.97468W, 22-VIII-2013, DB Weissman, CAS; 1♂, same data except VI-1986, DB Weissman, CAS; 7♂, 2♀, Los Gatos, Francis Oaks Way, 37.226611N, 121.97468W, 120 m, 6-VII-1987, DB Weissman, CAS; 2♂, Uvas Canyon County Park, 15 miles west of Morgan Hill on Croy Road, 37.0855N, 121.7954W, 349 m, 19-20-VII-2005, JA Cole, JF Eguizabal, JAC; 6♂, 1♀, same data except LACM; 1♂, 2♀, same data except 2-3-VII-2003, JA Cole, LACM; 2♂, 2♀, same data except 22-VIII-2014, DB & DW Weissman, CAS; 1♂, same data except 6-IX-2002, JA Cole, JAC; 2♂, same data except LACM; 1♂, Mount Umunhum, 37.15255N, 121.89897W, 1008 m, 5-VII-2018, DW & DB Weissman, CAS; **Santa Cruz Co.**, 1♀, Loma Prieta, 37.110781N, 121.844676W, 2-VIII-1959, CAS; 1♀, Santa Cruz, 36.974117N, 122.030796W, 25-XI-1955, RL Lewis, CSCA; 1♂, Soquel, 36.98801N, 121.95663W, 18-XII-2016, DW Weissman, CAS; 4♂, same data except 9-IX-2014, DW Weissman, CAS; 1♂, Summit above Saratoga, 37.263832N, 122.023015W, 26-VIII-1968, J Smith, BMED; 6♂, 1♀, U.C. Santa Cruz Campus, 36.974117N, 122.030796W, 25-VI-1982, SI Weissman, CAS.

Neduba oblongata Cole, Weissman, & Lightfoot sp. n.

Fig. 9. (distribution), Fig. 11 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 4B (male calling song), Plate 6E (ventral sclerite), Plate 11B (female subgenital plate).

Common name. Mount Hamilton Shieldback.

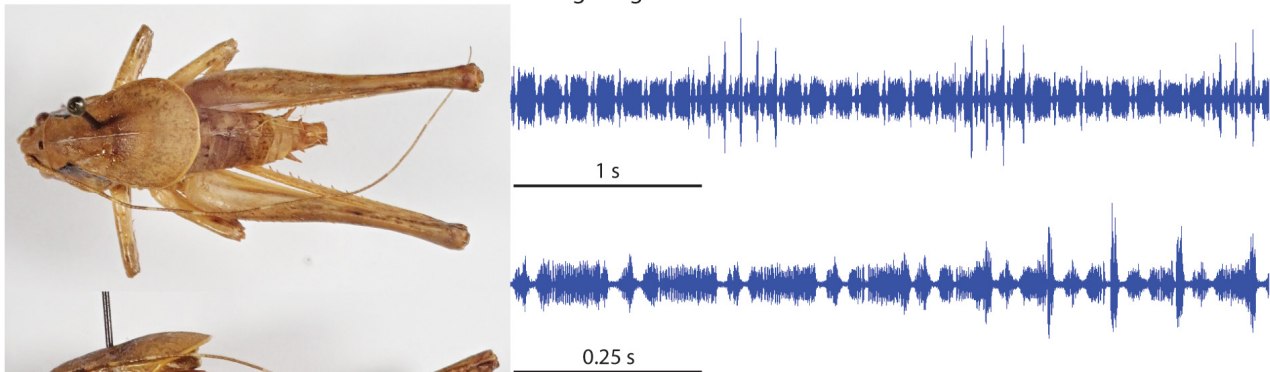
History of recognition. None.

Type material. HOLOTYPE MALE: USA, CA, Santa Clara Co., Mount Hamilton, 2.6 road mi. W observatory, 37.341883N, 121.643002W, 1036 m, 12-VI-1982, DB Weissman, S82-23 [stop], R82-47 [recording], T82-2 [karyotype], 127 [teeth] 3.5 [mm stridulatory file length], deposited at CAS, Entomology type #19713.

PARATYPES (n=10): USA, CA, Santa Clara Co., 1♂, Mount Hamilton, 0.3 mi. W observatory, 37.341883N, 121.643002W, 1260 m, 6-VII-1997, DB Weissman, CAS; 3♂, Mount Hamilton, 15 mi. W observatory, 37.341883N, 121.643002W, 488 m, 12-VI-1982, DB Weissman, CAS; 3♂, 1♀, Mount Hamilton, 2.6 mi. W observatory, 37.341883N, 121.643002W, 1036 m, 12-VI-1982, DB Weissman, CAS; 2♂, Mount Hamilton, 6.5 mi. W observatory, 37.32864N, 121.65729W, 686 m, 8-VIII-2015, DB & DW Weissman, LACM

Measurements. (mm, ♂n = 8, ♀n = 1) Hind femur ♂18.44–20.61, ♀22.01, pronotum total length ♂8.65–11.01, ♀9.66, prozona length ♂3.65–5.21, ♀4.95, metazona dorsal length ♂4.80–6.27, ♀4.71, pronotum constriction width ♂2.50–3.14, ♀3.55, metazona dorsal width ♂6.00–7.39, ♀6.43, head width ♂4.26–4.85, ♀5.18, ovipositor length ♀18.58.

male HOLOTYPE CA: Santa Clara Co. S82-23 calling song PARATOPOTYPE CA: Santa Clara Co. 26.0°C R82-55



male terminalia PARATOPOTYPE CA: Santa Clara Co. JAC000002252



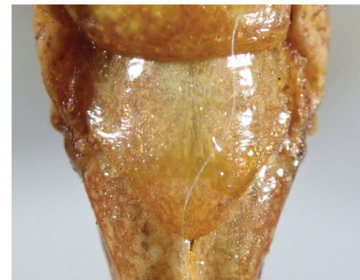
female PARATOPOTYPE CA: Santa Clara Co. S82-23



ventral sclerite HOLOTYPE



female terminalia PARATOPOTYPE JAC000002253



karyotype PARATOPOTYPE CA: Santa Clara Co. S82-23 T82-2

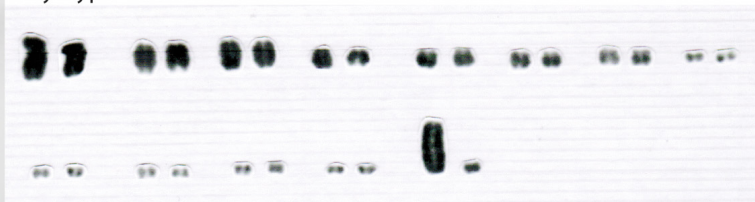


FIGURE 11. *N. oblongata* male and female habitus, calling song, male and female terminalia, karyotype.

Distribution. Known only from Mount Hamilton in the Diablo Range, Santa Clara County, California.

Habitat. Oak woodland and chaparral.

Seasonal occurrence. Available records indicate adult activity extends throughout the summer from mid-June (12-VI-1982, DB Weissman, CAS) through mid-August (8-VIII-2015, DB & DW Weissman, CAS).

Stridulatory file. (n = 4) length 2.8–3.5 mm, 114–134 teeth, tooth density 39.1 ± 2.3 (36.3–41.3) teeth/mm.

Song. (n = 9) Unique. PTR is bimodal and switches between a slow rate $7.45 \pm 0.59 \text{ s}^{-1}$ and a fast rate of $11.2 \pm 1.28 \text{ s}^{-1}$.

Karyotype. (n = 4) $2n_{\text{♂}} = 26$ (2m + 22t + XtYt), S82-23, T82-2, paratopotype.

Recognition. Stridulatory file, male genitalia, song, and geography. A low stridulatory file tooth density separates this species (36–41 teeth/mm) from *N. carinata*, which has a significantly higher density (38–55 teeth/mm; two-sample *t*-test, $P = 0.007$). The ventral sclerite is robust with a straight shaft, low convex apex, and a minute lateral process. Other Carinata Group species have a longer lateral process, and the shaft of Convexa Clade species is curved. Santa Lucia Mountains *N. carinata* males may have a minute lateral process but the whole sclerite is not as robust as in *N. oblongata*. The ventral sclerite of *N. diabolica*, which inhabits the same mountain range, has a more conical apex, a longer lateral process, and a curved shaft. The calling song is unique among Carinata Group species in having a bimodal PTR. The female subgenital plate is pentagonal and flat, identical to *N. carinata*, both of which are separated from *N. diabolica* by the lack of a medial groove. This species is geographically restricted to the Mount Hamilton vicinity in the Diablo Range of California.

Etymology. *l. oblongata* oblong, referring to the fusiform habitus and enlarged, oval pronotum.

Notes. The two highest peaks in the Diablo Range, Mount Hamilton (1284 m) and Mount Diablo (1173 m) are mountain habitat islands separated by a mere 67 km, yet each harbors a distinct Carinata Group species (see *N. diabolica* below). This contrasts with a single (albeit variable) species, *N. carinata*, distributed across 200 km of the South Coast Ranges. The Santa Clara Valley is thus implicated as an isolating barrier between the Diablo Range and the Coast Ranges, while the Vallecitos Valley is a potential biogeographic break between populations in the north and south of the Diablo Range. The bimodal PTR in the male calling song is reminiscent of the songs of Sierranus Group species (see below). Given the evolutionary distance between the Carinata Group and the Sierranus Group (Figs. 3–5), the mostly likely explanation for shared bimodal PTR is convergent evolution. A preexisting receiver response may exist in *Neduba* females (e.g. Basolo 1996; Ryan & Rand 1999) that selects for male songs with an elaborate pattern or additional OPT.

Material examined. Type series only. See Type material above.

Neduba ambagiosa Cole, Weissman, & Lightfoot sp. n.

Fig. 9 (distribution), Fig. 12 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 1B–C (live habitus), Plate 4C (male calling song), Plate 6I (male ventral sclerite), Plate 6G–H (male ventral sclerites, *ambagiosa* x *carinata* hybrids), Plate 9D (male titillators), Plate 11C (female subgenital plate).

Common name. Ambiguous Shieldback.

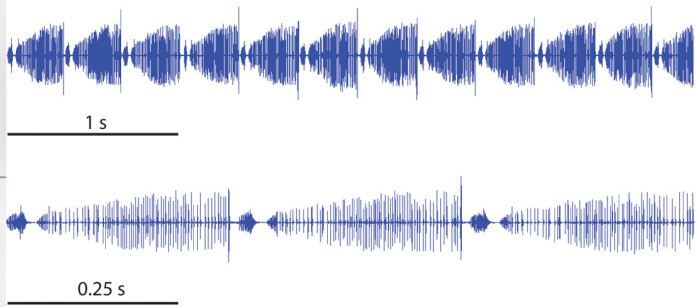
History of recognition. Individuals of this species were encompassed in the type series of *N. convexa* (Caudell 1907).

Type material. HOLOTYPE MALE: USA, CA, Lake Co., Middle Creek, 2.7 mi. S of Middle Creek Campground on Elk Mountain Road, 39.21569N, 122.93381W, 430 m, 6-VIII-2014, JA Cole, DB Weissman, JAC000001944 [specimen barcode], S14-64 [stop], JCR140918_00 [recording], 110T [teeth] 3.4 [mm stridulatory file length], genitalia extracted and cleared in vial and excised tegmen in gelcap below specimen, deposited at CAS, Entomology type #19706.

PARATYPES (n = 27): USA, CA, Lake Co., 6♂, 3♀, Middle Creek Campground, 7 miles northwest of Upper Lake on Elk Mountain Road, 39.2537N, 122.9502W, 610 m, 3-6-VII-2003, JA Cole, LACM; 1♂, 1♀, same data except JAC; 5♂, 4♀, Middle Creek, 2.7 miles south of Middle Creek Campground on Elk Mountain Road, 39.21569N, 122.93381W, 430 m, 6-VIII-2014, JA Cole, DB Weissman, LACM; Mendocino Co., 4♂, 3♀, Tranquility, 1 mile south of Caspar, 39.349009N, 123.815849W, 7-VII-1982, JR Helfer, CAS.

Measurements. (mm, ♂n = 16, ♀n = 9) Hind femur ♂17.59–22.4, ♀19.95–22.36, pronotum total length ♂7.82–11.14, ♀6.90–8.84, prozona length ♂3.26–4.91, ♀3.75–5.12, metazona dorsal length ♂4.35–6.23, ♀2.93–3.87,

male HOLOTYPE CA: Lake Co. JAC000001944 calling song PARATOPOTYPE CA: Lake Co. 24.5°C JCR140816_01



male terminalia PARATOPOTYPE CA: Lake Co. JAC000001947



female PARATOPOTYPE CA: Lake Co. JAC000001952



ventral sclerite HOLOTYPE



subgenital plate PARATOPOTYPE CA: Lake Co. JAC000001950



male PARATOPOTYPE CA: Lake Co. JAC000001938



karyotype PARATOPOTYPE CA: Lake Co. S14-64 T14-24 JAC000001949



FIGURE 12. *N. ambagiosa* male and female habitus, calling song, male and female terminalia, and karyotype.

pronotum constriction width ♂1.55–2.93, ♀2.30–3.15, metazona dorsal width ♂5.43–7.00, ♀4.20–6.15, head width ♂3.75–4.80, ♀4.42–5.10, ovipositor length ♀13.43–18.81.

Distribution. North Coast Ranges of California. The type locality is in the vicinity of Clear Lake.

Habitat. Understory of chaparral and mixed conifer forests, riparian corridors, and canyon bottoms. On leaf litter, poison oak, and on tree trunks.

Seasonal occurrence. mid-June (16-VI-1978, DB Weissman, CAS) through November (15-XI-1953 JR Helfer, CAS). Nymphs from December through July.

Stridulatory file. (n = 13) length 2.6–3.9 mm, 94–139 teeth, tooth density 34.2 ± 2.6 (30.8–40.9) teeth/mm.

Song. (n = 11) PTR 2.9 ± 0.3 s⁻¹, identical to topotype *N. convexa*. PTF 13.0 ± 0.9 kHz. Males are nocturnal singers. A genetically identified hybrid population (Fig. 4; see also Notes under *N. carinata*) from Solano County, California has a significantly faster pulse rate of 3.1 ± 0.2 s⁻¹ (ANCOVA, $P = 1.08 \times 10^{-5}$).

Karyotype. (n = 9) $2n\♂ = 26$ (2m + 22t + XtYt). T14-24, S14-64, paratopotype.

Recognition. A low stridulatory file tooth density (30–40) will separate this species from *N. carinata* and *N. diabolica* distributed to the south. The ventral sclerite apex is usually conical to pyramidal, rarely flat, with a short to medium-length lateral process. The length of the lateral process is shorter than most *N. convexa*, a species of the Sierra Nevada, northern Central Valley and Cascade Range, but is longer than that of *N. oblongata* in the Diablo Range. The lateral process is shorter than the shaft, separating this taxon morphologically from *N. longiplutea* distributed farther north in the North Coast Ranges. Curved apical margins and a distinct central groove on the triangular subgenital plate will separate females of this species from *N. carinata*, *N. diabolica*, and *N. oblongata* which are pentagonal with straight apical margins. The subgenital plate of *N. longiplutea* to the north is longer than wide with a bifurcate apex in contrast to the subequal length and width and entire, acute apex of this species. Calling song will separate this species from *N. carinata*, *N. oblongata*, and *N. diabolica* as all are species with similar length MPT and OPT and fast PTR.

Etymology. *l. ambagiosa* circuitous, indirect, roundabout, referring to the distribution being the southwestern extent of a ring of Convexa Clade taxa around the Central Valley (Fig. 8).

Notes. This species has exchanged genes with populations of *N. carinata* (see also Notes section under *N. carinata* species account). In addition to DNA evidence (Fig. 4), males from a population along Putah Creek in Solano County have a high stridulatory file tooth density as in *N. carinata* but sing with *N. convexa* song, albeit with a faster PTR that may be influenced by *N. carinata* alleles. The geography of this hybrid population suggests that other populations from the northern and eastern Bay Area may also have hybrid characteristics. Stridulatory files from north Bay Area populations that we have examined are within the range for this species. Populations in inland locations such as Solano County may experience gene flow that is otherwise prevented across the Coast Ranges by San Francisco Bay. A precopulatory pair was observed (JAC pers. obs.) at the type locality (Fig. 2G, Plate 1B). After phonotaxis the female oriented directly behind the male and palpated the male with her antennae.

Material examined. DETERMINED (n = 51): **All USA, CA, Alameda Co.,** 1♂, Berkeley, Strawberry Canyon, 37.871593N, 122.272747W, 4-VII-1959, RW Thorp, CAS; **Humboldt Co.,** 1♂, Scotia, 40.482357N, 124.100881W, 18-VII-1958, JR Helfer, CAS; **Lake Co.,** in addition to type material (above), 2♂, 1♀, Anderson Springs, 38.775N, 122.69194W, 29-VII-1961, JS Buckett, BMED; 1♀, Anderson Springs, 38.775N, 122.69194W, 7-VIII-1955, JS Buckett, BMED; 1♂, Blue Lakes, 39.17111N, 123.01111W, 414 m, 30-VII-1949, HA Hurt, BMED; 1♂, SR20, mile marker 114, 39.01101N, 122.4908W, 423 m, 5-VIII-2014, JA Cole, DB Weissman, JAC sound record; **Marin Co.,** 1♂, 2.9 km Samuel P Taylor State Park, 38.02583N, 122.72667W, 61 m, 27-IX-1981, VF Lee, CAS; 1♂, Lagunitas, 38.011312N, 122.702208W, 5-VII-2009, EC VanDyke, CAS; 1♂, 1♀, Lake Lagunitas, 37.946869N, 122.594742W, 24-VI-1958, DC Rentz, CAS; 1♂, McClures Beach, 38.187421N, 122.965276W, 15-VII-1960, JS Buckett, BMED; 1♂, same data except CAS; 1♂, same data except 2-X-1960, JS Buckett, BMED; 1♂, same data except 6-VIII-1964, JS Buckett, BMED; 2♂, Tomales Bay State Park, beach area, 38.166667N, 122.916667W, 16-VI-1978, DB Weissman, CAS; **Mendocino Co.,** 5♂, Mendocino, 39.307674N, 123.799459W, 37 m, 1960, ER Tinkham, CAS; 1♀, same data except 10-XI-1959, JR Helfer, CAS; 1♂, same data except, 10-XI-1961, JR Helfer, CAS; 1♂, same data except 15-X-1959, JR Helfer, CAS; 1♀, same data except 15-XI-1953, JR Helfer, CAS; 1♂, 1♀, same data except 20-X-1962, JR Helfer, CAS; 1♀, same data except 22-X-1961, JR Helfer, CAS; 1♀, same data except, 3-X-1958, JR Helfer, CAS; 1♂, same data except 3-XI-1959, JR Helfer, CAS; 1♂, same data except 3-XI-1961, JR Helfer, CAS; 1♂, same data except 30-X-1959, JR Helfer, CAS; 1♀, same data except 5-XII-1958, JR Helfer, CAS; 3♂, Ukiah, 39.15017N, 123.20778W, 196 m, 2014, JN Hogue, CSUN; 1♂, 3♀, Mendocino Co., 20-VII-1923, ER Leach, CAS;

Napa Co., 1♂, end of Atlas Peak Road 10 mi. airline N of Napa, 38.450743N, 122.262753W, 6-VII-1973, JA Sutro, CAS; 1♀, north side Howell Mountain, 2 miles NNE Angwin, 38.602527N, 122.435787W, 396 m, 18-X-1974, HB Leech, CAS; **San Francisco Co.**, 5♂, Lands End, 37.787707N, 122.505528W, 17-X-1909, FX Williams, CAS; **Solano Co.**, 1♀ nymph, Green Valley, 38.227515N, 122.151579W, 34 m, 16-VI-1953, AA Grigarick, BMED; **Sonoma Co.**, 1♂, Bodega Bay, 38.33325N, 123.048057W, 20-VII-1974, LD & MD Anderson, UCR; QUESTIONABLE PLACEMENT (n = 20): **Alameda Co.**, 1♀, Oakland Hills, 37.804372N, 122.270803W, 6-IX-1948, CD MacNeill, CAS; **Marin Co.**, 1♂, McClures Beach, Pt. Reyes Peninsula, 38.187421N, 122.965276W, 2-X-1960, JS Buckett, CAS; 1♀, Mill Valley, 37.89076N, 122.523586W, 2-VIII-1925, EP VanDuzee, CAS; 1♀ nymph, same data except 24-VI-1923, EP VanDuzee, CAS; 1♀ nymph, same data except 25-VI-1925, EP VanDuzee, CAS; 1♀, same data except 26-VII-1926, EP VanDuzee, CAS; 1♀, same data except 27-VI-1925, EP VanDuzee, CAS; 1♀, same data except 5-VII-1925, EP VanDuzee, CAS; 1♀, same data except 7-XI-1925, EP VanDuzee, CAS; 2♂, Mount Tamalpais, NE slope, 37.927425N, 122.591924W, 700 m, R Hunt, BMED; **Mendocino Co.**, 1♀, Navarro, 39.151843N, 123.541956W, 18-XII-1973, DO Clark, CSCA; 1♂, VanDamme State Park, 39.27639N, 123.77333W, 13-X-1979, T Tyler, CSCA; **Napa Co.**, 1♀, Hwy 121, 6 mi. NW of Napa, 38.403064N, 122.4184W, no collector, CSCA; 1♀ nymph, Lake Berryessa, 38.58903N, 122.229496W, 20-V-1961, CD MacNeill, CAS; **Solano Co.**, 1♂, Vallejo, 38.104086N, 122.256637W, 18 m, 6-VIII-1956, D Haug, CSCA; **Sonoma Co.**, 1♂ nymph, Cazadero, 38.533246N, 123.08528W, 36 m, 5-VII-1962, R Bartges, BMED; 1♀, Jenner, 38.449636N, 123.115559W, 17-X-1937, no collector, BMED; 1♀ nymph, Kenwood, 38.4138N, 122.546094W, 126 m, 14-V-1960, TH Gantenbein, BMED; 1♀ nymph, Stillwater Cove, 38.545833N, 123.298611W, 23-V-1954, EI Schlinger, BMED; HYBRIDS WITH *N. CARINATA*: **Napa Co.**, 1♀, Monticello Dam, 38.513394N, 122.104351W, 8-X-1969, F Andrews, CSCA; **Solano Co.**, 3♂, Lake Solano County Park, 5 mi. SW of Winters off SR128, 38.49576N, 122.03399W, 51 m, 30-VII-2016, JA Cole, LACM; 12♂, 3♀, same data except 31-VII-1-VIII-2013, JA Cole, LACM; 7♂, same data except 31-VII-2014, JA Cole, DB Weissman, LACM; 2♂, 1♀, same data except 31-VII-1-VIII-2013, JA Cole, JAC; 1♀, same data except 25-VII-2019, JA Cole, JAC

***Neduba diabolica* (Scudder, 1899)**

Fig. 9 (distribution), Fig. 13 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 4D (male calling song), Plate 6F (male ventral sclerite), Plate 9E (male titillators), Plate 11D (female subgenital plate).

Common name. Mount Diablo Shieldback.

History of recognition. Originally described in *Tropizaspis* from a female taken at “Monte Diablo, California” (Scudder 1899). Rentz & Birchim (1968) assigned the majority of South Coast Range *Neduba* populations to this species and synonymized variety *picturata* (Scudder 1899) under this name. We reassign all other South Coast Range populations to *N. carinata*. The type of *picturata* was collected during the Northwestern Boundary Survey (Caudell 1907), which makes *picturata* a synonym of *N. steindachneri* (see discussion under that species) and not *N. diabolica*.

Type material. The female holotype is housed in ANSP. Type not examined by us but images available at OSFO (Cigliano *et al.* 2020). TOPOTYPES EXAMINED (n = 23): **USA, CA, Contra Costa Co.**, 1♀, Mount Diablo State Park, 37.862703N, 121.93107W, 1021 m, 1-IX-2002, DB Weissman, CAS; 3♂, Mount Diablo State Park, 37.862703N, 121.93107W, 670-1160 m, 30-VI-1990, DB & DD Weissman, CAS; 3♂, Mount Diablo State Park, Fire Interpretive Trail, 37.8807N, 121.9172W, 1131 m, 20-21-VII-2005, JA Cole, JF Eguizabal, LACM; 1♂, Mount Diablo State Park, Juniper Camp, 37.8785N, 121.9339W, 886 m, 27-28-VI-2008, JA Cole, W Chatfield-Taylor, W Ericson, JAC; 1♂, 1♀, same data except LACM; 1♂, Mount Diablo State Park, Juniper Camp, 37.862703N, 121.93107W, 886 m, 28-VIII-1982, DB Weissman, CAS; 1♂, 1♀, Mount Diablo State Park, Lookout Point, 37.862703N, 121.93107W, 7-VI-1967, DC & KA Rentz, CAS; 2♂, Mount Diablo State Park, near North Gate Entrance, 37.862703N, 121.93107W, 229 m, 13-VII-1982, DB Weissman, CAS; 1♂, 2♀, Mount Diablo State Park, summit, 37.862703N, 121.93107W, 1021 m, 11-VIII-1990, DB Weissman & DW Weissman, CAS; 1♂, same data except 13-VII-1982, DB Weissman, CAS; 2♂ nymphs, 1♀ nymph, Russelman Park, Mount Diablo East Slope, 19-IV-1931, EP VanDuzee, CAS; 1♂ nymph, same data except 24-IV-1932, EC VanDyke, CAS.

Measurements. (mm, ♂n = 8, ♀n = 3) Hind femur ♂20.09–22.49, ♀21.80–23.09, pronotum total length ♂9.50–

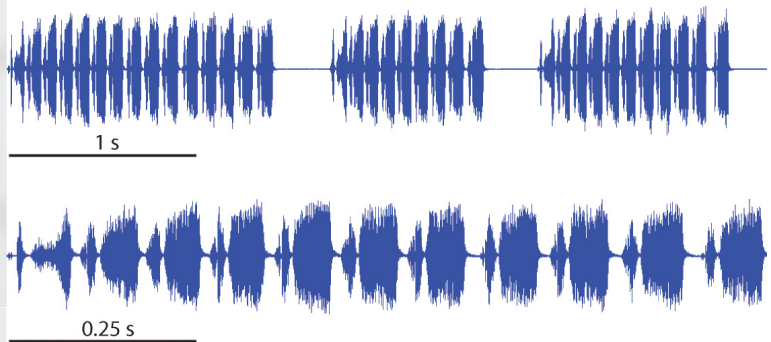
11.02, ♀9.40–9.98, prozona length ♂4.38–4.92, ♀4.81–5.34, metazona dorsal length ♂4.86–6.10, ♀4.59–4.75, pronotum constriction width ♂2.55–3.21, ♀2.55–3.10, metazona dorsal width ♂6.30–6.86, ♀5.89–6.05, head width ♂4.60–5.95, ♀4.95–5.39, ovipositor length ♀16.47–18.04.

Distribution. Known only from Mount Diablo at the north end of the Diablo Range, California. Not known from Mt. Hamilton, also in the Diablo Range, some 67 km southeast of Mt. Diablo where *N. oblongata* occurs. The Vallecitos Valley is a possible biogeographic break between these two species (See *N. oblongata* species account above).

Habitat. Oak woodland and chaparral habitats. Males call from the interior of large bushes, especially in canyon bottoms.

Seasonal occurrence. Adults have been taken from late June (27-VI-2008, JA Cole, W Chatfield-Taylor, W Ericson, LACM) to September (1-IX-2002, DB Weissman, CAS). Nymphs were collected 7-VI-1967 (Rentz & Birchim 1968).

male TOPOTYPE CA: Santa Clara Co. S82-113 calling song TOPOTYPE CA: Santa Clara Co. 25.0°C S90-61 R90-103



male terminalia TOPOTYPE CA: Santa Clara Co. JAC000002133



female TOPOTYPE CA: Santa Clara Co. S02-65



ventral sclerite
TOPOTYPE
S90-61, R90-103



female terminalia TOPOTYPE
JAC000002135



karyotype TOPOTYPE CA: Santa Clara Co. S90-61 T90-12

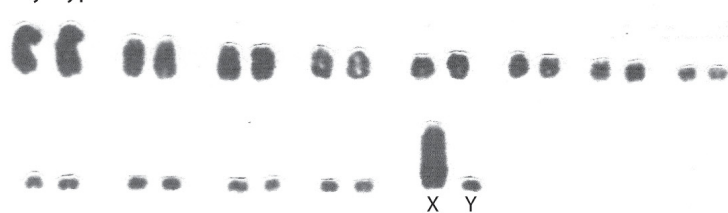


FIGURE 13. *N. diabolica* male and female habitus, calling song, male and female terminalia, karyotype.

Stridulatory file. (n = 4) length 3.0–3.5 mm, 132–145 teeth, tooth density 43.2 ± 4.5 (37.7–48.3) teeth/mm.

Song. (n = 12) The song of *N. diabolica* consists of bouts of uniform rate “lispering” as in *N. carinata*. PTR $10.8 \pm 0.7 \text{ s}^{-1}$ is identical to *N. carinata*. PTF $13.3 \pm 2.3 \text{ kHz}$; a high frequency lab recording measured PTF at 19.2 kHz. PTdc $80.4 \pm 8.0\%$ is significantly higher than that found in *N. carinata* songs (ANOVA, $P = 2.36 \times 10^{-3}$). PTdc is a temperature-invariant song character (linear regression, $P = 0.188$), and thus can be compared among recordings that lack temperature control. Males are nocturnal singers. Bout length is variable, but the bouts of *N. diabolica* males tend to be shorter and more even in length than those of *N. carinata* males.

Karyotype. (n = 4) $2n\text{♂} = 26$ (2m + 22t + XtYt) T90-12, S90-61, topotype. This corrects the information of Ueshima and Rentz (1979).

Recognition. The high stridulatory file tooth density (37–48) is shared only with *N. carinata* in the Carinata Group. The ventral sclerite is narrow with a high convex to pyramidal apex and a poorly developed anterolateral process. In contrast, ventral sclerites of *N. oblongata* have a low convex apex and a minute lateral process. Except for *N. radicata*, all other Convexa Clade taxa have long anterolateral processes. The female subgenital plate is pentagonal and flat as in *N. carinata* and *N. oblongata*, but those two species lack a distinct medial groove, which is present in this species. Songs of *N. diabolica* males are qualitatively similar to those of *N. carinata* but have a higher duty cycle. The distribution is restricted to the vicinity of Mount Diablo, California.

Notes. This species exhibits a mosaic of characters. DNA places *N. diabolica* with the Convexa Clade, the song type and stridulatory file are like those of *N. carinata*, and the genitalia resemble those of *N. radicata*. Mount Diablo has remained above sea level since the early Miocene (Bartow 1991) and lies at the junction of the distributions of the southern Carinata and northern Convexa Clades. The mixture of characters found in *N. diabolica* suggests past introgression. By maintaining its species status, we recognize that *N. diabolica* is a phylogenetically distinct, philopatric lineage that inhabits an ancient region of high endemism and provided it remains protected (Mount Diablo is a California State Park), this lineage may persist into the future with its mixture of characters. The name *picturata* Scudder was originally described to differentiate insects with a mottled color pattern as opposed to uniform or striped coloration. These color pleomorphisms are shared by all species in the Carinata Group.

Material examined. See Type material above.

Neduba longiplutea Cole, Weissman, & Lightfoot, sp. n.

Fig. 9. (distribution), Fig. 14 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 4E (male calling song), Plate 6J (male ventral sclerite), Plate 9F (male titillators), Plate 11E (female subgenital plate).

Common name. Trinity Alps Shieldback.

History of recognition. Apparently confused with *N. convexa*, 1 male and 1 female from CA, Trinity Co., Big Flat, 15-VIII-1960, PH Benson (Rentz & Birchim 1968).

Type material. HOLOTYPE MALE: USA, CA, Humboldt Co., East Fork Campground, 5.2 mi. W of Willow Creek, Six Rivers National Forest, 40.90582N, 123.7068W, 471 m, 6-VIII-2014, JA Cole, DB Weissman, JAC000002182 [specimen barcode], DNA125 [tissue], SING0458 [DNA extraction], JCT14-2 [karyotype], deposited at CAS, Entomology type #19711.

PARATYPES (n = 10): 5♂, 2♀, same data as holotype, LACM; 2♂, same data as holotype, CAS; 1♂, same data as holotype, JAC.

Measurements. (mm, ♂n = 8, ♀n = 2) Hind femur ♂18.35–20.00, ♀21.41–21.61, pronotum total length ♂8.17–9.30, ♀7.60–7.78, prozona length ♂2.92–3.75, ♀3.93–3.96, metazona dorsal length ♂4.73–5.69, ♀3.64–3.85, pronotum constriction width ♂1.96–2.90, ♀2.21–2.51, metazona dorsal width ♂5.90–6.36, ♀5.20–5.40, head width ♂4.08–4.30, ♀4.45–4.81, ovipositor length ♀15.68–16.45.

Distribution. Trinity Alps in the North Coast Ranges of California.

Habitat. Forest understory, on ferns, leaf litter, and occasionally arboreal. Some CSCA specimen labels indicate range grass.

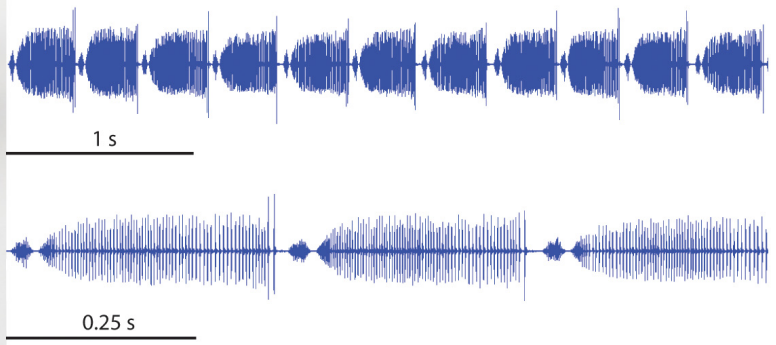
Seasonal occurrence. Midsummer through fall, from July (19-VII-1934, EC VanDyke, CAS) to October (17-X-1995, Spadoni, CSCA). Nymphs from May through July.

Stridulatory file. (n = 4) length 3.4–3.9 mm, 114–125 teeth, tooth density 33.7 ± 3.0 (31.0–36.8) teeth/mm.

male PARATOPOTYPE CA:Trinity Co.
JAC000002187



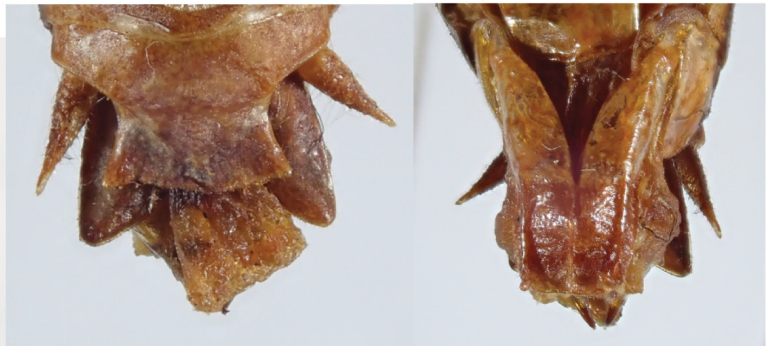
calling song PARATOPOTYPE CA:Trinity Co. 24.4°C JCR140823_02



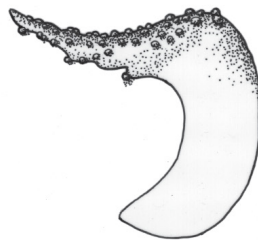
female PARATOPOTYPE CA:Trinity Co.
JAC000002189



male terminalia PARATOPOTYPE CA:Trinity Co. JAC000002187



ventral sclerite
HOLOTYPE



female terminalia PARATOPOTYPE
JAC000002189



male HOLOTYPE CA:Trinity Co. JAC000002182



karyotype PARATOPOTYPE CA:Trinity Co. S14-65 T14-26

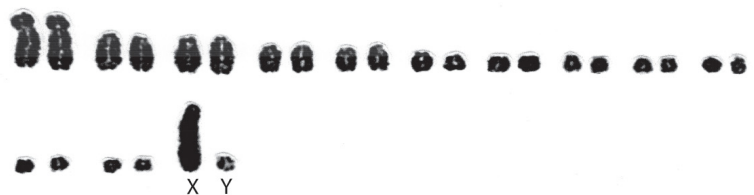


FIGURE 14. *N. longiplutea* male and female habitus, calling song, male and female terminalia, karyotype.

Song. (n = 4). PTR $2.7 \pm 0.3 \text{ s}^{-1}$, PTF $14.4 \pm 2.7 \text{ kHz}$, indistinguishable from topotype *N. convexa*.

Karyotype. (n = 4) $2n\text{♂} = 26 (2m + 22t + XtYt)$. T14-25, S14-65, paratopotype.

Recognition. Male genitalia unique: the lateral process is as long or longer than the short, thick shaft. Female subgenital plate longer than wide and has a bifurcate apex. The subgenital plate of *N. convexa* has similar proportions but the apex is usually entire, rarely bifurcate.

Etymology. *l. longi* long + *plutea* barrier, screen, low wall, parapet. Descriptive of the long lateral process of the male ventral sclerite.

Notes. This species replaces *N. convexa* to the west. Populations may be large and widespread, judging from an 80 km acoustic transect through Humboldt and Trinity Counties, California (JAC and DBW, pers. obs.) and from the number of nymphs in museum collections. The song is identical to that of *N. convexa*. Color patterns are variable and beautifully match the complex background of the forests of the Trinity Alps.

Material examined. DETERMINED (n = 63): **All USA, CA, Humboldt Co.,** 1♀ adult, 1♀ nymph, Bullrun Flat, Garberville, 40.100145N, 123.795029W, 27-VII-1934, EC VanDyke, CAS; 3♂, 1♀, Hoopa, 41.050408N, 123.674224W, 524 m, 19-VIII-1959, Tabor, Graham, Gallian, CSCA; 1♂, Humboldt County State Park, 40.70501N, 123.91582W, 6-VIII-1957, J Keefe, CSCA; 1♂ nymph, Johnsons Bar, 41.350401N, 123.872012W, 16-VII-1964, D Ramsey, CSCA; 1♂, Miranda, 40.234586N, 123.823646W, 19-VII-1934, EP VanDuzee, CAS; 1♀, Orick, 41.28679N, 124.059794W, 10 m, 17-X-1995, Spadoni, CSCA; 1♀ nymph, same data except 4-VII-1931, EC VanDyke, CAS; 1♂, 2♀ nymphs, Weott, 40.321897N, 123.921706W, 12-VII-1929, EC VanDyke, CAS; 1♂, 2♀ nymphs, same data except 13-VII-1929, EC VanDyke, CAS; 4♂, 4♀ nymphs, same data except 15-VII-1929, EC VanDyke, CAS; **Te-hama Co.,** 1♀, N Yollabolly, 40.17556N, 122.98W, 27-IX-1964, D Sale, CSCA; **Trinity Co.,** in addition to type material (above), 1♂, 1♀ nymphs, Burnt Ranch, 40.809027N, 123.474208W, 449 m, 1-VI-1964, G Harmon, CSCA; 1♂ nymph, Carrville, 41.064868N, 122.70419W, 18-V-1934, EC VanDyke, CAS; 1♂ nymph, same data except 25-VI-1931, EC VanDyke, CAS; 1♂, 1♀ nymphs, same data except 26-VI-1913, EC VanDyke, CAS; 2♀ nymphs, Carrville, same data except 27-V-1934, EC VanDyke, CAS; 1♀ nymph, Coffee Creek, 23-VI-1931, EC VanDyke, CAS; 1♀, East Weaver Lake, 40.81389N, 122.98556W, 25-IX-1964, FL Blanc, GM Buxton, CSCA; 1♂, 8♀, Grizzly Lake, 41.010046N, 123.049925W, 2166 m, 10-15-IX-1964, Buxton, Gurney, Forbes, Kamp, Thompson, CSCA; 3♀, Grizzly Meadows, 41.017084N, 123.05198W, 10-15-IX-1964, Buxton, Gurney, Forbes, Kamp, Thompson, CSCA; 1♀, Hyampom, 40.617364N, 123.452536W, 392 m, 27-VII-1962, J Reed, CSCA; 1♀, same data except CAS; 1♂, 4♀, Lamb Gap, South Fork Mountain, 40.507087N, 123.497257W, 19-IX-1962, FL Blanc, CSCA; 1♀, Ruth, 40.269591N, 123.321414W, 829 m, CSCA; 1♂, 1♀, Sids Place Hwy 36, 40.419033N, 123.456698W, 1109 m, 19-IX-1962, FL Blanc, CSCA; 1♂, 4♀, Weaver Bally, 40.815976N, 122.99364W, 2129 m, 9-VIII-1964, Buxton, Gurney, Forbes, Kamp, Thompson, CSCA; QUESTIONABLE PLACEMENT (n = 2): **Humboldt Co.,** 1♀, Mad River Mountains, 40.925112N, 124.115737W, 19-VII-1934, EC VanDyke, CAS; 1♀, same data except no date, EC VanDyke, CAS.

Neduba radicata Cole, Weissman, & Lightfoot, sp. n.

Fig. 9 (distribution), Fig. 15 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 1D (live habitus), Plate 4F (male calling song), Plate 6K (male ventral sclerite), Plate 9G (male titillators), Plate 11F (female subgenital plate).

Common name. Lake Tahoe Shieldback.

History of recognition. Confused with *N. convexa*, specimen from CA: El Dorado Co., Ice House Road, 22-X-1965, D.C. Rentz, 1 male (Rentz & Birchim 1968).

Type material. HOLOTYPE MALE: **USA, CA, El Dorado Co.,** Stanford University Sierra Camp, Fallen Leaf Lake, 38.901076N, 120.061626W, 1940 m, 9-VII-1988, DB Weissman, CAS, S88-60 [stop], R88-75A [recording], T88-8 [karyotype], genitalia extracted and cleared in vial and excised tegmen in gelcap below specimen, deposited in CAS, Entomology type #19679.

PARATYPES (n = 36): **USA, CA, El Dorado Co.,** 8♂, 1♀, China Flat Campground, El Dorado National Forest, 2 mi. SE of Kyburz off US50, 38.7535N, 120.2671W, 1470 m, 20-21-VII-2012, JA Cole, LACM; 1♂, same data except JAC; 4♂, same data except 12-VIII-2002, JA Cole, LACM; 1♂, same data JAC; 2♂, same data except 19-VII-2015, JA Cole, DB Weissman, LACM; 1♂, Emerald Bay State Park, Lake Tahoe, 38.964888N, 120.090884W, 1890

m, 8-VII-2016, DI Weissman, CAS; 1♀ nymph, same data as holotype except 10-VII-1935, FE Blaisdell, CAS; 1♀ nymph, same data as holotype except 20-VII-1936, FE Blaisdell, CAS; 1♀, same data as holotype except 3-VIII-1989, BI Weissman, CAS; 2♂, 2♀, same data as holotype except 9-VII-1988, DB Weissman, CAS; 1♂ nymph, same data as holotype except VII-1915, LS Rosenbaum, CAS; 1♀ nymph, same data as holotype except VII-1931, OH Swezey, CAS; 6♂, 1♀, Loon Lake, 38.997163N, 120.3095W, 1950 m, VIII-1991, BI Weissman, CAS; **Placer Co.**, 1♂, Finning Mill Rd. at Forest Hill Rd., 39.0586N, 120.7696W, 1097 m, 20-VII-2012, JA Cole, JAC; 1♂, Squaw Valley, foot trail by Squaw Creek, 39.21169N, 120.198611W, 1920 m, 1-VIII-1988, VF Lee, CAS.

Measurements. (mm, ♂n = 20, ♀n = 4) Hind femur ♂18.00–20.91, ♀19.05–22.36, pronotum total length ♂8.70–10.16, ♀7.35–8.46, prozona length ♂3.38–4.36, ♀3.80–4.62, metazona dorsal length ♂4.82–6.47, ♀3.32–4.66, pronotum constriction width ♂2.10–2.65, ♀2.55–2.87, metazona dorsal width ♂6.35–7.55, ♀5.28–5.62, head width ♂4.20–4.75, ♀4.50–5.22, ovipositor length ♀12.78–15.54.

Distribution. High elevations in the central and northern Sierra Nevada of California.

Habitat. Mixed conifer woodland. Taken from understory tangles and leaf litter in coniferous forest, under logs, in a small shrub in an open field, and from riverbanks. One male paratype sang from 2.4 m above ground in thicket of branches. He dropped to the ground when approached (JAC pers. obs.).

Seasonal occurrence. Midsummer through fall, from July (1-VII-1950, HL McKenzie, CSCA) through November (17-XI-1967, HR Ingham, CSCA). Nymphs occur from early June through August, thus overlapping broadly with adult activity.

Stridulatory file. (n = 6) length 3.3–3.9 mm, 115–135 teeth, tooth density 35.4 ± 3.4 (30.8–40.9) teeth/mm.

Song. (n = 19) PTR is significantly faster than all other Convexa Clade lineages (ANCOVA, $P = 1.08 \times 10^{-5}$), owing to significantly shorter MPTL of 202.5 ± 53.6 ms (ANCOVA, $P = 4.27 \times 10^{-11}$). MPT often have a characteristic amplitude modulation pattern, with a gradual increase in amplitude followed by an abrupt increase at the middle of the PT (Plate 4F). Males may sing in the late afternoon as well as at night.

Karyotype. (n = 7) $2n♂ = 26$ (2m + 22t + XtYt), T88-8, S88-60, paratype.

Recognition. The male ventral sclerite has straight, thick shaft, the apex rounded with the highest point lateral to the central axis, and the short lateral process directed 45° anterior to plane of shaft. This genital morphology may only be confused with *N. diabolica* and some *N. carinata*, both of which have higher stridulatory file tooth densities and lipping songs and are distributed in the South Coast Ranges. The female subgenital plate is distinct from all other Carinata Group species: wider than long with a strongly bifurcate apex. The song PTR is faster and MPTL shorter than all other Convexa Clade taxa. This species is the only *Neduba* found in high elevation yellow pine forest in the central and northern Sierra Nevada Mountains of California.

Etymology. *l. radicata* having roots, having found a home.

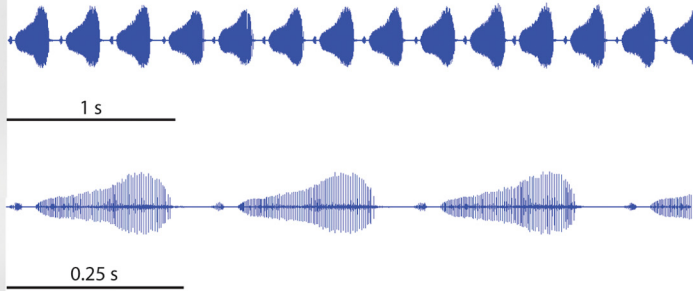
Notes. At China Flat Campground, El Dorado County, California, two males were observed emerging from leaf litter to sing in understory tangles. Acoustical activity commenced before dusk at this locality during overcast conditions after a rainstorm. At the southern extent of the range along Finning Mill Road, males were singing before sunset at 2019 h. This species is sympatric with *N. radocantans* (Sierranus Group) in El Dorado County, California.

Specimens examined. (n = 21) **All USA, CA, El Dorado Co.**, in addition to type material (above), 1♂, Kelsey, 38.798791N, 120.820768W, 24-VII-1939, J Labadie, CSCA; 1♀, Pollock Pines, 38.761292N, 120.586594W, 1207 m, 1-VII-1950, HL McKenzie, CSCA; 1♀ nymph, Snowline Camp, 38.746292N, 120.624373W, 21-VI-1948, CD MacNeill, CAS; 1♂, Strawberry, 38.796852N, 120.145187W, 1768 m, 1-X-1954, ME Gardner, BMED; 1♀, same data except WJ Wall, BMED; 1♀ nymph, same data except 28-VII-1950, ME Gardner, BMED; 1♀ nymph, same data except 3-VIII-1952, WJ Wall, BMED; 1♂ nymph, Strawberry Valley, 38.796582N, 120.145187W, 12-VIII-1912, EC VanDyke, CAS; 1♂ nymph, same data except 5-VIII-1912, EC VanDyke, CAS; 1♂, US50 3.7 mi. W Kyburz, 38.76427N, 120.35897W, 1112 m, 19-VII-2015, JA Cole, DB Weissman, JAC sound record; **Nevada Co.**, 1♂, junction SR20&I-80, 4-X-1972, AM Shapiro, BMED; **Placer Co.**, Cisco, 39.301569N, 120.546874W, VI-1910, C VanGeldern, CAS; 3♂, Emigrant Gap, 39.300456N, 120.668268W, 1567 m, 17-XI-1967, HR Ingham, CSCA; 1♀, Michigan Bluff, 39.042956N, 120.741319W, 1073 m, 11-V-1962, G Buxton, CSCA; **Sierra Co.**, 1♂, 10 mi. S Downieville, 39.41439N, 120.826891W, 28-VII-1962, WJ Turner, CSCA; 1♂, Goodyears Creek, 39.540911N, 120.88824W, 10-VII-1925, EB Nast, CAS; 1♂, St. Charles Hill, 39.56795N, 120.911061W, 7-VII-1925, EB Nast, CAS; **Yuba Co.**, 1♂ nymph, Challenge, 39.487389N, 121.223572W, 1-VII-1963, J Vercamp, CAS; 1♂, same data except 20-VIII-1964, R Whitely, CAS; 1♀, same data except VIII-1963, E Ball Jr, CAS.

male HOLOTYPE CA: El Dorado Co.
S88-60 R88-75A



calling song PARATYPE CA: El Dorado Co. 24.1°C JCR120808_03



female PARATYPE CA: El Dorado Co. S91-96



male terminalia PARATYPE CA: El Dorado Co. JAC000002285



ventral sclerite
HOLOTYPE



female terminalia PARATYPE JAC000002299



male PARATOPOTYPE CA: El Dorado Co.
S88-60 R88-75B



karyotype PARATYPE CA: El Dorado Co. S88-60 T88-8

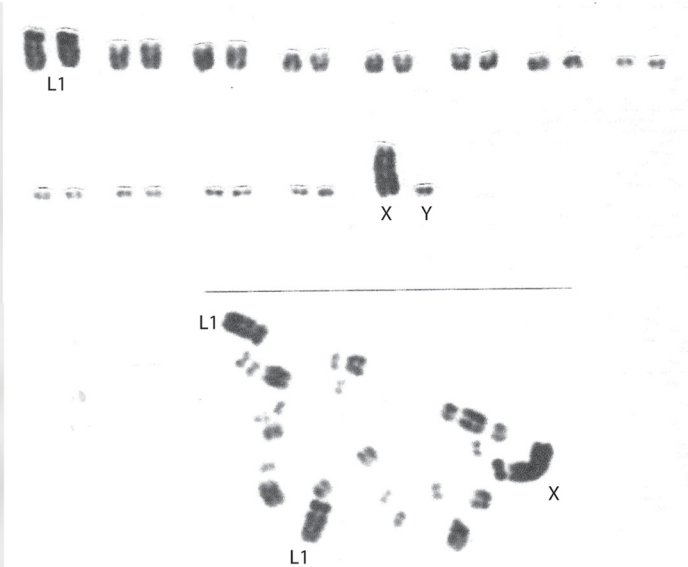


FIGURE 15. *N. radicata* male and female habitus, calling song, male and female terminalia, karyotype.

Neduba convexa Caudell, 1907

Fig. 9 (distribution), Fig. 16 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 4G (male calling song), Plate 7A–C (male ventral sclerites), Plate 9H (male titillators), Plate 11G (female subgenital plate).

Common name. Convex Shieldback.

History of recognition. This taxon was described as a variety of *N. carinata* (Caudell 1907). The type series included specimens from widely separated localities in California: Mount Shasta and Napa County. We resolved the taxonomy in relation to topotypes from the Mount Shasta type locality designated by Rentz & Birchim (1968). The North Coast Range type material from Napa County belongs to *N. ambagiosa* (see species account above).

Type material. The type specimen is a lectotype male from Mt. Shasta, Siskiyou Co., in the USNM. Images of the type are available at OSFO (Cigliano *et al.* 2020). TOPTYPES EXAMINED (n = 19): USA, CA, Siskiyou Co., 7♂, McBride Camp, 4 mi. E of Mount Shasta City on Rd A10, 41.409294N, 122.117727W, 1433 m, 2-IX-1983, DB Weissman, CAS; 1♂, same data except 29-VI-1992, DB Weissman, CAS; 7♂, McBride Springs Campground, 4 mi. NE of Mount Shasta City, 41.3529N, 122.28328W, 1487 m, 1-2-VIII-2013, JA Cole, LACM; 3♂, same data except JAC; 1♂, same data except 22-25-VIII-2019, JA Cole, JAC.

Measurements. (mm, ♂n = 27, ♀n = 5) Hind femur ♂18.38–20.60, ♀21.42–24.22, pronotum total length ♂8.50–10.36, ♀7.78–9.50, prozona length ♂2.95–4.45, ♀3.39–4.60, metazona dorsal length ♂5.03–6.55, ♀4.39–5.17, pronotum constriction width ♂2.35–3.06, ♀2.57–3.04, metazona dorsal width ♂5.38–6.95, ♀5.55–6.05, head width ♂4.06–4.87, ♀5.03–5.80, ovipositor length ♀15.80–21.19.

Distribution. Widely distributed in the northern Central Valley and Cascade Range of Northern California, extending east along the junction of the Sierra Nevada and Cascade Range to the Diamond Mountains.

Habitat. Understory vegetation, tangles, and leaf litter of chaparral and mixed conifer forests. Also, in remaining northern Central Valley riparian forests.

Seasonal occurrence. Specimens suggest a long summer and fall adult activity from July (1-VII-2000, JA Cole, LACM) through November (10-XI-1948, HP Chandler, CAS). Nymphs have been collected from early April through late August. Adult activity will commence earlier in the lower elevations of the Central Valley.

Stridulatory file. (n = 8) length 3.1–3.9 mm, 106–145 teeth, tooth density 35.3 ± 2.8 (29.7–38.2) teeth/mm.

Song. (n = 14) The male song is of the “zwee-zwee type with PTR 2.6 ± 0.3 s⁻¹ at 25°C, MPTL 308.1 ± 51.1 ms, and PTF 14.0 ± 0.8 kHz. OPT are well developed. A distinct amplitude increase commences at the middle of each MPT. Males are nocturnal and may sing in aggregations.

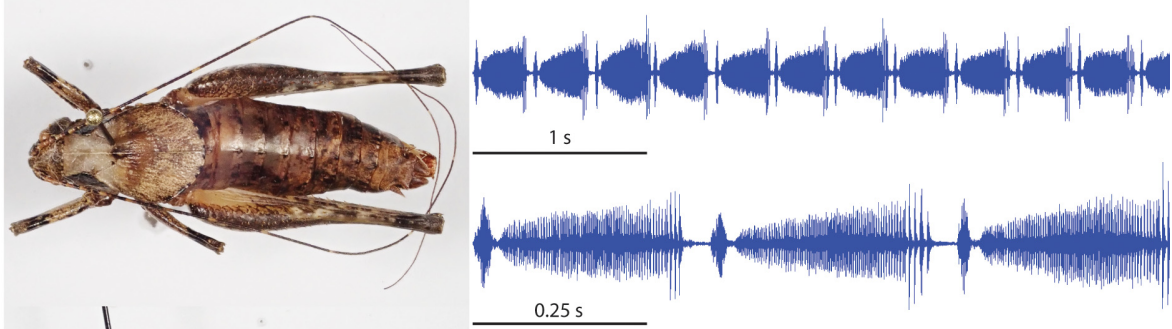
Karyotype. (n = 15) $2n♂ = 26$ (2m + 22t + XtYt). T83-48, S83-119, topotype.

Recognition. *N. convexa* can be confused with *N. longiplutea* distributed to the west, but the latter has a male ventral sclerite lateral process that is longer than the shaft, unlike the reverse condition in the former. To the south and north of *N. convexa* are *N. radicata* and *N. cascadia*, respectively, both of which have small lateral process on the male ventral sclerite. *N. ambagiosa* is also similar but males usually have a more conical ventral sclerite apex and that is a Coast Range species. Females may often be separated from *N. longiplutea* by the lack of a bifurcate subgenital plate apex, but this is variable in *N. convexa*. The *N. radicata* subgenital plate is wider than long with a deep notch, and that of *N. cascadia* does not have curved apical margins. The song of *N. radicata* to the south has a faster PTR, whereas the song of *N. cascadia* to the north has a slower PTR.

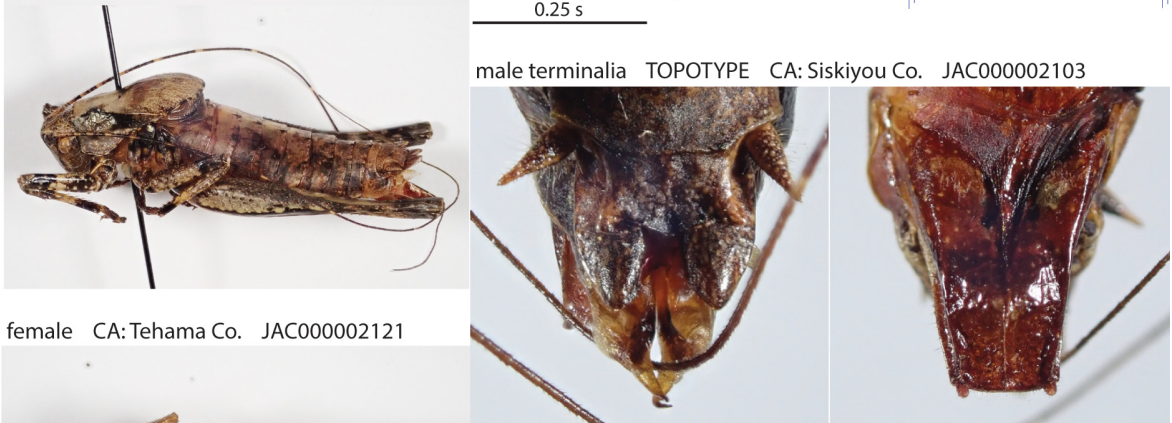
Notes. This species has a wide range and can be locally abundant. *N. convexa* was probably widespread in the Central Valley riparian forests before modification of the region for agriculture. Local variation is evident. Males from the populations along the Feather River Drainage and Laufman Campground in the Diamond Mountains tend to have flatter ventral sclerite apices (Plate 7C) and are genetically distinct (Figs. 3–5), but these populations are not reliably separable using any character. Further study may conclude that cryptic species are present along this east-west transect across the northern rim of the Central Valley and the Sierra Nevada. The physiology of this species is apparently adapted for activity at cold temperatures. On Mount Shasta, males sang between 10–15°C. When brought into the laboratory at standard temperature, individuals became hyperactive and did not survive long (JAC pers. obs.).

Material examined. (n=88) All USA, CA, Butte Co., 1♀ nymph, Chico, 39.728494N, 121.837478W, 59 m, 7-V-1968, T Kone, B Wilkey, W Wiard, CSCA; 6♂, Sacramento River State Park, Indian Fishery Day Use Area, 39.70522N, 121.93905W, 42 m, 18-VII-2015, JA Cole, DB Weissman, LACM; Lassen Co., 3♂, 2♀,

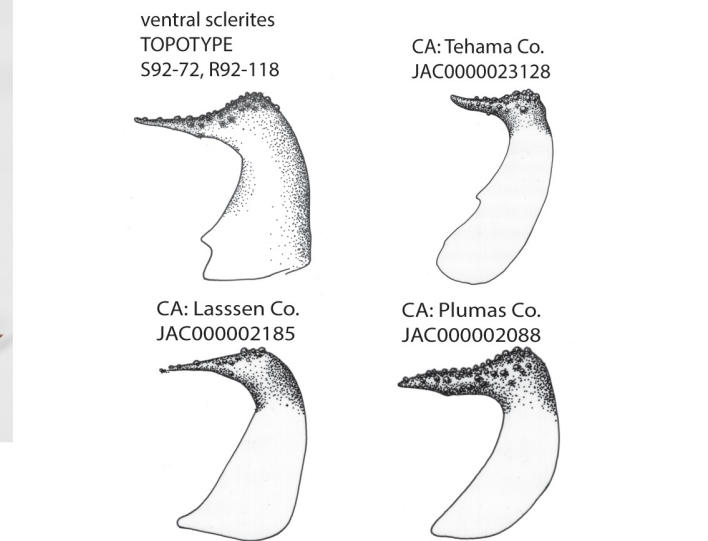
male TOPOTYPE CA: Siskiyou Co. JAC000002106 calling song TOPOTYPE CA: Siskiyou Co. 25.5°C S92-72 R92-118



male terminalia TOPOTYPE CA: Siskiyou Co. JAC000002103



female CA: Tehama Co. JAC000002121



female terminalia CA: Plumas Co. JAC000002094



karyotype TOPOTYPE CA: Siskiyou Co. S83-119 T83-48

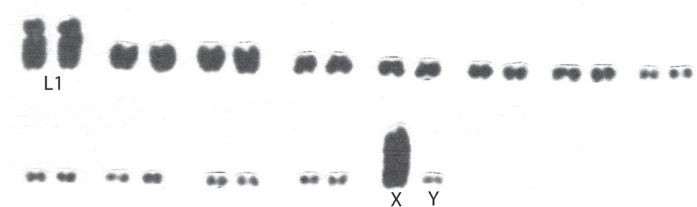


FIGURE 16. *N. convexa* male and female habitus, calling song, male and female terminalia, karyotype.

Dyer Mountain Rdg., 40.239055N, 121.03246W, 2279 m, 27-VIII-1968, FL Blanc, CSCA; 1♂, Laufman Campground, Plumas National Forest, 3.5 mi. S of Milford on Milford Grade Rd., 40.135N, 120.3483W, 1554 m, 13-14-VIII-2002, JA Cole, LACM; 1♂, same data except JA Cole, JAC; 2♂, same data except 18-VII-2012, JA Cole, LACM; 5♂, same data except 8-VIII-2014, JA Cole, DB Weissman, LACM; **Plumas Co.**, 1♂, Almanor, 40.217386N, 121.17413W, 1377 m, 16-VII-1940, no collector, CAS; 2♂, Hallsted Campground, 0.25 mi. W of Twain on SR 70, 40.0174N, 121.0745W, 864 m, 1-4-VII-2000, JA Cole, LACM; 3♂, same data except 13-16-VII-2004, JA Cole, LACM; 1♂, 2♀, same data except JAC; 1♂, same data except 15-17-VIII-1997, JA Cole, LACM; 4♀, same data except 7-10-IX-2001, JA Cole, LACM; 1♂, same data except 15-17-VIII-1998, JA Cole, LACM; 1♂, Johnsville, 39.76073N, 120.695498W, 1573 m, 16-VII-1973, RA Belmont, BMED; 1♂, same data except 9-VIII-1961, JS Buckett, BMED; 1♂, same data except 25-VIII-1961, JS Buckett, BMED; 1♂, same data except 9-X-1974, H Pini, BMED; 1♀, Meadow Valley, 39.929612N, 121.060791W, 1153 m, 30-X-1954, B Forbs, BMED; 2♂ adults, 1♂ nymph, same data except 5-VII-1924, EC Van Dyke, CAS; 1♀, Quincy, 39.936836N, 120.947176W, 27-IX-1967, J Badaj, CSCA; **Shasta Co.**, 1♂, Bridge Bay Rd., yacht area, 40.75611N, 122.32167W, 4-VIII-1980, no collector, CAS; 1♂, Burney Fall, 41.010716N, 121.652765W, 853 m, 10-XI-1948, HP Chandler, CAS; 1♂, Crystal Lake, 40.934999N, 121.556861W, 1585 m, 2-IX-1953, HP Chandler, CAS; 1♀ nymph, Hat Creek, 40.829684N, 121.508994W, 1003 m, 10-VII-1952, GF Pronin, CAS; 2♂, same data except 11-VIII-1964, RE Pinger, CSCA; 1♀, same data except 19-VIII-1951, no collector, CAS; 1♀ nymph, same data except 20-VIII-1951, GF Pronin, CAS; 1♂, 4♀, same data except 22-VII-1965, S Seminoff, CSCA; 1♀ nymph, same data except 23-VI-1951, GF Pronin, CAS; 1♂, same data except 25-VIII-1951, GF Pronin, CAS; 1♀ nymph, Iron Mountain Mine, 40.675427N, 122.52807W, 305 m, 30-VII-1947, HP Chandler, CAS; 1♂, Lamoine, 40.977927N, 122.430847W, 377 m, 2-IX-1970, RE Whipp, CSCA; 1♀, Whiskeytown, 40.63876N, 122.559737W, 390 m, 10-X-1976, TR Haig, CSCA; **Siskiyou Co.**, in addition to type material (above), 1♀, Castle Lake, 41.227294N, 122.383254W, 1554 m, IX-1953, HP Chandler, CAS; 1♀, Dunsmuir, 41.208209N, 122.271953W, 698 m, 7-VII-1970, V Pierce, CSCA; 1♀, Specimen Gulch, 41.13986N, 123.124485W, 25-VII-1967, AD & GJ Keuter, CAS; **Tehama Co.**, 1♂ nymph, 7 mi. NE Red Bluff, 40.25019N, 122.141936W, 4-IV-1961, T Gallion, CSCA; 11♂, 1♀, Potato Patch Campground, Lassen National Forest, 21.5 mi. SW of Chester off SR36 and SR32, 40.1894N, 121.5315W, 1128 m, 19-20-VII-2012, JA Cole, LACM; 4♂, same data except JAC; ♂3, ♀2, same data except 7-VIII-2014, JA Cole, DB Weissman, CAS.

Neduba cascadia Cole, Weissman, & Lightfoot, sp. n.

Fig. 9 (distribution), Fig. 17 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 1F–H (live habitus), Plate 4H (male calling song), Plate 7E (male ventral sclerite), Plate 11H (female subgenital plate).

Common name. Cascade Shieldback.

History of recognition. None.

Type material. HOLOTYPE MALE: **USA, OR, Jackson Co.**, Wildcat Campground, Hyatt Lake Complex, Cascade-Siskiyou National Monument, 42.18283N, 122.44775W, 1531 m, 27-29-VII-2016, JA Cole, JAC000002023 [specimen barcode], DNA218 [genomic], SING0616 [DNA extraction], JCR160727_02 [recording], 125 [teeth], 3.7 [mm stridulatory file length], tegmen in gelcap below specimen, deposited in CAS, Entomology type #19708.

PARATYPES (n = 12): 5♂, same data as holotype, LACM; 4♂, same data as holotype, CAS; 1♂, same data as holotype, JAC; 1♀, same data as holotype except 28-VIII-2019, DB Weissman & DC Lightfoot, CAS; 1♀, Woodruff Meadow, 30 mi. SW Crater L., 42.885125N, 122.509206W, 6-VIII-1960, JR Helfer, CAS.

Measurements. (mm, ♂n = 7, ♀n = 1) Hind femur ♂18.05–18.95 ♀19.91, pronotum total length ♂9.20–9.81, ♀8.85, prozona length ♂3.01–4.65, ♀4.55, metazona dorsal length ♂5.10–6.80, ♀4.30, pronotum constriction width ♂2.07–2.30, ♀2.55, metazona dorsal width ♂6.50–7.25, ♀6.49, head width ♂4.10–4.68, ♀5.02, ovipositor length ♀16.00.

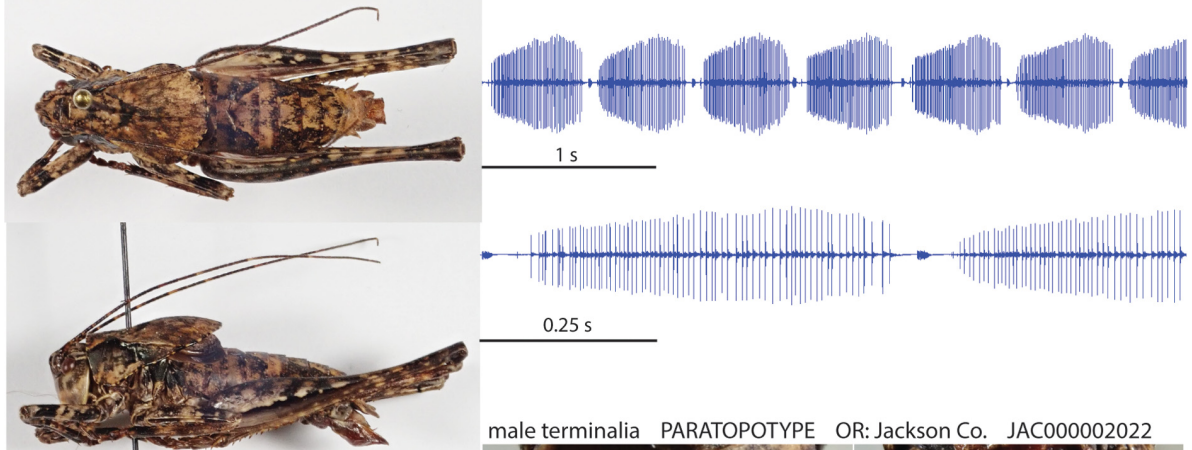
Distribution. Southern Cascade and Siskiyou mountain ranges of southern Oregon.

Habitat. Understory and edges of coniferous forest.

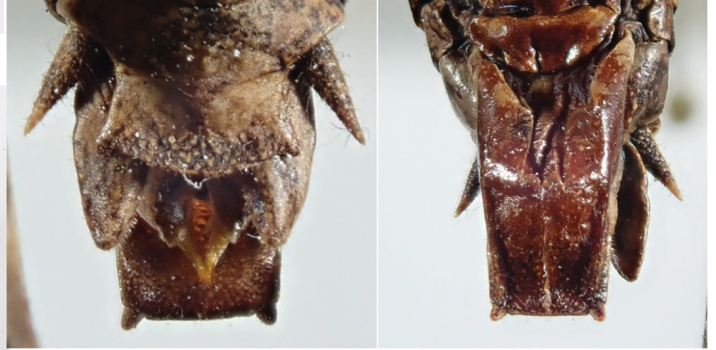
Seasonal occurrence. Scant records are from mid-July through late August. Adult activity probably lasts from midsummer through fall until first frosts.

Stridulatory file. (n = 4) length 3.4–3.7 mm, 125–133 teeth, tooth density 36.7 ± 2.1 (33.8–38.8) teeth/mm.

male HOLOTYPE OR: Jackson Co. JAC000002023 calling song PARATOPOTYPE OR: Jackson Co. 19.9°C JCR160727-01



male terminalia PARATOPOTYPE OR: Jackson Co. JAC000002022



female PARATOPOTYPE OR: Jackson Co. JAC000002032



ventral sclerite TOPOTYPE JAC000002025



female terminalia JAC000002032



male PARATOPOTYPE OR: Jackson Co. JAC000002030



karyotype PARATOPOTYPE OR: Jackson Co. S19-70 T19-16

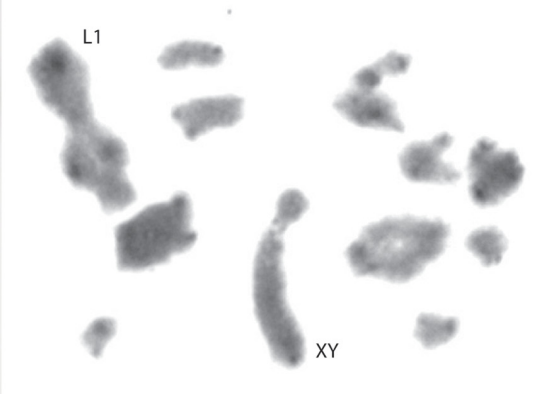


FIGURE 17. *N. cascadia* male and female habitus, calling song, male and female terminalia, karyotype.

Song. (n = 6) Typical Convexa Clade “zwee-zwee” song type but with a significantly slower PTR of $1.8 \pm 0.1 \text{ s}^{-1}$ (ANCOVA $P = 1.08 \times 10^{-5}$) and longer MPTL of $498.2 \pm 65.5 \text{ ms}$ (ANCOVA $P = 4.27 \times 10^{-11}$) than all other Convexa Clade taxa. PTF is $13.9 \pm 2.2 \text{ kHz}$.

Karyotype. (n=2) $2n \text{♂} = 26 (2m + 22t + Xt + Yt)$ T19-16, S19-90, paratopotype.

Recognition. The male ventral sclerite of *N. cascadia* has a blunt apex with scattered large tubercles and a short lateral process that blends into the shaft by an obtuse angle. This contrasts with *N. convexa* and *N. longiplutea*, both distributed to the south, which have the ventral sclerite apex low if not flat and a long lateral process with numerous fine tubercles that are arranged in rows. *N. steindachneri* to the north has a mushroom-shaped ventral sclerite with few large tubercles and a blunt, recurved lateral process. The female subgenital plate is unique among the Convexa Clade in having straight apical margins. The slow PTR separates the song of *N. cascadia* from all other Carinata Group species; *N. steindachneri* to the north has the fastest PTR in this species Group.

Etymology. *cascadia*, reflecting the southern Cascade Range distribution.

Notes. The distribution of this species lies between that of *N. steindachneri* to the north and *N. convexa* to the south. Further studies are needed to determine the limits of the ranges of northern Carinata Group taxa. Museum specimens from intermediate localities are nymphs and are only tentatively identified as this species. The calling songs and genitalia of all three species differ, so sympatry may be expected if these differences confer reproductive isolation. That calling song extremes of PTR occur in two species with adjacent ranges suggests prezygotic reproductive isolation mediated by calling song.

Material examined. In addition to type material (above), QUESTIONABLE PLACEMENT (n = 3): **USA, OR, Jackson Co.**, 2♀ nymphs, Little Applegate River, 42.198722N, 123.045356W, 701 m, 6-VIII-1950, B Malkin, CAS; 1♀ nymph, Union Creek, 42.906905N, 122.445598W, 7-31-VIII-1950, B Malkin, CAS.

Neduba steindachneri (Herman, 1874)

Fig. 9 (distribution), Fig. 18 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 1E (live habitus), Plate 4I (male calling song), Plate 7D (male ventral sclerite), Plate 9I (male titillators), Plate 11I (female subgenital plate).

Common name. Steindachner’s Shieldback.

History of recognition. Originally described in *Tropizaspis* from Fox Island, Puget Sound, Washington. Caudell (1907) synonymized this species under *N. carinata*. This species was subsequently removed from synonymy on the basis of the wide distance between type localities, but without examination of specimens (Rentz & Birchim 1968). **NEW COMBINATION:** *N. picturata* (Scudder 1899) is transferred under the synonymy of this species, rather than *N. diabolica*, given the type was collected during the Northwestern Boundary Survey (Caudell 1907). This survey, from 1857-1861, was led by B.R. Kennerly, along the 409-mile-long Canadian-US border between the Rocky Mountains and Point Roberts on coastal Washington.

Type material. The syntype series of males and females is in NMW Vienna. Lectotype male here chosen as the adult whose images appear, along with collection labels, on the OSFO (Cigliano *et al.* 2020). Label data of this specimen is as follows:

Small square label: “Stein-/dachner /1869[typed]/Califor [handwritten over label]

Wide rectangular label [handwritten]: Type n. sp. steindachneri/Fox Island Pouget Sound/1874 (<http://orthoptera.speciesfile.org/Common/basic/ShowImage.aspx?TaxonNameID=1141747&ImageID=208936>)

TOPOTYPES EXAMINED (n = 4): WA, Pierce Co., 4♂, Puget Sound, Fox Island, 47.235925N, 122.626948W, 16-VIII-1986, DB Weissman, CAS

Measurements. (mm, ♂n = 20, ♀n = 1) Hind femur ♂16.72–21.00, ♀19.80, pronotum total length ♂7.61–9.55, ♀7.56, prozona length ♂3.34–4.41, ♀1.94, metazona dorsal length ♂4.15–5.83, ♀5.62, pronotum constriction width ♂1.95–2.55, ♀2.60, metazona dorsal width ♂5.65–6.90, ♀5.50, head width ♂3.71–4.45, ♀4.69, ovipositor length ♀14.18.

Distribution. Central Oregon Cascade and Coast Ranges north to coastal British Columbia.

Habitat. Understory of fir and fir-oak forests. On grasses, low branches, *Ribes*, and leaf litter.

Seasonal occurrence. Summer through fall, from July (6-VII-1926, CL Hubbs, CAS) through September (19-IX-2015, JA Cole, LACM).

Stridulatory file. (n = 11) length 3.5–4.0 mm, 108–127 teeth, tooth density 31.3 ± 2.3 (27–35.3) teeth/mm.

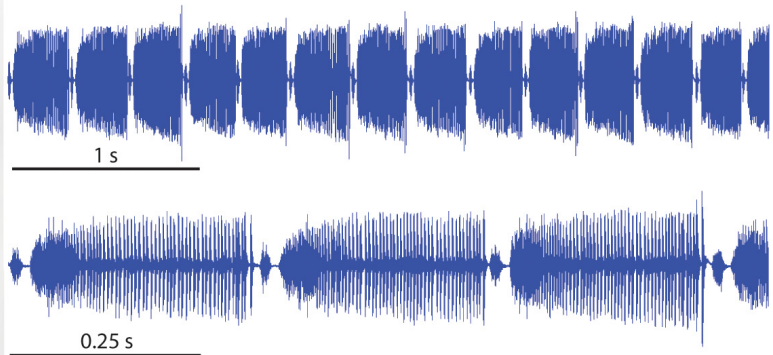
Song. (n = 26) Male songs are of the zwee-zwee type with PTR $3.7 \pm 0.4 \text{ s}^{-1}$, faster than all other Convexa Clade species except some males of *N. radicata*. Males sometimes add partial PT when initiating song bouts. MPTL is $250.4 \pm 47.6 \text{ ms}$. The OPT is poorly developed or absent. PTF is $13.1 \pm 1.7 \text{ kHz}$. Males are nocturnal singers.

Karyotype. (n = 5) $2n_{\text{♂}} = 26$ (2m + 22t + XtXt) T86-74, S86-95, topotype.

male WA: Kitsap Co. JAC000002396



calling song TOPOTYPE WA: Pierce Co. 24.5°C S86-95 R86-185



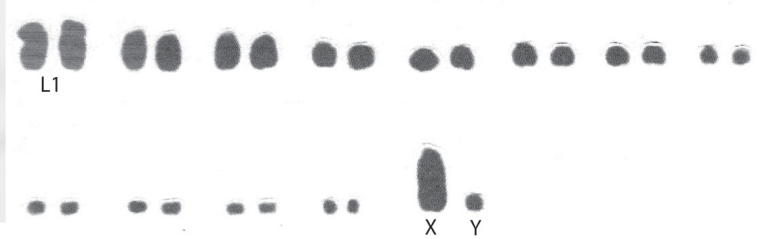
female WA: Mason Co.



male terminalia OR: Benton Co. JAC000002374



karyotype TOPOTYPE WA: Pierce Co. S86-95 T86-74



female terminalia WA: Mason Co. ventral sclerite
TOPOTYPE
S86-95, R86-182

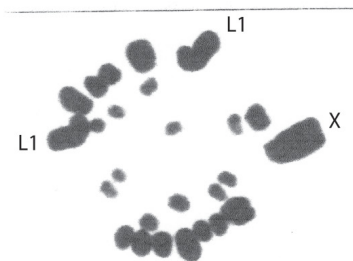
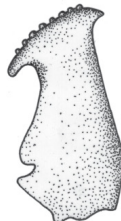


FIGURE 18. *N. steindachneri* male and female habitus, song, male and female terminalia, karyotype.

Recognition. The male ventral sclerite is mushroom-shaped with a short, broad shaft and a wide, evenly curved apex with a short, blunt, recurved anterolateral projection. Tubercles are large, sparse, and confined to the apex. The

titillators of *N. steindachneri* begin curvature after the midpoint of the shaft and are not as strongly curved dorsally ($>90^\circ$) as seen in most other Carinata Group species (Plate 9). Stridulatory file tooth density (27–35 teeth/mm) is lower than that of *N. convexa* (2-sample *t*-test, $P = 5.48 \times 10^{-3}$) and also trends lower than *N. cascadia* (33–39 teeth/mm). The female subgenital plate is pentagonal, flat, subequal in length and width, and with curved apical margins and a strongly pointed apex, which separates this species from *N. cascadia* females which have straight apical margins and from *N. convexa* and *N. longiplutea* females which have plates that are longer than wide. The song is unique in having reduced or absent OPT. The PTR is faster than all other *convexa* clade species. This species has the most northern range of any *Neduba* (Fig. 9).

Notes. *N. steindachneri* is locally common in the forest understory of the western slopes of Oregon and Washington Cascade Range and primarily the eastern slopes of the Oregon and Washington coastal ranges. A phylogeographic break separates populations north and south of the Willamette River (Figs. 3–4) that suggests historical isolation that indicates historical isolation. Hybridization with *N. cascadia* is possible and should be sought from populations in central Oregon, where the ranges of these two species overlap.

Material examined. (n = 28) **USA, OR, Benton Co.,** 8♂, McDonald-Dunn Forest, Corvallis, 44.60382N, 123.33253W, 144 m, 18-IX-2015, JA Cole, LACM; 1♂, same data except JAC; 5♂, same data except 19-VII-1982, DC Lightfoot, CAS; **Columbia Co.,** 1♀, Wilson Creek, 46.07701N, 123.02315W, EH Nast, CAS; **Hood River Co.,** 1♂, 1♀, Hood R., 45.70556N, 121.52028W, 122 m, 17-VII-1931, RH Beamer, CAS; **Marion Co.,** 1♂, Sublimity, Silver Creek Falls, 45.000267N, 122.840916W, 167 m, 19-VIII-1945, W Blehm, CAS; **Multnomah Co.,** 3♂, Dabney State Park, 45.51766N, 122.35429W, 22 m, 19-IX-2015, JA Cole, JAC; 5♂, Oxbow Regional Park Day Use Area, SE Gordon Creek Rd., 1.2 mi. SE jct. Hurlburt Rd., 45.49821N, 122.27871W, 59 m, 19-IX-2015, JA Cole, JAC; 1♂ same data except JAC; 1♂, SE Gordon Creek Rd., 2.7 mi. S jct. Hurlburt Rd., 45.4784N, 122.28107W, 257 m, 19-IX-2015, JA Cole, JAC sound record; **Tillamook Co.,** 1♂, Tillamook, 45.51667N, 123.71667W, 30-VII-1926, CL Hubbs, CAS; **WA, Kitsap Co.,** 1♂, Holly, 47.557593N, 122.978488W, 3 m, 6-VII-1926, CL Hubbs, CAS; 5♂, Margarete Ranch, Port Orchard, 47.47137N, 122.65009W, 1525 m, 13-14-VIII-2013, JA Cole, LACM; 2♂, same data except JAC; **Mason Co.,** 1♂, 1♀, Lake Cushman, 47.487964N, 123.266471W, 244 m, 27-VIII-1919, P Putnam, CAS; **Pierce Co.,** see Type material (above). QUESTIONABLE PLACEMENT: **OR, Douglas Co.,** 1♂ nymph, Drain, 43.658731N, 123.318699W, 9-VI-2014, EC VanDyke, CAS.

Material from databases not examined by us (n = 7): CANADA, BC, Departure Bay, 49.20, 123.98W, 1925, GJ Spencer, Symbiota Collections of Arthropods Network (SCAN, <https://scan-bugs.org/portal>); UBC Campus 49.26N, 123.25W, 3-X-1946, D Evans, SCAN; Gailano Island, 48.93N, 123.45W, 4-IX-1971, J Scudder, SCAN; same data except 1971, J Scudder, SCAN; same data except 11-X-1976, GGE Scudder, SCAN; same data except 1976, GGE Scudder, SCAN; Vancouver Island, 49.66667N, 125.83333W, 9-VIII-2007, J Miskelly, SINA.

Propsti Group

The Propsti Group contains a single species, the Santa Catalina Island endemic (Fig. 8) *N. propsti*. The Group is defined by having a single spine on the fore tibia located on the posterior margin, a pair of prosternal spines, darkened male tegminal apices, and a female subgenital plate that is over half again as long as wide. Only *N. lucubrata* from mainland California shares this suite of characters, but this species has a smaller body size, a male subgenital plate that narrows from base to apex along the lateral carinae, and a song that consists of a bout (chirp) structure (Plate 5C) whereas the song of *N. propsti* is continuous (Plate 4J). The karyotype is unique.

Neduba propsti Rentz & Weissman, 1981

Fig. 19 (distribution), Fig. 20 (male and female habitus, calling song, drumming, male and female tremulation karyotype), Plate 2A (live habitus), Plate 4J (male calling song), Plate 7F (male ventral sclerite), Plate 10A (male titillators), Plate 11J (female subgenital plate).

Common name. Santa Catalina Island Shieldback.

History of recognition. Described as a Santa Catalina Island endemic (Rentz & Weissman 1981). Listed under *Aglaothorax* in OSFO for unspecified reasons (Cigliano *et al.* 2020).

Type material. The holotype male is in the CAS collection. Images of the holotype are available at OSFO (Cigliano *et al.* 2020).

Measurements. (mm, ♂n = 9, ♀n = 5) Hind femur ♂20.86–23.47, ♀24.10–25.89, pronotum total length ♂8.30–9.45, ♀9.15–9.89, prozona length ♂4.15–5.55, ♀5.15–5.93, metazona dorsal length ♂3.90–4.90, ♀3.88–4.15, pronotum constriction width ♂2.44–3.13, ♀2.98–3.22, metazona dorsal width ♂6.37–7.01, ♀6.27–7.22, head width ♂4.25–4.95, ♀5.18–5.54, ovipositor length ♀18.04–19.14.

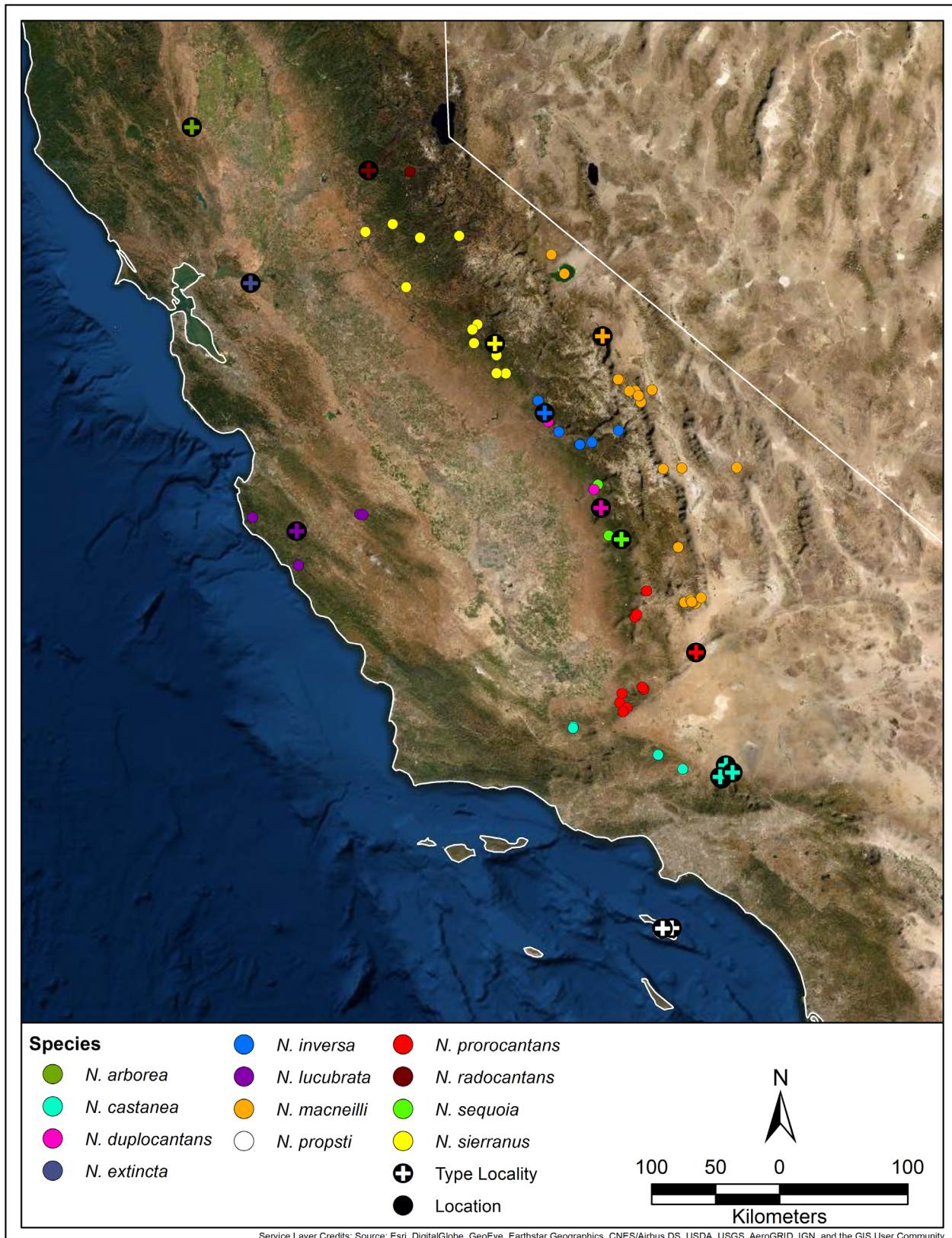
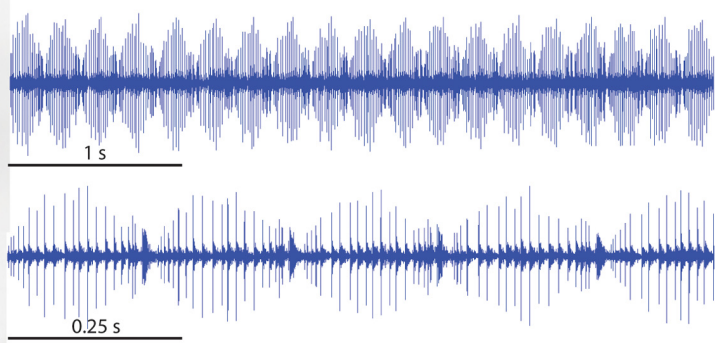


FIGURE 19. Distribution of Propsti, Castanea, Lucubrata, Sierranus, and Sequoia Group species mapping records reported in this work.

male CA: Los Angeles Co.



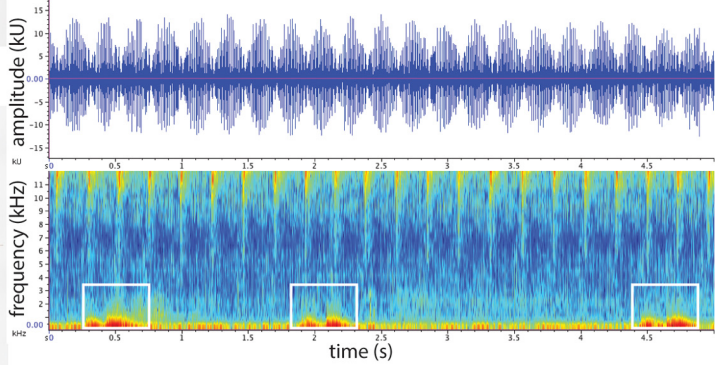
calling song CA: Los Angeles Co. 25.0°C JCR130721_01



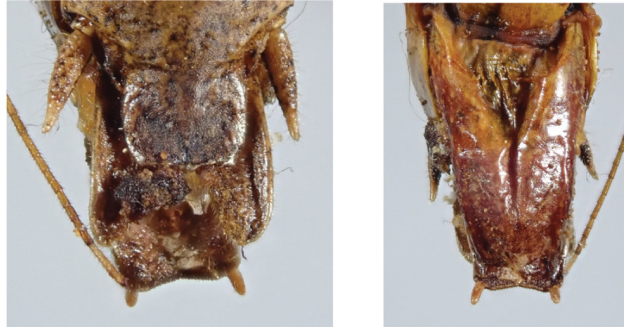
female CA: Los Angeles Co.



calling song with drumming (white boxes)
CA: Los Angeles Co. 24.4°C JCR130722_01



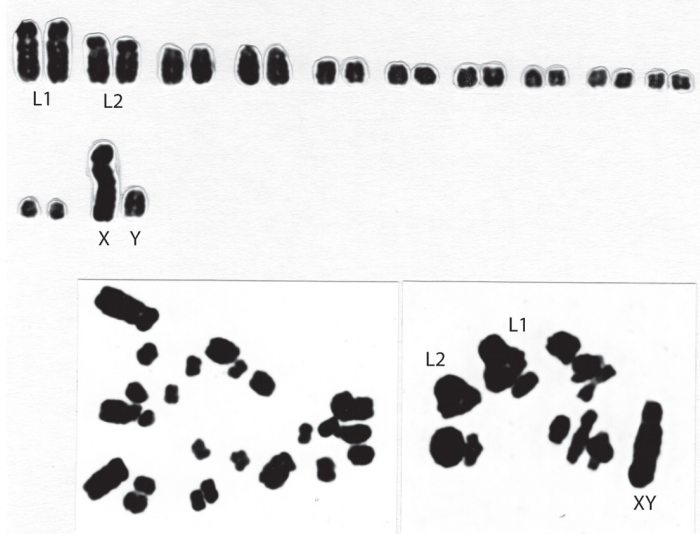
male terminalia CA: Los Angeles Co.



ventral sclerite
CA: Los Angeles Co.



karyotype CA: Los Angeles Co. S85-70 T85-12



female terminalia
CA: Los Angeles Co.



FIGURE 20. *N. propsti* male and female habitus, calling song, male and female terminalia, karyotype.

Distribution. Restricted to Santa Catalina Island, Los Angeles County, California, USA. Probably found throughout the island in suitable habitat.

Habitat. Dense chaparral vegetation, often on steep hillsides and in canyon bottoms. Individuals prefer to sit on the inner twigs of tangles. Also, in gardens on non-native vegetation. One individual taken from ornamental eucalyptus (JAC, pers. obs.).

Seasonal occurrence. Adult records from mid-June (14-VI-1985, S Bennett, CAS) through July (28-VII-1981 DB Weissman, CAS).

Stridulatory file. (n = 5) length 3.2–3.9 mm, 94–111 teeth, tooth density 30.4 ± 2.1 (28.2–33.0) teeth/mm.

Song. (n = 10) Continuous 200 ms MPTL at a brisk PTR of 4.4 ± 0.4 s⁻¹. PT consist of the least amount of pulses (toothstrikes) of any species (~20). PTF approaches the ultrasonic at 18.5 ± 3.5 kHz. A captive male drummed at irregular intervals while stridulating (Fig. 20); the drums were audible and induced considerable substrate vibration in the cage.

Karyotype. (n = 4) Unique. $2n\♂ = 24$ (4m + 18t + XmYt). T85-12, S85-70, topotype.

Recognition. Shares the following morphological characters with *N. lucubrata*: a single apical spine on the fore tibiae, prosternal spines, and tegmina darkened apically. The stridulatory file has a lower tooth density (28–33 teeth/mm) than any other species except those of the Castanea Group. Male genitalia of *N. propsti* are similar to those of *N. castanea* and *N. macneilli*, but the arms of the titillators of *N. propsti* have a shaft that is straight and not swollen at a distance of 1/6 from the base as in the latter two species (Plate 10). The song is unique in having short MPTL produced continually at a rapid PTR. Females have the longest subgenital plate of any species, approximately 1.5 times longer than wide. This is the only nedubine on Santa Catalina Island (Figs. 8, 19) with the most southerly distribution of any *Neduba*.

Notes. *N. propsti* is an early branching lineage (Figs. 3–5) that has apparently been isolated on Santa Catalina Island for a long time. The island has never been connected to mainland California (Legg *et al.* 2004) being the product of tectonic uplift. Males may be wary and cease calling at the slightest disturbance, as much as a single leaf falling, and jump with little provocation (JAC pers. obs.). This is one of a handful of *Neduba* species that drum (Weissman 2001; see also *N. castanea*, *N. macneilli*, and *N. lucubrata* below). Drumming was observed in captivity by a single male without a female present (JAC pers. obs) and not in the field; the context of drumming in the mating system is not known in this species.

Material examined. (n = 14) **All USA, CA, Los Angeles Co.:** 3♂, Hermit Gulch Campground, Avalon Canyon, Santa Catalina Island, 33.38265N, 118.33951W, 91 m, 9-10-VII-2013, JA Cole, LACM; 1♂ same data except JAC; 2♀, Santa Catalina Island, 33.383361N, 118.417576W, 1-VII-1983, DB Weissman, CAS; 1♀, same data except 20-VII-1982, S Bennett, CAS; 1♀, same data except 28-VII-1981, S Bennett, LACM; 1♂, same data except 30-VI-1973, DB Weissman, CAS; 4♂, Santa Catalina Island, Toyon Bay, 33.383N, 118.416W, 14-VI-1985, S Bennett, CAS; 1♀, same data except 5-VII-1986, S Bennett, CAS.

Castanea Group

The Castanea Group is readily recognizable on account of the robust habitus, the short hind femora, by having only one spine on the anterior margin of the fore tibiae, and by the lack of prosternal spines. The lateral carinae of the male subgenital plate converge apically, although not as dramatically as in the Sierranus and Sequoia Groups, and the styli vary from articulate to rudimentary to absent. The posterior margins of the abdominal tergites have only slight crenulations. Superficially the species of this group resemble sympatric *Aglaothorax ovata*. Karyotypes also separate the two species in this group from all other *Neduba*. Castanea Group species occupy the dry slopes of central and southern California mountain ranges (Fig. 8).

Neduba castanea (Scudder, 1899)

Fig. 19 (distribution), Fig. 21 (male and female habitus, calling song, drumming, male and female tremulation karyotype), Plate 2B–C (live habitus), Plate 5A (male calling song), Plate 7I (male ventral sclerite), Plate 10B (male titillators), Plate 11K (female subgenital plate).

Common name. Chestnut Shieldback.

History of recognition. Scudder (1899) described *Tropizaspis castanea* from Los Angeles County, California. Caudell (1907) transferred this species to *Aglaothorax* based on habitus, in particular the pronotal shape, but the species was moved to *Neduba* once the male genitalia were examined (Rentz 1988; Rentz & Birchim 1968). Our fieldwork shows that *N. castanea* is the only *Neduba* species found in mainland Los Angeles County (i.e. exclusive of the Channel Islands), where it is limited to the fringes of the Mojave Desert.

Type material. The holotype male is housed at ANSP. Images of the type are available at OSFO (Cigliano *et al.* 2020). PARATYPE (n = 1): USA, CA, Los Angeles Co., 1♀, Los Angeles Co., VII, Coquillett, USNM; TOPOTYPES EXAMINED (n = 26): USA, CA, Los Angeles Co., 2♂, County road N4 near Llano, 34.505828N, 117.817841W, 1280 m, 6-VIII-1988, DB Weissman & DC Lightfoot, CAS; 1♂, County Road N6, 2 mi. NW of Devil's Punchbowl, 34.4267N, 117.8697W, 1250 m, 6-VIII-1988, DB Weissman & DC Lightfoot, CAS; 1♂, Devil's Punchbowl County Park, 34.4138N, 117.8587W, 1445 m, 17-VIII-1982, DB Weissman, CAS; 1♂, Devil's Punchbowl County Park, 34.4138N, 117.8587W, 1445 m, 30-VIII-1975, PH Sullivan, CAS; 1♂, Devil's Punchbowl Road 1 mi. NW of Devil's Punchbowl, 34.42382N, 117.86816W, 1341 m, 20-VI-2018, JA Cole, JAC; 1♂, Juniper Hills, Devil's Punchbowl Road (County Road N6), 2 miles east of Longview Road, 34.4267N, 117.8697W, 1316 m, 2005, JA Cole, LACM; 3♂, 1♀ nymph, same data except 13-VI-2003, JA Cole, JN Hogue, LACM; 1♂, same data except JAC; 2♂, same data except 14-VI-2015, JA Cole, GE Bell, T Farwell, LACM; 1♂, same data except JAC; 2♂, same data except 14-VI-2017, JA Cole, LACM; 3♂, 1♀, same data except 18-VI-2008, JA Cole, LACM; 1♀ nymph, same data except 20-VI-2003, JA Cole, JN Hogue, LACM; 1♂, same data except 7-VII-2004, JA Cole, LACM; 1♂, 1♀, Largo Vista Rd. (county Road N4), 1 mi. S of Fort Tejon Rd., 34.4530N, 117.7649W, 1277 m, 22-VI-2008, JA Cole, LACM; 1♀, same data except 22-VI-2008, JA Cole, JAC.

Measurements. (mm, ♂n = 14, ♀n = 6) Hind femur ♂16.99–21.20, ♀18.50–23.87, pronotum total length ♂9.90–13.20, ♀10.08–13.20, prozona length ♂3.84–5.69, ♀4.83–6.92, metazona dorsal length ♂5.60–8.67 ♀4.72–6.76, pronotum constriction width ♂2.70–3.68, ♀2.95–3.85, metazona dorsal width ♂7.24–8.49 ♀6.75–8.25, head width ♂4.94–5.85, ♀5.05–6.81, ovipositor length ♀14.92–20.25.

Habitat. Pinyon-juniper (*Juniperus* spp.-*Pinus monophylla* Torr & Frém.), Joshua tree (*Yucca brevifolia* Engelm.) woodlands, *Ceanothus* scrub, and yellow pine forest. Specimens were taken from pinyon pine, juniper, mountain mahogany (*Cercocarpus* sp.), and Joshua tree.

Distribution. Dry north slope of Transverse Ranges of California including the San Gabriel, San Bernardino, Liebre, and San Emigdio Mountains.

Seasonal occurrence. Adult specimens have been taken from mid-June in foothill regions (13-VI-2003, JA Cole & JN Hogue, LACM) into September at high elevation (12-IX-2015, DA Gray, CAS). Females were last instar nymphs at the earliest date of occurrence listed above.

Stridulatory file. (n = 5), length 3.7–4.6 mm, 79–99 teeth, tooth density 21.6 ± 1.1 (19.8–22.7) teeth/mm.

Song. (n = 24) A continuous series of long MPTL (373.1 ± 51.5 ms) with widely spaced toothstrikes delivered at PTR of 2.6 ± 0.7 s⁻¹. The sound resembles a finger running along the teeth of a comb. The PTF of 13.7 ± 2.1 kHz extends comfortably into the audible range. There is a significant high frequency component, however, with 18.7 kHz PTF measured in one high frequency laboratory recording. Males begin calling at sunset. The population from McGill Campground on Mount Pinos, Ventura County, California has a significantly slower PTR than that of the type locality (2-sample *t*-test, *P* = 0.002). Males may also produce audible substrate vibrations via drumming. Drums precede bouts of stridulation (Fig. 21).

Karyotype. (n = 5) $2n♂ = 22 (4m + 16t + XmYt)$, shared only with *N. macneilli*. T88-69, S88-72, topotype.

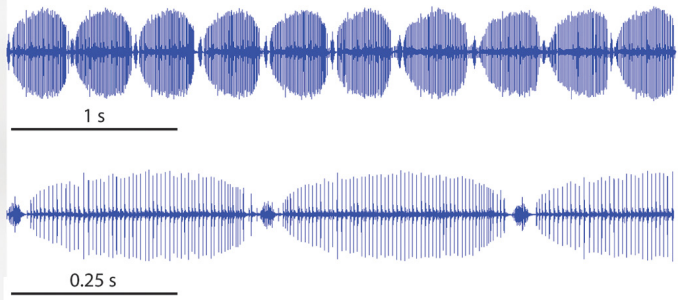
Recognition. Morphological and color pattern differences thought to separate *N. castanea* from *N. macneilli* (per Rentz & Birchim 1968) are unreliable. The development of the styli on the subgenital plate, from absent to slight swellings to articulated, may vary within a population and even between the left and right sides of a single specimen. Both species exhibit the full range of variation in color patterns. Female *N. castanea* have round, highly convex subgenital plates, whereas those of *N. macneilli* are subtriangular with a bluntly pointed apex. Geographically *N. castanea* replaces *N. macneilli*, which is a Sierra Nevada species, in the Transverse Ranges of southern California.

Notes. We treat *N. castanea* and *N. macneilli* as closely related sister species based on reproductive isolation via allopatry. Both inhabit the same life zone in different geographic regions of California. *N. castanea* and *N. macneilli* are sympatric with *Aglaothorax ovata*, and all three species share a similar robust habitus suggesting convergent evolution of body form in their habitat. Enlarged pronotal size may be adaptive for signal transmission in open

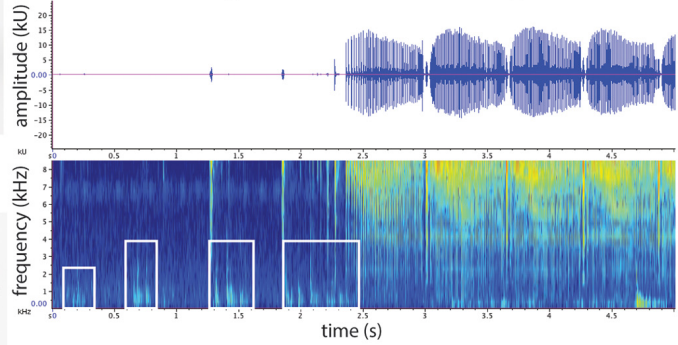
male TOPOTYPE CA: Los Angeles Co.
JAC000002043



calling song TOPOTYPE CA: Los Angeles Co. 25.8°C JCR150614_02



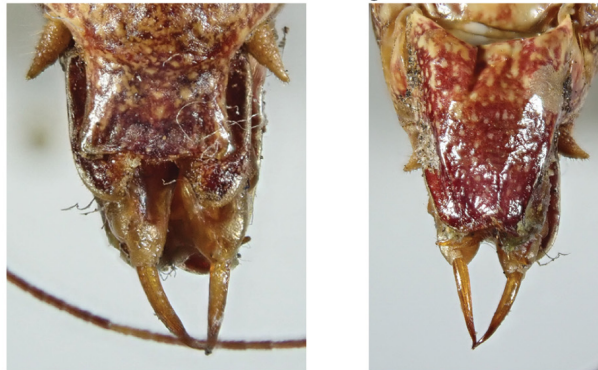
calling song with drumming (white boxes)
TOPOTYPE CA: Los Angeles Co. 23.3°C JCR171002_00



female TOPOTYPE CA: Los Angeles Co.
JAC000002036



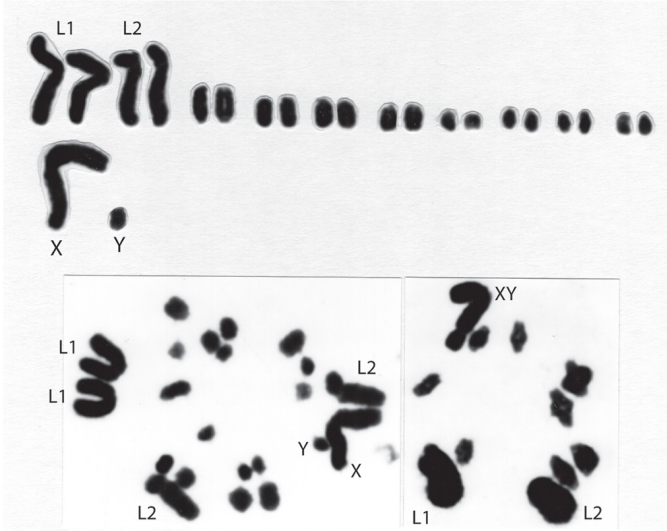
male terminalia TOPOTYPE CA: Los Angeles Co. JAC000002041



ventral sclerite
TOPOTYPE
S88-73



karyotype TOPOTYPE CA: Los Angeles Co. S88-72 T88-69



female terminalia TOPOTYPE
JAC000002038



FIGURE 21. *N. castanea* male and female habitus, calling song, male and female terminalia, karyotype.

habitats such as pinyon-juniper and Joshua tree woodlands, where trees and bushes are widely spaced, compared with the dense forest understories inhabited by other *Neduba* species Groups. Drumming was observed during courtship in the field at the Largo Vista Road locality (see Type material above), during which a male alternated drumming and stridulating. The signaling did not result in copulation in this observed instance (JAC pers. obs.).

Material examined. (n = 26) **All USA, CA, Kern Co.,** 3♀, McGill Campground, Los Padres National Forest, 34.82539N, 119.09791W, 12-IX-2015, DA Gray, LACM; 11♂, 1♀, McGill Campground, Los Padres National Forest, 34.81505N, 119.10014W, 2271 m, 8-9-VIII-2017, JA Cole, LACM; 1♂, 1♀, same data except JAC; **Los Angeles Co.,** in addition to type material (above), 5♂, Sierra Highway, 0.6 miles west of Crown Valley Road, Acton, 34.4936N, 118.1834W, 929 m, 17-VI-2003, JA Cole, JN Hogue, LACM; 1♂, same data except 18-19-VI-2008, JA Cole, JAC sound record; 1♂, Spunky Canyon, 2 mi. SW of Green Valley, 34.6023N, 118.3863W, 1047 m, 16-VI-2012, JA Cole, LACM; 2♂, same data except 26-VII-2001, JA Cole, LACM.

Neduba macneilli Rentz & Birchim, 1968

Fig. 19 (distribution), Fig. 22 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 2D (live habitus), Plate 5B (male calling song), Plate 7J–K (male ventral sclerites), Plate 10C (male titillators), Plate 11L (female subgenital plate).

Common name. MacNeill's Shieldback.

History of recognition. *N. macneilli* was described from the eastern Sierra Nevada mountains of California by Rentz & Birchim (1968). The type locality is 1 mile west of Tom's Place, Mono County, California. Tinkham (1944) referred to this species under the name *carinata*.

Type material. The male holotype is housed at ANSP. Images of the holotype are available at OSFO (Cigliano *et al.* 2020). **PARATYPES** (n = 2): **USA, CA, Mono Co.,** 2♂, Rock Creek, 1 mi. W Tom's Place, 37.5586N, 118.7025W, 2143 m, 10-IX-1966, DC & KA Rentz, CAS;

TOPOTYPES (n = 16): 4♂, 1♀, Tom's Place, 37.5586N, 118.7025W, 2143 m, 28-VIII-1986, DB & BI Weissman, DCF Rentz, CAS; 8♂, 1♀, Tom's Place, 1 mi. W, 37.5586N, 118.7025W, 2143 m, 15-16-VII-2012, JA Cole, LACM; 2♂, same data except JAC.

Measurements. (mm, ♂n = 19, ♀n = 4) Hind femur ♂16.35–21.50, ♀22.55–28.10, pronotum total length ♂9.89–11.85, ♀10.15–12.13, prozona length ♂4.59–6.30, ♀4.61–6.68, metazona dorsal length ♂4.90–6.20, ♀4.78–5.54, pronotum constriction width ♂2.58–3.85, ♀3.15–3.42, metazona dorsal width ♂6.65–7.81, ♀6.96–7.55, head width ♂4.13–5.83, ♀5.93–6.25, ovipositor length ♀17.14–19.35.

Distribution. Eastern slope of the Sierra Nevada Mountains of California.

Habitat. Yellow pine forest and pinyon-juniper woodlands. Specimens were taken from *Purshia tridentata* Pursh (DC) and *Pinus monophylla*.

Seasonal occurrence. Adult specimens have been taken from mid-July (10-VII-2003, JA Cole & JF Eguizabal, LACM) through October (22-X-1939, ER Tinkham, CAS).

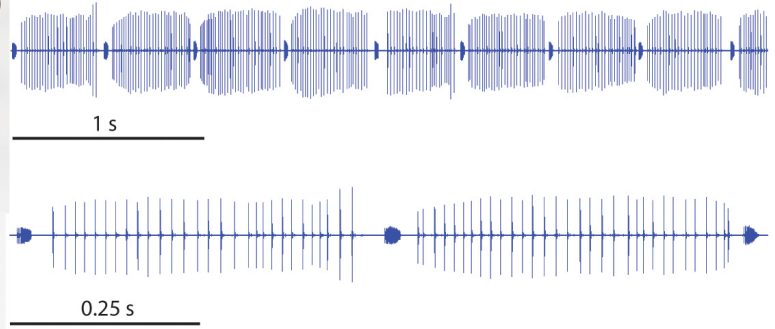
Stridulatory file. (n = 19) length 3.4–4.4 mm, 71–99 teeth, tooth density 23.1 ± 1.8 (19.8–26.4) teeth/mm.

Song. (n = 43) The song of this species was published in Morris *et al.* (1975). The calling song of *N. macneilli* is not distinguishable from that of *N. castanea* (see discussion under the former species). In addition to calling song, 2 of 5 recorded males of *N. macneilli* (identified as *N. castanea* in Weissman (2001)) from 1.3 m E Walker Pass, Kern Co. (S88-68), produced an audible drumming by visibly tapping the substrate in the laboratory simultaneously with both hind legs. Of many males recorded from various populations, these were the only males of *N. macneilli* ever heard drumming. A courting topotypic male produced short PT accompanied by obvious body movements (tremulations) that could have caused substrate vibration. This male was displaying to a female nymph (JAC, pers. obs., 15-VII-2012).

Karyotype. (n = 14) $2n♂ = 22$ (4m + 16t + XmYt), identical to that of *N. castanea*, and corrects the result of Ueshima and Rentz (1979). T86-83, S86-98, topotype.

Recognition. Males are indistinguishable from *N. castanea*. The female subgenital plate is subtriangular, in contrast to the rounded plate of *N. castanea*. This species inhabits the southeastern Sierra Nevada, whereas *N. castanea* inhabits the Transverse Ranges.

male TOPOTYPE CA: Mono Co. JAC000002237 calling song CA: Mono Co. 23.3°C JCR160924_02



male terminalia TOPOTYPE CA: Mono Co. JAC000002243



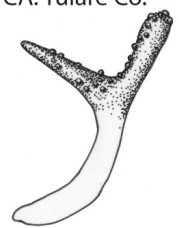
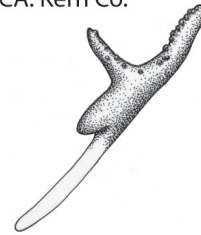
female CA: Kern Co. JAC000002231



TOPOTYPE
S86-98, R86-216

ventral sclerites
CA: Kern Co.

CA: Tulare Co.



karyotype TOPOTYPE CA: Mono Co. S86-98 T86-83



female terminalia CA: Kern Co.
JAC000002231

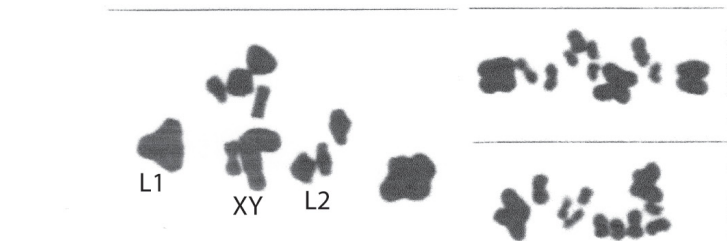


FIGURE 22. *N. macneilli* male and female habitus, calling song, male and female terminalia, karyotype.

Notes. Color pattern features that were used to separate *N. macneilli* and *N. castanea* (Rentz & Birchim 1968) are variable and are correlated with habitat rather than with lineage. The darker, mottled coloration of *N. macneilli* matches the background in higher elevation pinyon-juniper woodlands, while the lighter coloration typical of *N. castanea* is more cryptic in Joshua tree woodlands of the lower, arid foothill slopes. Both *N. castanea* and *N. macneilli* may have greenish or bluish abdominal pleura when alive (Plate 2C), colors that are invariably lost in museum specimens even if gutted and stuffed. Only freeze-drying retains such colors.

Material examined. (n = 110). **All USA, CA, Inyo Co.**, 1♂, 4 Jeffrey Campground, Inyo National Forest, 37.24759N, 118.56942W, 2479 m, 10-11-IX-2016, JA Cole, J Bailey, JAC sound record; 1♂, 8.1 mi. W of Big Pine on road to Sage Flat Camp, 37.164839N, 118.43694W, 2195 m, 28-VIII-1986, DB & BI Weissman, DCF Rentz, CAS; 11♂, 1♀, Big Pine Canyon, 37.164931N, 118.289546W, 16-VIII-1938, ER Tinkham, CAS; 1♂, same data except J Davis, CAS; 2♂, same data except 22-VIII-1948, ER Tinkham, CAS; 9♂, same data except 24-X-1939, ER Tinkham, CAS; 5♂, Glacier Lodge Rd. SR168, 1.38 mi. NE of Aspendell, 37.25047N, 118.58169W, 2497 m, 10-IX-2016, JA Cole, J Bailey, LACM; 1♀, Glacier Lodge, 11 mi. W of Big Pine, 37.164762N, 118.48971W, 4-VIII-1931, ER Tinkham, CAS; 5♂, 5♀, Lone Pine Canyon, 36.606044N, 118.062865W, 3-VIII-1931, ER Tinkham, CAS; 2♂, Lone Pine, 9 mi. W, 36.605934N, 118.225457W, 7-VIII-1961, JS Buckett, BMED; 2♂, Mouth Big Pine Canyon, 37.164931N, 118.289546W, 22-X-1939, ER Tinkham, CAS; 1♂, Sage Flat Camp, 8 mi. W of Big Pine, 37.082856N, 118.392482W, 2243 m, 19-VIII-1982, DB Weissman, CAS; 1♂, Sage Flat, 6 mi. SW of Big Pine on Glacier Lodge Rd., 37.1279N, 118.4037W, 2204 m, 13-VII-2003, JA Cole, JF Eguizabal, LACM; 1♂, same data except JAC; 1♂, same data except 4-VIII-2004, JA Cole, LACM; 1♀, Saline Valley, Grapevine Canyon Road Station 3, 36.58917N, 117.58472W, 1958 m, 18-VIII-1959, B. Banta, CAS; **Kern Co.**, 6♂, 2♀, 1.3 mi. E of Walker Pass on SR178, 35.66245N, 118.003532W, 1460 m, 5-VIII-1988, DB Weissman & DC Lightfoot, CAS; 1♂, 1♀, Freeman Canyon, 1.5 miles southeast of Walker Pass on SR178, 35.6509N, 118.0055W, 1470 m, 10-VII-2003, JA Cole, JF Eguizabal, LACM; 2♂, 2♀, same data except 14-VII-2005, JA Cole, LACM; 4♂, SR178, 4.1 mi. W of Walker Pass, 35.662431N, 118.099936W, 1280 m, 5-VIII-1988, DB Weissman & DC Lightfoot, CAS; 2♂, 1♀, Walker Pass, 35.662453N, 118.02674W, 1600 m, 18-VIII-1982, DB Weissman, CAS; 1♂, Walker Pass, 35.67669N, 118.04383W, 1416 m, 21-22-VII-2015, JA Cole, DB Weissman, JAC sound record; 1♂, Walker Pass, 35.662453N, 118.02674W, 1537 m, 21-IX-1967, RE Love, CAS; 4♂, 4♀, Walker Pass, 35.662453N, 118.02674W, 1537 m, 22-VIII-1938, ER Tinkham, CAS; 2♂, same data except 29-IX-1960, JR Helfer, CAS; 3♂, Walker Pass, 35.662453N, 118.02674W, 1524 m, 7-IX-1966, DC & KA Rentz, CAS; 1♂, Walker Pass Campground, BLM, 15 mi. E of Onyx off SR178, 35.689934N, 117.952753W, 1537 m, 13-14-VII-2012, JA Cole, JAC sound record; 2♂, Walker Pass Recreation Area, BLM, 15 miles east of Onyx off SR178, 35.6646N, 118.037W, 1537 m, 13-14-VII-2005, JA Cole, LACM; 1♂, same data except 23-24-VI-2008, JA Cole, JAC sound record; **Mono Co.**, in addition to type material (above), 2♂, 13 mi. N of Lee Vining, 38.145913N, 119.121816W, 2164 m, 24-VIII-1957, ER Tinkham, CAS; 1♂, French Camp, Inyo National Forest, 0.25 mi. S of Tom's Place on Rock Creek Rd., 37.5505N, 118.6836W, 2249 m, 16-VII-2012, JA Cole, LACM; 11♂, Mono Lake, 38.007604N, 119.014763W, 1958 m, 11-VIII-1938, ER Tinkham, CAS; 7♂, Mouth of Tioga Pass, nr. Mono Lake, 38.007604N, 119.014763W, 1-VIII-1931, ER Tinkham, CAS; **Tulare Co.**, 2♂, Kennedy Meadow, 26 miles northwest of Pearsonville via Nine Mile Canyon Road and Kennedy Meadows Road, 36.0518N, 118.1288W, 1883 m, 11-13-VII-2003, JA Cole, JF Eguizabal, LACM.

Lucubrata Group

The Lucubrata Group contains one early branching species (Figs. 3–5) that inhabits the South Coast Ranges of California (Figs. 8, 19). This group is defined by having one spine on the posterior margin of the fore femora, a pair of well-developed prosternal spines, and in having the apices of the tegmina darkened. This suite of characters is shared only with the Propsti Group. The lateral carinae of the male subgenital plate taper regularly to a narrow apex and styli are rudimentary. Male subgenital plates of the Carinata, Propsti, and Castanea Groups have subparallel lateral carinae and well-developed articulate styli. The song of the Lucubrata Group is delivered in bouts (Plate 5C), as opposed to the continuous PT of the Propsti Group (Plate 4J). The karyotype is unique.

Neduba lucubrata Cole, Weissman, & Lightfoot, sp. n.

Fig. 19 (distribution), Fig. 23 (male and female habitus, calling song, drumming, male and female terminalia, karyotype), Plate 2E (live habitus), Plate 5C (male calling song), Plate 7G–H (male ventral sclerites), Plate 10D (male titillators), Plate 12A (female subgenital plate).

Common name. Midnight Shieldback.

History of recognition. None.

Type material. HOLOTYPE MALE, USA, CA, Monterey Co., Miller's Lodge, 0.6 miles west jct. Arroyo Seco Road and G16, 36.25466N, 121.43208W, 192 m, 22-VII-2015, JA Cole, DB Weissman, JAC000002197 [specimen barcode], DNA161 [tissue], SING0503 [DNA extraction], JCT15-08 [karyotype], genitalia in vial under specimen, deposited in CAS, Entomology type #19712.

PARATYPES (n = 32): All USA, CA, Monterey Co., 4♂, 1♀, same data as holotype, LACM; 2♂, 1♀, Arroyo Seco Rd., 0.6 mi. W of intersection with G16, 36.235139N, 121.473392W, 274 m, 29-VII-1983, DB Weissman, CAS; 3♂, Bottcher's Gap, Los Padres National Forest, 19 miles north of Big Sur off SR1 on Palo Colorado Road, 36.355N, 121.8138W, 652 m, 20-21-VIII-2012, JA Cole, LACM; 1♂, same data except 7-8-IX-2002, JA Cole, LACM; 7♂, Nacimiento-Ferguson Rd., at bridge of Nacimiento River, 8.4 miles east of SR1, 36.0135N, 121.4216W, 587 m, 19-20-VIII-2012, JA Cole, LACM; San Benito Co., 9♂, Short Fence Trailhead, Coalinga Road, Laguna Mountain Recreation Area, BLM, 36.36403N, 120.8784W, 670 m, 10-11-VIII-2017, JA Cole, LACM; 2♂, same data except 10-11-VIII-2017, JA Cole, JAC; 2♂, Upper Sweetwater Campground, Coalinga Road, Laguna Mountain Recreation Area, BLM, 36.36067N, 120.85256W, 848 m, 10-11-VIII-2017, JA Cole, LACM.

Measurements. (mm, ♂n = 24, ♀n = 2) Hind femur ♂16.35–20.74, ♀21.61–22.90, pronotum total length ♂7.04–9.03, ♀8.95–9.17, prozona length ♂2.65–4.78, ♀4.02–4.18, metazona dorsal length ♂3.85–5.10, ♀4.77–5.15, pronotum constriction width ♂1.85–2.66, ♀2.70–3.35, metazona dorsal width ♂5.36–6.25, ♀5.76–6.35, head width ♂3.90–4.70, ♀5.11–5.46, ovipositor length ♀16.50–16.60.

Distribution. Santa Lucia and Diablo Ranges in the South Coast Range, California.

Habitat. Mixed woodland and chaparral. Taken from twigs in tangles, poison oak, and California sage (*Artemisia californica* Less.). Males call approximately 1 m above ground level in thick tangles. At dusk two males and one female emerged for nocturnal activity from a pack rat nest, suggesting that this structure served as a daytime shelter for an aggregation of individuals. These individuals retreated into the nest when disturbed.

Seasonal occurrence. Adults from late July (22-VII-2015, JA Cole and DB Weissman, LACM) through early September (8-IX-2002, JA Cole, LACM).

Stridulatory file. (n = 7) length 3.2–3.8 mm, 121–186 teeth, tooth density 45.9 ± 4.2 (38.4–50.0) teeth/mm.

Song. (n = 31) Brief bouts separated by long intervals between bouts. PTR is 4.0 ± 0.5 s⁻¹. Males may add one PT to each successive bout, for example three successive bouts may consist of 3 PT, 4 PT, then 5 PT, and then the cycle recommences at 3 PT. PTF is 14.9 ± 0.8 kHz. Males may accompany stridulation with audible drumming, which is generated by the abdomen striking the substrate (Weissman 2001; JAC pers. obs.). Drumming coincides with partial PT at the beginning of a bout (Fig. 23). Drumming does not occur frequently and may not occur in all populations. Drumming was observed at the Monterey County localities of Arroyo Seco (one of two males, DBW, JAC, pers. obs.) and Bottcher's Gap (JAC, pers. obs.), but not at any San Benito County localities.

Karyotype. (n = 8) Unique. $2n♂ = 24$ (2m + 20t + XtYt). T83-37, S83-107, paratopotype.

Recognition. With a single apical protibial spine, dark apical tegminal spots and prosternal spines, this species may be confused only with *N. propsti*, a larger species that does not occur on the California mainland. The female subgenital plate length and width are subequal, in contrast with the elongated subgenital plate of *N. propsti*. The song, which consists of short stridulation bouts accompanied by drumming, is unique.

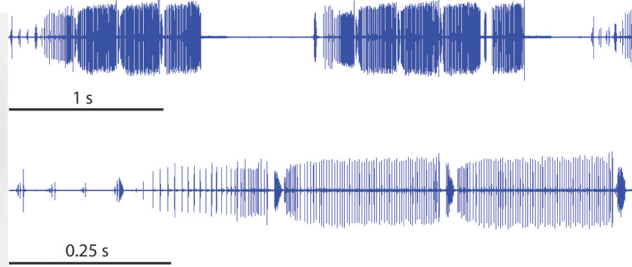
Etymology. *l. lucubrata* burning the midnight oil, descriptive of male acoustic activity continuing throughout the night.

Notes. This species shares morphological and genitalic characteristics with *N. propsti* as well as with the species of the Sierranus and Castanea Groups. Santa Lucia Range and Diablo Range populations are genetically distinct (Figs. 3–5) but are separable neither morphologically nor bioacoustically. The chirping song structure combined with abdominal drumming makes *N. lucubrata* the most acoustically distinct species of *Neduba*. Selection for mate recognition may have driven the evolution of distinctive song phrasing in *N. lucubrata*, as within its distribution are found two sympatric nedubines: *N. carinata* and a small *Aglaothorax* species. Females may require silent periods

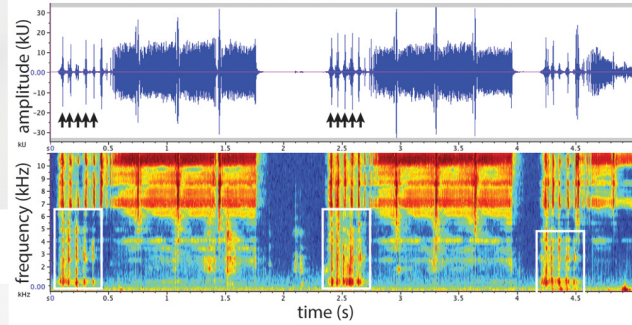
male HOLOTYPE CA: Monterey Co.
JAC000002197



calling song PARATOPOTYPE CA: Monterey Co. 24.5°C JCR150802_04



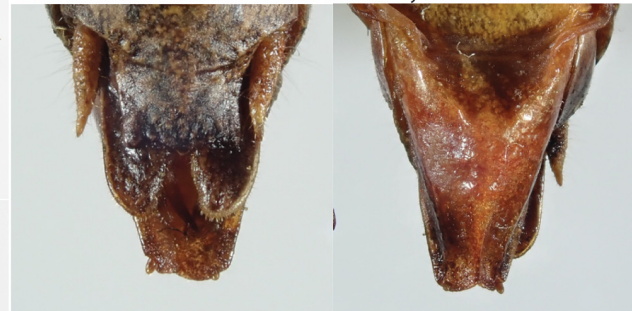
calling song with drumming (arrows and white boxes)
PARATOPOTYPE CA: Monterey Co. 24.5°C JCR150802_04



female PARATOPOTYPE CA: Monterey Co.
JAC000002198



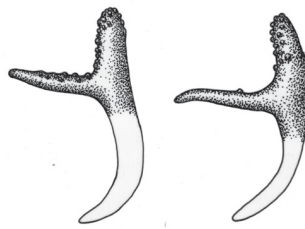
male terminalia PARATOPOTYPE CA: Monterey Co. JAC000002195



ventral sclerite
HOLOTYPE
JAC000002197

PARATYPE
Monterey Co.
JAC000002199

female terminalia PARATOPOTYPE
CA: Monterey Co. JAC000002198



male PARATYPE CA: San Benito Co.
JAC000002216



karyotype PARATOPOTYPE CA: Monterey Co. S83-107 T83-37

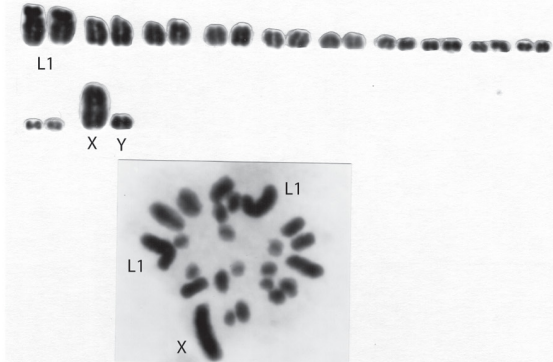


FIGURE 23. *N. lucubrata* male and female habitus, calling song, male and female terminalia, karyotype.

of an appropriate intermediate length between bouts to recognize a conspecific male signal (Cole 2016): intermediate length gaps between PT bouts will contrast with the continuous PT production of sympatric *N. carinata* as well and the long periods of silence between pulse production in *Aglaothorax*.

Material examined. Type series only. See Type material above.

Sierranus Group

The Sierranus Group is composed of 3 species (*sierranus*, *arborea*, and *radocantans*). Like the Sequoia Group, all Sierranus Group species have a single spine on the posterior margin of the forefemur, a pair of prosternal spines, and the entire male tegmen ivory or white. The male subgenital plate has lateral carinae that converge to the apex, which is devoid of styli, petal-like and often reflexed. The stridulatory file tooth density is the highest of all *Neduba* species groups (59–77 teeth/mm), and this character alone separates it from all Sequoia Group species except *N. inversa*. The Sierranus Group is distributed in the central and northern Sierra Nevada while the Sequoia Group occupies the southern portions of that mountain range (Figs. 8, 19). Within this Group are morphologically cryptic species defined by song and/or karyotype. Body part measurements and stridulatory files offer the only means to identify males that lack song data. Females may also be identified by body part measurements and sometimes the shape of the subgenital plate. Species are parapatric in the Sierra Nevada (Fig. 19) and thus geography will serve to narrow species possibilities. Molecular data show hybridization (Fig. 4) between species with adjacent ranges.

Neduba sierranus (Rehn & Hebard, 1910)

Fig. 19 (distribution), Fig. 24 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 2F–G (live habitus), Plate 5D (male calling song), Plate 8A (male ventral sclerite), Plate 10E (male titillators), Plate 12B (female subgenital plate).

Common name. Yosemite Shieldback.

History of recognition. Described in *Aglaothorax* from Yosemite Valley (Rehn & Hebard 1910) and transferred to *Neduba* (Rehn & Hebard 1912). The Tulare and Kern County records in Rentz and Birchim (1968) belong to Sequoia Group species that are described in this work (*N. sequoia* and *N. prorocantans*).

Type material. The holotype male is in ANSP. Images of the holotype are available at OSFO (Cigliano *et al.* 2020). **TOPOTYPES:** All USA, CA, Mariposa Co., 2♂, Carl Inn, Yosemite, 12-VIII-1938, ER Tinkham, CAS; 4♂, Yosemite National Park, Wawona, 37.53694N, 119.65528W, 1223 m, 27-VIII-1982, DB & BI Weissman, CAS; 4♂, 4♀, Yosemite National Park, Wawona Area, Redwood Estates, 37.53694N, 119.65528W, 1250 m, 23-25-VI-1989, DB Weissman, CAS.

Measurements. (mm, ♂_n = 14, ♀_n = 5) Hind femur ♂18.11–22.25, ♀21.92–23.60, pronotum total length ♂7.87–9.90, ♀8.54–9.00, prozona length ♂3.80–4.99, ♀4.35–4.91, metazona dorsal length ♂4.01–5.45, ♀3.83–4.50, pronotum constriction width ♂2.60–3.23, ♀2.85–3.20, metazona dorsal width ♂5.47–6.67, ♀5.64–6.05, head width ♂4.50–5.40, ♀5.20–5.65, ovipositor length ♀13.75–14.84.

Distribution. Western slope of the Central Sierra Nevada of California, distributed between the Merced and Mokelumne River watersheds in the vicinity of Yosemite National Park.

Habitat. Mixed conifer forests. Males call from dense understory vegetation and from pine needle litter, most commonly 15 cm or less from the ground but occasionally as high as 3 m above the ground in conifers. This species is associated with mountain misery (*Chamaebatia foliosa* Benth.), incense cedar (*Calocedrus decurrens* (Torr.) Florin), western bracken fern (*Pteridium aquilinum* (L.) Kuhn), and white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.).

Seasonal occurrence. Adults have been taken from early July (9-VII-1968, TR Haig, CSCA) into mid-September (12-IX-2015, JA Cole, LACM). Last instar nymphs from late June into early July.

Stridulatory file. (n = 7) length 2.9–3.6 mm, 196–234 teeth, tooth density 66.1 ± 5.9 (58.8–75.5) teeth/mm.

Song. (n = 14) The calling song of this species was published in Morris *et al.* (1975). The song of *N. sierranus*, like all other species in the Sierranus Group, has a complex pattern of several OPT between MPT, and gives the song a “fluttering” quality as perceived by a human listener. The PTF is 16.2 ± 1.2 kHz, and at this high carrier

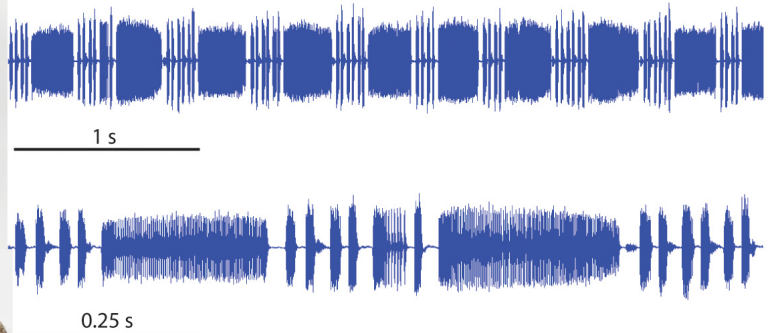
frequency the songs of these insects are difficult for many humans to hear, and a listener must be in close proximity to the singing male to detect him. The PTR of $1.7 \pm 0.3 \text{ s}^{-1}$ is the fastest rate among the *Sierranus* Group (ANCOVA, $P = 3.96 \times 10^{-9}$).

Karyotype. ($n = 9$) $2n_{\text{♂}} = 21$ (18t + XtXtYm), shared only with *N. duplocantans*. T89-20, S89-47, topotype.

male TOPOTYPE CA: Mariposa Co.
S82-110 R82-160



calling song TOPOTYPE CA: Mariposa Co. 25.0°C S89-47 R89-59



female TOPOTYPE CA: Mariposa Co. S89-47



male terminalia CA: Madera Co. JAC000002360



ventral sclerite
TOPOTYPE
S89-47, R89-59



female CA: Madera Co. JAC000002360



karyotype TOPOTYPE CA: Mariposa Co. S89-47 T89-20

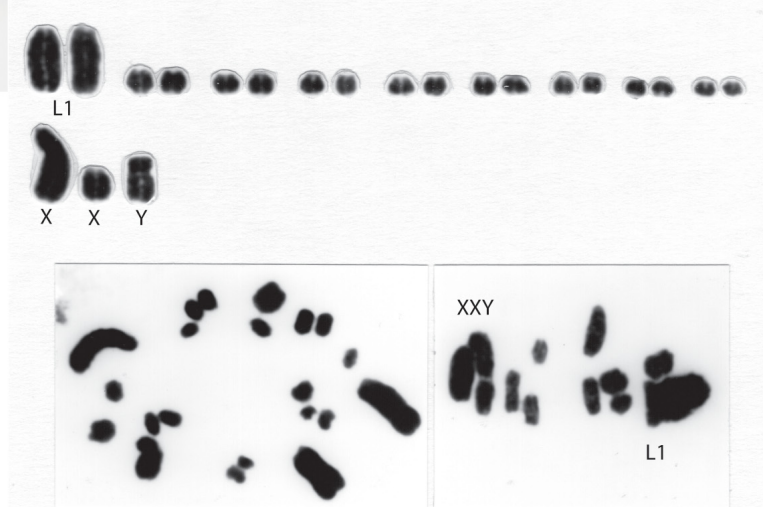


FIGURE 24. *N. sierranus* male and female habitus, calling song, male and female terminalia, karyotype.

Recognition. Males may be identified by the combination of a high stridulatory file tooth density (62–70 teeth/mm) and a pronotum that is not strongly constricted. *N. sierranus* has two parapatric neighbors that also have high tooth densities: *N. inversa* to the south and *N. radocantans* to the north, but those species have stronger pronotum constrictions. The PTR is faster than all other species with multiple OPT (*N. arborea*, *N. radocantans*, and *N. inversa*). Karyotype also separates this species from *N. radocantans* and *N. inversa*. The subtriangular subgenital plate that is longer than wide is unique among the Sierranus and Sequoia groups.

Notes. Based on comparison of rDNA and mtDNA topologies (Fig. 4), this species has hybridized with its parapatric neighbors to the south and north: *N. inversa* and *N. radocantans*, respectively. The three species are morphologically cryptic. Species status for Sierranus Group lineages is based on song and karyotype. Song differences between these three species may reinforce prezygotic isolation if hybrids between species that differ in chromosome arrangement suffer reduced fitness.

Material examined. DETERMINED (n = 23): **Calaveras Co.**, 1♂, 1♀, Golden Pines RV Resort and Campground, 38.29808N, 120.28773W, 1570 m, 14-15-VIII-2015, JA Cole, LACM; **Madera Co.**, 4♂, 2♀, Narrow Gauge Inn, Fish Camp, 37.45506N, 119.64345W, 1435 m, 11-12-IX-2015, JA Cole, LACM; 1♀, Narrow Gauge Inn, Fish Camp, 37.45506N, 119.64345W, 1435 m, 11-12-IX-2015, JA Cole, JAC; **Mariposa Co.**, in addition to type material (above), 1♂, 1 mi. W El Portal, 37.67465N, 119.80238W, 29-VII-1965, RP Allen, CSCA; 1♀, Hites Cove, 37.64083N, 119.84806W, 9-VII-1968, TR Haig, CSCA; 1♂, Jerseydale Campground, Sierra National Forest, 13.5 miles northeast of Mariposa, 37.5451N, 119.8386W, 1131 m, 10-11-VIII-2002, JA Cole, LACM; 1♂, 1♀, same data except JAC; 3♂, same data except 28-29-VII-2012, JA Cole, LACM; **Tuolumne Co.**, 3♂, Mill Creek Campground, Stanislaus National Forest, FR5N21 off Mono Way (SR108), 38.30168N, 119.93763W, 1918 m, 23-24-VIII-2019, JA Cole, J Bailey, SA Downing, LACM; 2♂, same data except JAC; QUESTIONABLE PLACEMENT (n = 5): **Amador Co.**, 1♀, Ponderosa Rd., 1.5 mi. N of Mokelumne River, 38.34889N, 120.77306W, 21-VIII-1984, RW, BMED; **Calaveras Co.**, 1♀, West Point, 38.399079N, 120.527426W, 18-VIII-1929, CAS; **Madera Co.**, 1♀, Bass Lake, 37.324666N, 119.566254W, 20-VII-1934, FE Blaisdell, CAS; 1♀, Oakhurst, 37.328N, 119.649315W, 914 m, 29-VI-1946, HP Chandler, CAS; **Tuolumne Co.**, 1♀, Jamestown, 37.953258N, 120.422695W, 429 m, 1978, Schultz, CSCA.

Neduba arborea Cole, Weissman, & Lightfoot sp. n.

Fig. 19 (distribution), Fig. 25 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 3B (live habitus), Plate 5F (male calling song), Plate 8C (male ventral sclerite), Plate 12C (female subgenital plate).

Common name. Arboreal Shieldback.

History of recognition. None.

Type material. HOLOTYPE MALE: USA, CA, Colusa Co., SR20, mile marker 11.36, 39.1056N, 122.31903W, 129 m, 19-VII-2015, JA Cole, DB Weissman, JAC000001958 [specimen barcode], JCR150803_01 [recording], DNA159 [tissue], SING0501 [extraction], JCT15-05 [karyotype], tegmen removed in gelcap below specimen, 219 [tooth count], 3.4 mm [file length], genitalia in vial below specimen, deposited in CAS, Entomology type #19707.

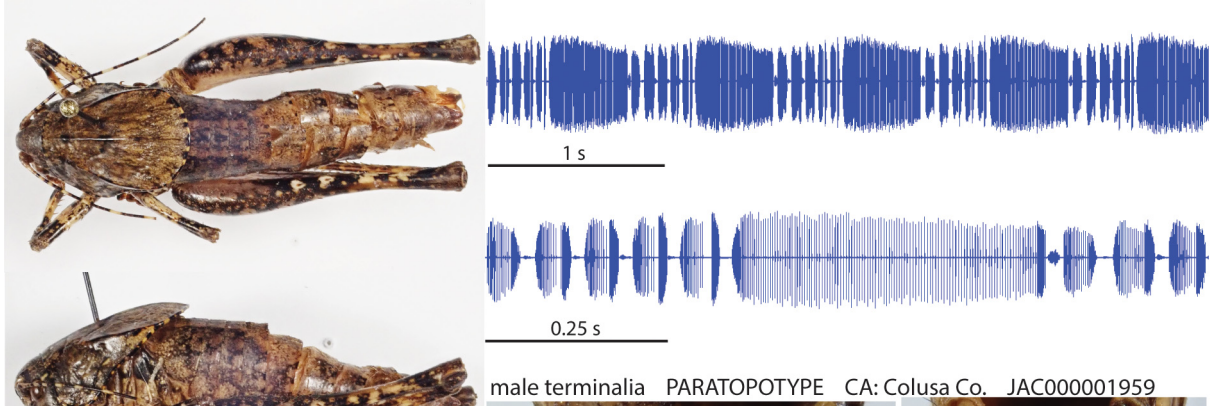
PARATYPES (n = 6): **Colusa Co.**, 2♀, SR20, 11.5 miles west of I-5 at mile post 11.22., 39.10567N, 122.32102W, 150 m, 22-IV-2007, DB Weissman, LACM; 1♂, 1♀, SR20, mile marker 11.36, 39.1056N, 122.31903W, 129 m, 19-VII-2015, JA Cole, DB Weissman, CAS; 1♂, SR20, mile marker 11.4, 39.10547N, 122.31759W, 423 m, 5-VIII-2014, JA Cole, DB Weissman, LACM; 1♀, same data except CAS.

Measurements. (mm, ♂n = 3, ♀n = 2) Hind femur ♂22.23–23.27, ♀22.44–24.09, pronotum total length ♂10.54–11.60, ♀10.09–10.49, prozona length ♂4.55–5.19, ♀4.94–5.76, metazona dorsal length ♂5.58–6.41, ♀4.33–5.55, pronotum constriction width ♂3.10–3.56, ♀3.08–3.58, metazona dorsal width ♂7.00–7.35, ♀6.72–6.80, head width ♂5.87–6.08, ♀5.72–5.87, ovipositor length ♀16.40–16.60.

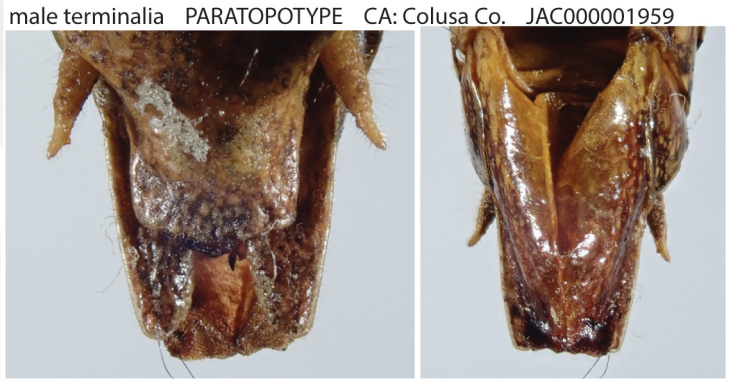
Distribution. East slopes of the North Coast Ranges bordering the California Central Valley. The type locality is along the Cortina Ridge.

Habitat. Oak woodland. Topotype males sang from ground level or from oak branches 1 m or more above the ground.

male HOLOTYPE CA: Colusa Co. JAC000001958 calling song PARATOPOTYPE CA: Colusa Co. 25.0°C JCR150806_00



female PARATOPOTYPE CA: Colusa Co. JAC000001960



male terminalia PARATOPOTYPE CA: Colusa Co. JAC000001959



male PARATOPOTYPE CA: Colusa Co. JAC000001959

ventral sclerite HOLOTYPE



female terminalia PARATOPOTYPE CA: Colusa Co. JAC000001954



karyotype PARATOPOTYPE CA: Colusa Co. S14-61 JCT14-06

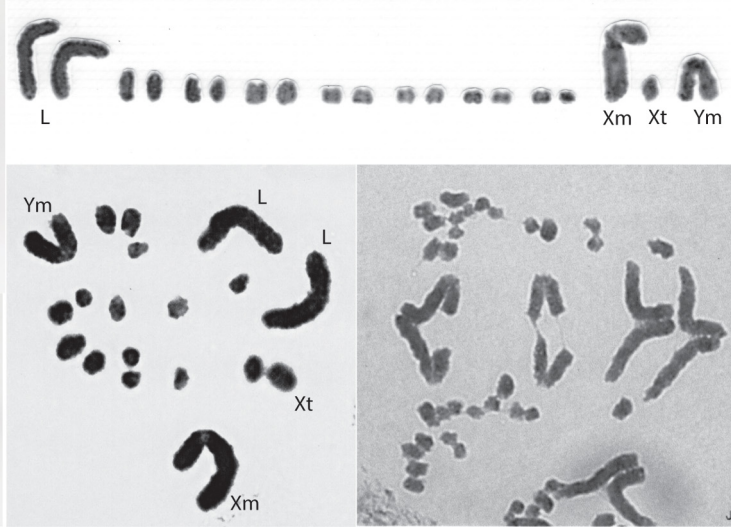


FIGURE 25. *N. arborea* male and female habitus, calling song, male and female terminalia, karyotype.

Seasonal occurrence. Limited records show that nymphs occur in April (11-IV-2007, DB Weissman, CAS) and adults are active by mid-July (19-VII-2015, JA Cole and DB Weissman, CAS) into August (5-VIII-2014, JA Cole, DB Weissman, CAS).

Stridulatory file. (n = 3), length 3.2–3.5 mm, 190–219 teeth, tooth density 60.9 ± 3.1 (58.9–64.4) teeth/mm.

Song. (n = 4) Similar to *N. sierranus* in consisting of several OPT (10.6 ± 3.7 (5.0–15.3)) that are interspersed between MPT. The PTR of 1.20 ± 0.03 is intermediate: slower than *N. sierranus*, faster than *N. radocantans*, and statistically indistinguishable from *N. inversa*. PTF is 16.9 ± 0.5 kHz.

Karyotype. (n = 3) Unique. $2n\♂ = 19$ (16t + XmXtYm). JCT14-06, S14-61, paratopotype.

Recognition. Both sexes have the largest body size (pronotum length more than 10 mm) of any Sierranus Group species and are noticeably robust in comparison with the typical fusiform shape of *Neduba*. The male pronotum is weakly constricted as in *N. prorocantans* and *N. sierranus*, but not only is *N. arborea* larger than those species but the stridulatory file tooth density is greater (59–62 teeth/mm) than the former (47–52 teeth/mm) and less than the latter (62–70 teeth/mm). *N. inversa* is also separated from this species by a higher tooth density (64–68 teeth/mm) and a strong pronotum constriction. The oval, highly convex female subgenital plate is distinctive. Song PTR will separate this species from all others in the Sierranus Group, but not from *N. inversa* in the Sequoia Group, a smaller species with a strong pronotum constriction. The karyotype is unique. This is the only extant Sierranus or Sequoia Group species known from the Coast Ranges of California.

Etymology. *l. arborea* “of the trees” in reference to the male habit of singing from oak branches above the understory.

Notes. The discovery of a member of the Sierranus Group in the Coast Ranges is significant as *N. extincta*, the only other species in either the Sierranus or the Sequoia Group distributed west of the Central Valley is, as the name suggests, extinct (Rentz 1977). Female nymphs were the first individuals of this species to be encountered. DNA from these females indicated that the population was distinct from known Sierranus Group taxa. Once males were collected the unique karyotype provided more evidence for specific distinction. Further investigation of the North Coast Ranges should be undertaken as the Sierranus Group may have crossed the Central Valley on multiple occasions.

Material examined. Type series only. See Type material above.

***Neduba radocantans* Cole, Weissman, & Lightfoot, sp. n.**

Fig. 19 (distribution), Fig. 26 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 3A (live habitus), Plate 5E (male calling song), Plate 8B (male ventral sclerite), Plate 10F (male titillators), Plate 12D (female subgenital plate).

Common name. Raspy Shieldback.

History of recognition. None.

Type material. HOLOTYPE MALE: USA, CA, El Dorado Co., Finnon Reservoir, 5 mi. NE Placerville, 38.780862N, 120.732843W, 790 m, 5-6-VIII-1995, DB Weissman, S95-62 [stop], R95-49 [recording], T95-21 [testes], tegmen in gelcap and genitalia in vial below insect, deposited in CAS, Entomology type #19680.

PARATYPES (n = 17): USA, CA, El Dorado Co., 1♂, 2♀, same data as holotype; 4♂, 2♀, Finnon Reservoir, 5 mi. NE Placerville, 38.79978N, 120.74947W, 740 m, 8-9-VIII-2014, JA Cole, DB Weissman, LACM; 8♂, US50 3.7 mi. W Kyburz, 38.76427N, 120.35897W, 1112 m, 19-VII-2015, JA Cole, DB Weissman, LACM.

Measurements. (mm, ♂n = 12, ♀n = 4) Hind femur ♂18.26–20.50, ♀19.48–21.29, pronotum total length ♂7.96–9.70, ♀7.85–8.85, prozona length ♂3.46–5.07, ♀3.89–5.08, metazona dorsal length ♂3.92–5.50, ♀3.32–4.25, pronotum constriction width ♂2.20–2.63, ♀2.35–2.80, metazona dorsal width ♂5.47–6.41, ♀4.92–5.62, head width ♂4.40–4.75, ♀4.60–5.23, ovipositor length ♀13.45–18.05.

Habitat. Oak woodland understory and riparian. In tangles, leaf litter, and bunch grass under oaks. This species inhabits mixed conifer forests at lower elevations than does *N. radicata*, but the two overlap at the extremes of their elevational distributions.

Seasonal occurrence. Midsummer as indicated by scant records: July (19-VII-2015, JA Cole & DB Weissman, LACM) into August (9-VIII-2014, JA Cole, D.B. Weissman, LACM).

Distribution. West slope of the Sierra Nevada in the vicinity of the American River watershed.

male HOLOTYPE CA: El Dorado Co. S95-62



female PARATYPE CA: El Dorado Co. S95-62



female terminalia PARATOPOTYPE
CA: El Dorado Co. JAC000002307



calling song PARATOPOTYPE CA: El Dorado Co. 25.0°C JCR150804_01



male terminalia PARATYPE CA: El Dorado Co. JAC000002308



ventral sclerite
HOLOTYPE



karyotype PARATOPOTYPE CA: El Dorado Co. S95-62 T95-20

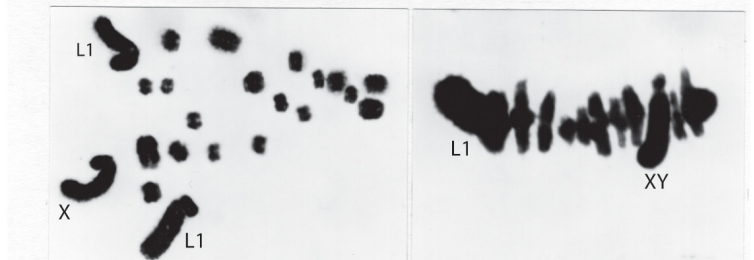
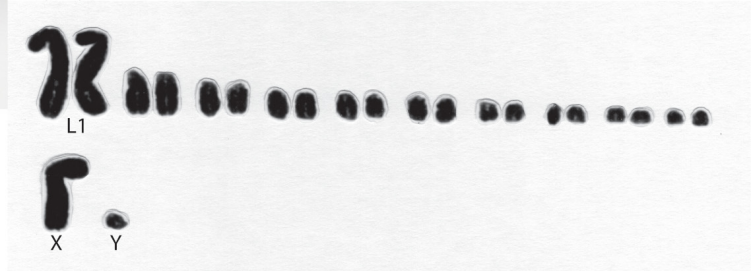


FIGURE 26. *N. radocantans* male and female habitus, calling song, male and female terminalia, karyotype.

Stridulatory file. (n = 5) length 3.2–3.4 mm, 200–250 teeth, tooth density 70.6 ± 5.5 (62.5–76.9) teeth/mm.

Song. (n = 19) Unique in the high PTN of 19.9 ± 3.9 (two-way ANOVA, $P = 1.93 \times 10^{-15}$). The greater portion of airtime spent producing OPT makes the PTR slower ($0.8 \pm 0.3 \text{ s}^{-1}$, ANCOVA, $P = 3.96 \times 10^{-9}$) than that of other Sierranus Group species. PTF is $16.2 \pm 1.2 \text{ kHz}$.

Karyotype. (n = 6) Unique. $2n\text{♂} = 22$ (2m + 18t + XmYt), T95-20, S95-62, paratopotype.

Recognition. Males have both a high stridulatory file tooth density (68–73 teeth/mm) and a strongly constricted pronotum. Male *N. sierranus* have a similar high tooth density but the pronotum constriction is weak. *N. inversa* is difficult to separate but tends to have a lower stridulatory file tooth density. Female hind femora are shorter than other Sierranus and Sequoia group species. The song has the slowest PTR and highest PTN of the Sierranus Group. The latter song feature is temperature-invariant and distinct to a human listener, and thus may be used to identify this species in song surveys that lack temperature correction. Inhabiting the vicinity of the American River drainage, this species ranges the farthest north of any in the Sierranus Group (Fig. 19).

Etymology. *l. rado* “scrape” + *cantans* “singing”. Refers to the rasping, abrasive sound quality of the numerous minor PT in the male song.

Notes. Distributed at the northern limit of the Sierranus Group, *N. radocantans* is sympatric with *N. radicata*, the species with the most southerly distribution in the Carinata Group where their elevational distributions overlap. Selection for mate recognition at a contact zone could have driven the evolution of the distinctive, elaborate song with numerous OPT in this species. The population near Kyburz, California was located with a bat detector while night driving. Males were common but no females could be found, even after trampling vegetation. *N. radicata* songs were heard in trees at this locality. The type locality of Finnon Lake is private property that is owned and managed by the Mosquito Volunteer Fire Association (www.gomvfa.org). The conservation prospectus of this area is unknown.

Material examined. Type series only, see Type material above.

Sequoia Group

The phylogenetically defined Sequoia Group includes the species *extincta*, *inversa*, *sequoia*, *prorocantans*, and *duplocantans*. Males of all but one of the four species are morphologically separated from the Sierranus Group by the lower stridulatory file tooth density (46–62 teeth/mm). Like the Sierranus Group, the species are diagnosed by song and karyotype and are morphologically cryptic; only measurements of body parts and stridulatory file tooth density differ. As in the Sierranus Group, each species occupies distinct watersheds in the Sierra Nevada, albeit farther south (Fig. 8). This group contains the only pair of fully sympatric *Neduba* species within the same species Group.

Neduba extincta Rentz, 1977

Fig. 19 (distribution).

Common name. Extinct Shieldback.

History of recognition. Described from a single male museum specimen deposited at CAS (Rentz 1977).

Type material. The holotype male is the only specimen known. Images of the holotype are available at OSFO (Cigliano *et al.* 2020).

Measurements. See Rentz (1977).

Distribution. Antioch Sand Dunes, Contra Costa County, California, on the western edge of the Central Valley.

Habitat. Historically known from the sandy banks of the San Joaquin River, elevation 9 m. The 55 acre Antioch Dunes National Wildlife Refuge is the only National Wildlife Refuge in the country established to protect endangered plants and insects.

Seasonal occurrence. The only known specimen was collected 1-VII-1937 (ES Ross, CAS).

Stridulatory file. (n = 1) length 3.2 mm, 167 teeth, tooth density 52.2 teeth/mm,

Song. Unknown.

Karyotype. Unknown.

Recognition. Description indicates large body size and absence of styli on subgenital plate. The stridulatory file tooth density places this species at the upper end of variation for the Sequoia Group. The tooth density of the single known specimen is less than the closest geographic relative, *N. inversa* (density 64–68 teeth/mm). The single specimen is the only Sequoia Group individual collected in the Central Valley west of the Sierra Nevada.

Notes. This species is one of four extinct North American Orthoptera species (Hoekstra 1998) and that status has not changed; David Rentz and DBW have searched for this species at the type locality on several occasions over the last few decades, visiting during summer months when *Neduba* are active and using a bat detector. On no occasion were individuals found. The lack of molecular, bioacoustical, and cytogenetic characters make this species difficult to place in context of this revision, but the stridulatory file tooth density is consistent with the Sequoia Group. Minimally destructive molecular work may be undertaken in the future to place *N. extincta* into phylogenetic context. Among the extant Sequoia Group species, *N. inversa* is distributed near the San Joaquin River watershed and is therefore a possible relative, and this lineage could have colonized the western edge of the Central Valley across riparian corridors. The description of *N. arborea* in this work reports the only other Sierranus or Sequoia Group members known west of the Sierra Nevada. Many *Neduba* populations were no doubt extirpated as the eastern slope of the Coast Ranges became more arid and as humans modified the Central Valley for agriculture. In the case of the Antioch dunes, sand mining and commercial development drove extinction of this species. Thorough collecting efforts are needed in the eastern slopes of the Coast Ranges to search for possible unknown populations.

***Neduba inversa* Cole, Weissman, & Lightfoot, sp. n.**

Fig. 19 (distribution), Fig. 27 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 3C (live habitus), Plate 5G (male calling song), Plate 8D (male ventral sclerite), Plate 10G (male titillators), Plate 12E (female subgenital plate).

Common name. Kings Canyon Shieldback.

History of recognition. Likely confused with *N. sierranus*.

Type material. HOLOTYPE MALE: USA, CA, Fresno Co., Bretz Mill Campground, Sierra National Forest, 24 mi. NE Trimmer on Big Creek Rd., 37.03775N, 119.24040W, 871 m, 13-VIII-2015, JA Cole, JCT15-15 [karyotype], 150820_01 [recording], 206 [teeth], 3.3 [mm file count], tegmen in gel capsule and genitalia in vial below insect deposited in CAS, Entomology type #19710. PARATYPES (n = 19): Fresno Co., 1♂, same data as holotype, CAS; 2♂, same data as holotype, LACM; 3♂, 1♀, Bretz Mill Campground, Sierra National Forest, 24 mi. NE Trimmer on Big Creek Rd., 37.0375N, 119.2388W, 1006 m, 29-30-VII-2012, JA Cole, LACM; 3♂, Princess Campground, Sequoia National Forest, 36.80456N, 118.94154W, 1797 m, 25-27-VII-2017, JA Cole, CAS; 7♂, 1♀, same data except LACM; 1♂, same data except JAC.

Measurements. (mm, ♂n = 17, ♀n = 2) Hind femur ♂20.22–24.12, ♀23.15–23.40, pronotum total length ♂8.17–10.54, ♀8.48–9.42, prozona length ♂3.57–5.11, ♀4.06–4.98, metazona dorsal length ♂4.29–5.95, ♀3.50–5.36, pronotum constriction width ♂2.22–2.95, ♀2.43–2.94, metazona dorsal width ♂5.68–6.63, ♀6.25–6.42, head width ♂4.84–5.47, ♀5.24–5.59, ovipositor length ♀15.81–16.78.

Distribution. West slope of the Sierra Nevada, between the San Joaquin and Kings River watersheds in the vicinity of Kings Canyon National Park.

Habitat. Understory of mixed conifer forests.

Seasonal occurrence. Available records are midsummer from July (1-VII-1935, EE Honeycutt, CAS) through mid-August (13-VIII-2015, JA Cole, LACM).

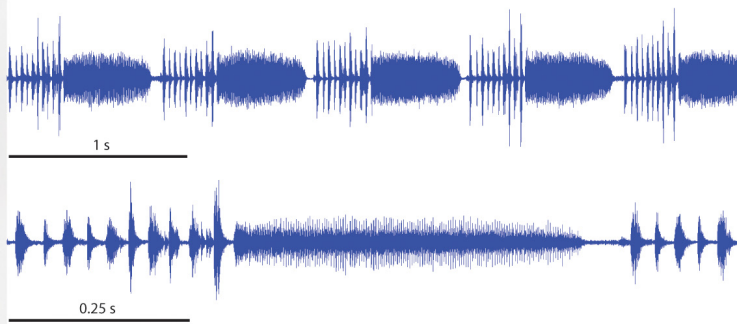
Stridulatory file. (n = 7) length 3.0–4.0 mm, 206–266 teeth, tooth density 66.3 ± 6.9 (55.5–78.3) teeth/mm.

Song. (n = 24) Qualitatively like Sierranus Group taxa, high frequency (PTF 15.9 ± 1.2 kHz) with a fluttering quality caused by multiple OPT (PTN 9.2 ± 3.4). PTR is significantly slower (1.3 ± 0.3 s⁻¹) than *N. sierranus* and faster than *N. radocantans* (ANCOVA, $P = 3.96 \times 10^{-9}$) but is indistinguishable from that of *N. arborea*.

Karyotype. (n = 5) $2n\♂ = 21$ (2m + 16t + XtXtYm). JCT15-15, paratopotype.

Recognition. Males have a high stridulatory file tooth density (64–68 teeth/mm) like *N. sierranus* and *N. radocantans*. A weakly constricted pronotum separates *N. sierranus* from this species. *N. radocantans* is morphologically separable only by its slightly higher stridulatory file tooth density (68–75 teeth/mm). This species belongs to

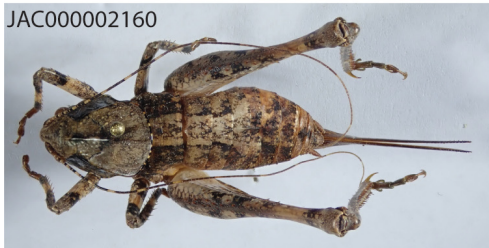
male HOLOTYPE CA: Fresno Co. JAC000002154 calling song PARATOPOTYPE CA: Fresno Co. 24.1°C JCR150830_01



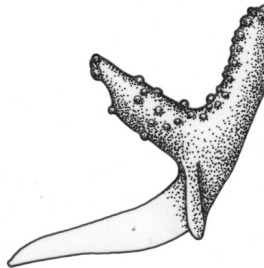
male terminalia PARATOPOTYPE CA: Fresno Co. JAC000002159



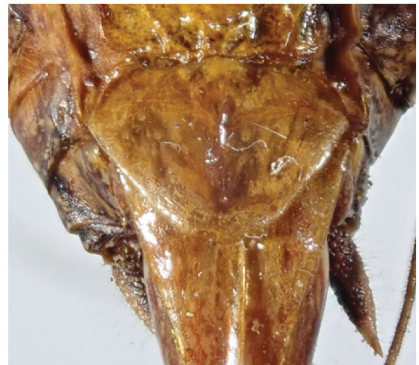
female PARATOPOTYPE CA: Fresno Co. JAC000002160



ventral sclerite HOLOTYPE



female terminalia PARATOPOTYPE CA: Fresno Co. JAC000002160



male PARATYPE CA: Fresno Co. JAC000002168



karyotype PARATOPOTYPE CA: Fresno Co. JCT15-15



FIGURE 27. *N. inversa* male and female habitus, calling song, male and female terminalia, karyotype.

the Sequoia Group lineage but has a Sierranus Group song with multiple OPT. The high PTN of *N. radocantans* will separate that otherwise cryptic species from *N. inversa*. Males of the neighboring species to the north, *N. sierranus*, have songs with a faster PTR than those of *N. inversa*. Songs from all population of the Sequoia Group to the south have only one OPT. Karyotypes also separate *N. inversa* from the geographically proximal species mentioned above. The distribution of this species lies between the San Joaquin and Kings River drainages in the vicinity of Kings Canyon National Park.

Etymology. *l. inversa* “to change, to pervert, to turn upside down,” in reference to the mosaic of characters possessed by this species, with the song of one clade but the genetics of another.

Notes. At the type locality the species was common, but the quiet male songs were drowned out by the incessant loud calls of the shield-back katydid *Cyrtophyllicus chlorum* Hebard. The distribution of *N. inversa* lies where the Sierranus and Sequoia Groups meet in the central Sierra Nevada (Figs. 8, 19). This species combines characters from the two lineages and gene flow between neighboring lineages has occurred during its evolutionary history (Fig. 4). The stridulatory file and the calling song with a fluttering sound, caused by numerous OPT, is similar to *N. sierranus* in the Sierranus Group, which is distributed to the north in the Yosemite Valley region. DNA places this species with Sequoia Group species to the south, however, and this species shares a karyotype with *N. prorocantans*. The remaining Sequoia Group species have simple songs with one OPT between any pair of MPT. Song alleles may have introgressed across species boundaries in this contact zone region (e.g. Cole 2016).

Material examined. Type series only, see Type material above.

Neduba prorocantans Cole, Weissman, & Lightfoot, sp. n.

Fig. 19 (distribution), Fig. 28 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 3D–E (live habitus), Plate 5H (male calling song), Plate 8E (male ventral sclerite), Plate 10H (male titillators), Plate 12F (female subgenital plate).

Common name. Incessant Shieldback

History of recognition. Records from Dougherty Creek, Kern River Canyon, CA (Rentz & Birchim 1968) were confused with *N. sierranus*.

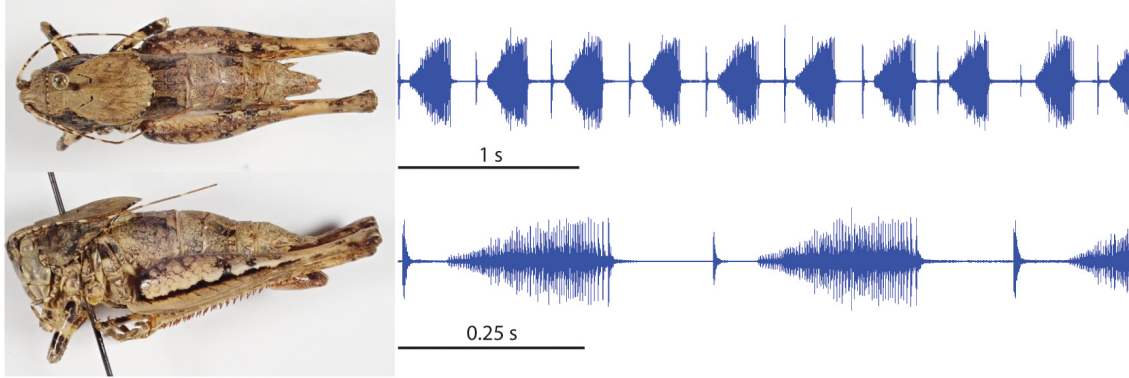
Type material. HOLOTYPE MALE: USA, CA, Kern Co., Tehachapi, Water Canyon Rd., 0.15 mi. S of intersection with Highline Rd., 35.307739N, 118.021738W, elev. 1463 m, 28-VIII-1983, DB Weissman, S83-115, R83-295 [recording], T83-46 [karyotype], 150 [teeth], 3.3 [mm file count], tegmen in gelcap and genitalia in vial below specimen, deposited at CAS, Entomology type #19681.

PARATYPES (n = 30): USA, CA, Kern Co., 3♂, 1♀, same data as holotype; 6♂, Hobo Campground overflow area, 3 miles west of Bodfish on Kern River Canyon Road, 35.5752N, 118.5305W, 700 m, 23-VI-2003, JA Cole, LACM; 1♂, horse trough spot, Tejon Ranch Conservancy, 34.97927N, 118.69159W, 1223 m, 3-VI-2017, L Pavliscak, LACM; 1♂, Kern River Rd. 1.1 mi. from jct. Caliente-Bodfish Rd., 35.59429N, 118.5141W, 1470 m, 21-VII-2015, JA Cole, DB Weissman, LACM; 1♂, Kernville, 37 Sierra Way, 35.7561N, 118.4203W, 828 m, 26-28-VII-2002, JA Cole, JAC; 2♂, same data except LACM; 2♂, same data except 27-VII-2004, JA Cole, LACM; 1♂, same data except 28-VII-2004, JA Cole, JAC; 1♀, Lopez Flat, Tejon Ranch Conservancy, 34.94264N, 118.63381W, 816 m, 3-VI-2017, JA Cole, K Halsey, LACM; 3♂, 1♀, Paradise Valley, Tehachapi Mountains, 34.91664N, 118.66759W, 7-VIII-1931, ER Tinkham, CAS; 1♂, Tehachapi Mountain Park, 35.06861N, 118.4825W, 1470 m, 20-VII-2015, JA Cole, DB Weissman, LACM; 2♂, Tehachapi Mountain Park, 35.06861N, 118.4825W, 1707 m, 28-VIII-1983, DB Weissman, CAS; 1♀, Tejon Ranch Conservancy, Indian Schoolhouse, Tejon Creek, 35.04512N, 118.67052W, 647 m, 1-IV-2018, K Moore, LACM; 4♂, Water Canyon Rd., 1.4 mi. below entrance to Tehachapi Mountain Park, 35.08258N, 118.49486W, 1571 m, 20-VII-2015, JA Cole, DB Weissman, LACM.

Measurements. (mm, ♂n = 14, ♀n = 2) Hind femur ♂19.60–22.59, ♀22.55–23.50, pronotum total length ♂8.25–10.15, ♀9.25–9.65, prozona length ♂3.83–5.09, ♀4.54–5.65, metazona dorsal length ♂4.07–5.35 ♀4.00–4.71, pronotum constriction width ♂2.44–3.50, ♀3.24–3.29, metazona dorsal width ♂4.99–6.80, ♀5.60–5.89, head width ♂4.70–5.57, ♀5.47–5.60, ovipositor length ♀8.75–9.41.

Distribution. West slope of the southern Sierra Nevada south of the Tule River watershed, south to the north slope of the Tehachapi Mountains.

male HOLOTYPE CA: Kern Co. S83-115 calling song PARATOPOTYPE CA: Kern Co. 25.0°C JCR150830_00



female PARATYPE CA: Kern Co. JAC000002279



male terminalia PARATOPOTYPE CA: Kern Co. S83-115 R83-291



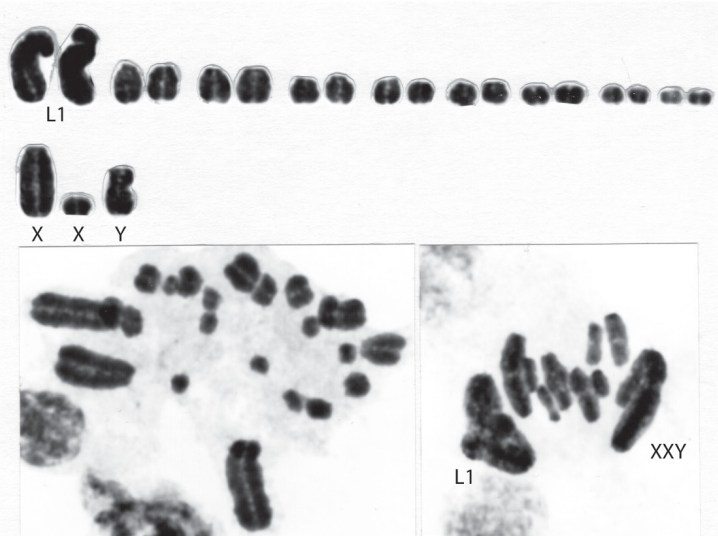
male PARATOPOTYPE CA: Kern Co. S83-115



ventral sclerite HOLOTYPE



karyotype PARATOPOTYPE CA: Kern Co. S83-115 T83-44



female terminalia PARATOPOTYPE CA: Kern Co. S83-115



FIGURE 28. *N. prorocantans* male and female habitus, calling song, male and female terminalia, karyotype.

Habitat. Forest understory, often in thick tangles of vegetation. Taken from poison oak, willow (*Salix* spp.), and thorny brambles in riparian areas. Nymphs were collected from under bark of fallen tree limbs and from leaf litter under a valley oak tree (*Quercus lobata* Née). Museum specimens (ER Tinkham, CAS) also indicate association with oaks.

Seasonal occurrence. Adults collected in the field from late June (23-VI-2003, JA Cole, LACM) through August (28-VIII-1983, DB Weissman, CAS). Last instar nymph collected in early June (3-VI-2017, LA Pavliscak, LACM) matured 19-VI-2017.

Stridulatory file. (n = 5) length 3.3–3.8 mm, 150–183 teeth, tooth density 49.1 ± 2.7 (45.5–52.4) teeth/mm.

Song. (n = 12) A continuous train of alternating MPT and OPT delivered at PTR 2.4 ± 0.3 s⁻¹. The PTdc is $62.1 \pm 9.7\%$, which is lower than that of *N. sequoia* (ANCOVA, $P = 3.75 \times 10^{-4}$). The PTF is high at 15.6 ± 1.2 kHz.

Karyotype. (n = 7) $2n\♂ = 21$ (2m + 16t + XtXtYm). T83-44, S83-115, type locality.

Recognition. This is the most morphologically distinctive species of the Sierranus and Sequoia Groups. Males combine a weakly constricted pronotum and a low stridulatory file tooth density (below 53 teeth/mm), lower than all other Sierranus and Sequoia Group species except *N. duplocantans* (47–52 teeth/mm) which has a more strongly constricted pronotum. Females have the shortest ovipositor of any Sierranus or Sequoia Group species, 10 mm or less in length. The song has a lower PTdc than that of the related *N. sequoia*. The karyotype is shared only by *N. inversa*. This species ranges the farthest south of any Sequoia or Sierranus Group species and occurs in the Tehachapi Mountains in addition to the Sierra Nevada.

Etymology. *l. proro* “to prolong, keep going” + *cantans* “singing,” describing the incessant and repetitive nature of the male calling song.

Notes. This species may be common in years of adequate rainfall and scarce in dry years, during which populations are localized around water sources. During the summer of 2001, a wet year for California, katydids were abundant in the Kernville area and males were seen walking and singing on bare soil on hillsides some distance from riparian or forested areas (JAC pers. obs).

Material examined. Type series only, see Type material above.

Neduba sequoia Cole, Weissman, and Lightfoot sp. n.

Fig. 19 (distribution), Fig. 29 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 3F–G (live habitus), Plate 5I (male calling song), Plate 8F–H (male ventral sclerite), Plate 10I (male titillators), Plate 12G (female subgenital plate).

Common name. Big Trees Shieldback

History of recognition. Likely confused with *N. sierranus*.

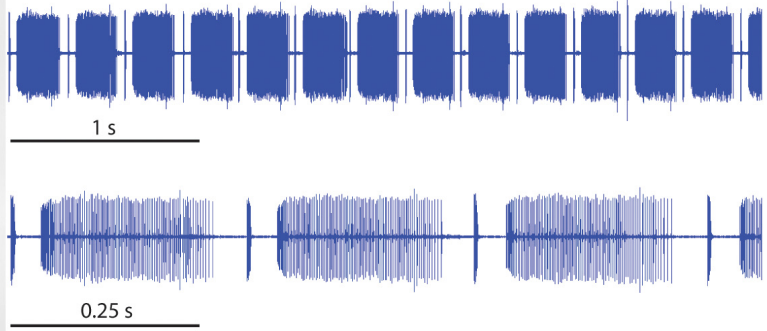
Type material. HOLOTYPE MALE: USA, CA, Tulare Co., Coy Flat Campground, Sequoia National Forest, 0.5 miles south of Camp Nelson off SR190, 36.1269N, 118.6183W, 1524 m., 30-31-VII-2012, JA Cole, DNA67 [tissue], SING357 [DNA extraction], JCR120914_00 [recording], genitalia in vial below specimen, deposited in CAS, Entomology type #19714. PARATYPES (n = 29): Tulare Co., 9♂, 1♀, same data as holotype, LACM; 1♂, same data as holotype JAC; 2♂, same data as holotype except, 20-VIII-2006, DB Weissman, DC Lightfoot, CAS; 11♂, 3♀, South Fork Campground, Sequoia National Park, 36.35029N, 118.76511W, 1112 m, 12-13-VIII-2015, JA Cole, LACM; 1m, same data except JAC; 1♂, Hwy 190 7 mi. E Springville, 36.156806N, 118.724278W, 707 m, 5-V-2011, DB Weissman, DBW.

Measurements. (mm, ♂n = 23, ♀n = 5) Hind femur ♂17.48–24.26, ♀22.03–24.14, pronotum total length ♂8.36–10.66, ♀9.50–10.05, prozona length ♂3.34–5.40, ♀4.78–5.96, metazona dorsal length ♂4.08–6.05, ♀3.79–4.72, pronotum constriction width ♂2.15–3.15, ♀2.57–2.96, metazona dorsal width ♂5.40–6.97, ♀5.85–6.65, head width ♂4.45–5.72, ♀5.10–5.90, ovipositor length ♀14.68–17.42.

Distribution. Western slope of the southern Sierra Nevada Mountains between the Kaweah River and Tule River watersheds, in the vicinity of Sequoia National Park.

Habitat. Understory of mixed conifer forests, especially in riparian habitats and mesic areas. At the South Fork localities, many adults were feeding on green leaves of mountain mahogany (*Cercocarpus*). Singing males at this locality were observed and recorded in young dead cedars at the forest edge.

male HOLOTYPE CA:Tulare Co. JAC000002314 calling song PARATOPOTYPE CA:Tulare Co. 22.8°C JCR120914_01



male terminalia PARATOPOTYPE CA:Tulare Co. JAC000002325

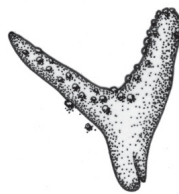
ventral sclerite HOLOTYPE



female PARATYPE CA:Tulare Co. JAC000002338



ventral sclerite PARATOPOTYPE JAC000002321



female terminalia PARATOPOTYPE CA:Tulare Co. JAC000002324



male PARATYPE CA:Tulare Co. JAC000002334



karyotype PARATOPOTYPE CA:Tulare Co. S06-80 T06-12

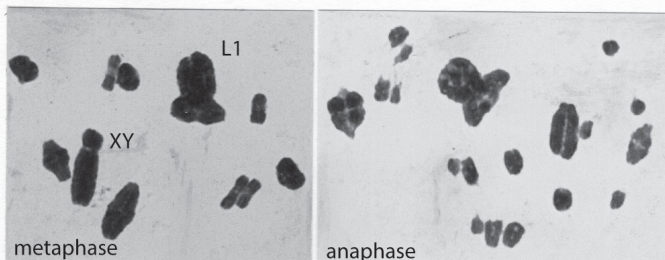
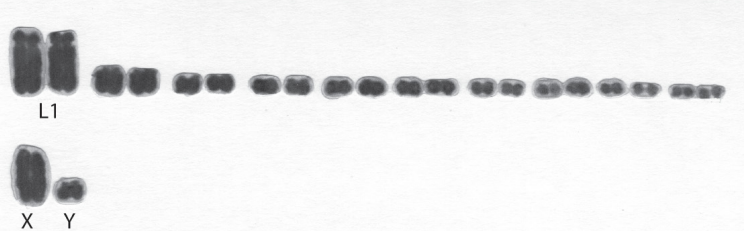


FIGURE 29. *N. sequoia* male and female habitus, calling song, male and female terminalia, karyotype.

Seasonal occurrence. Adults from late July (27-VII-1986, DJ Burdick, CAS) through August (20-VIII-2006, DB Weissman, CAS). Nymphs from May through mid-June.

Stridulatory file. (n = 18) length 2.7–3.7 mm, 152–203 teeth, tooth density 57.5 ± 3.4 (47.5–61.6) teeth/mm.

Song. (n = 19) A continuous series of alternating MPT and OPT as in other Sequoia Group species (except *N. inversa*). The PTR of 3.0 ± 0.5 s⁻¹ is significantly faster than *N. prorocantans*, which is distributed to the south, and is half the rate of syntopic *N. duplocantans*. PTdc of $75.1 \pm 8.7\%$ is significantly higher than all other Sequoia Group species (ANCOVA, $P = 3.75 \times 10^{-4}$). PTF is 14.3 ± 1.0 kHz.

Karyotype. (n = 4) Unique. $2n\♂ = 22$ (2m + 18t + XtYt). T06-12, S06-80, paratopotype.

Recognition. This is a plastic species that is difficult to recognize. A higher stridulatory file tooth density (55–59 teeth/mm) as well as larger body size will separate this species from the lower density (47–52 teeth/mm) of both *N. prorocantans* distributed to the south and *N. duplocantans*, with which it is sympatric. To the north, *N. inversa* has a greater stridulatory file tooth density (64–68 teeth/mm). The song PTR is faster than that of *N. prorocantans* but half that of *N. duplocantans*, whereas *N. inversa* sings with numerous OPT between MPT as in Sierranus Group taxa. The karyotype is unique. *N. sequoia* inhabits an area between the Kaweah River and Tule River watersheds, a range that it shares only with *N. duplocantans*.

Etymology. Named after Sequoia National Park and Sequoia National Forest of the southern Sierra Nevada of California.

Notes. This species is common at all localities where collected. Taxidermy of South Fork specimens showed the gut contents to be full of *Cercocarpus*. Collections were also made at oatmeal trails.

Material examined. DETERMINED (n = 2): **Tulare Co.**, in addition to type material (above), 1♀, Ash Mountain, Kaweah Power Station 3, 36.48606N, 118.83586W, 27-VII-1996, DJ Burdick, CAS; 1♀ nymph, Ash Mountain, Kaweah Power Station 3, 36.48606N, 118.83586W, 3-VI-1984, DJ Burdick, CAS. QUESTIONABLE PLACEMENT (n = 8): **Tulare Co.**, 2♀ nymphs, Sequoia National Park, Potwisha Campground, 36.517446N, 118.799821W, 13-VI-1923, EC VanDyke, CAS; 3♀ nymphs, same data except 13-VI-1929, EC VanDyke, CAS; 1♀ nymph, same data except 27-V-1928, EC VanDyke, CAS; 1♂, 1♀ nymphs, same data except 8-V-1931, EC VanDyke, CAS.

Neduba duplocantans Cole, Weissman, & Lightfoot, sp. n.

Fig. 19 (distribution), Fig. 30 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 3H (live habitus), Plate 5J (male calling song), Plate 12H (female subgenital plate).

Common name. Doubletime Shieldback.

History of recognition. None.

Type material. HOLOTYPE MALE: **USA, CA, Tulare Co.**, South Fork Road, 9.75 miles southeast of Three Rivers, 36.35334N, 118.78451W, elev. 970 m, 25-VI-2017, JA Cole, W Chatfield-Taylor, 170625_03 [recording], JCT17-1 [karyotype], 173 [teeth], 3.4 [mm], tegmen in gelcap below specimen, deposited in CAS, Entomology type #19709.

PARATYPES (n = 24): **Fresno Co.**, 1♀, Big Creek Road, 5 mi. S of Bretz Mill Campground, 36.97546N, 119.21088W, 810 m, 13-VIII-2015, JA Cole, LACM; **Tulare Co.**, 3♂, 8♀, same data as holotype, LACM; 2♂, same data as holotype, CAS; 1♀, same data as holotype, JAC; 1♂, 1♀, South Fork Campground, Sequoia National Park, 36.35209N, 118.76511W, 1112 m, 12-13-VIII-2015, JA Cole, CAS; 1♂, 6♀, same data except LACM.

Measurements. (mm, ♂n = 7, ♀n = 17) Hind femur ♂19.46–21.95, ♀21.44–22.69, pronotum total length ♂8.20–9.28, ♀8.10–8.95, prozona length ♂3.30–4.71, ♀3.48–5.28, metazona dorsal length ♂4.42–5.44, ♀3.09–4.75, pronotum constriction width ♂2.00–2.35, ♀2.03–2.95, metazona dorsal width ♂5.60–6.05, ♀5.20–6.41, head width ♂4.60–5.12, ♀4.85–5.85, ovipositor length ♀13.09–17.60.

Distribution. At present, known only from the vicinity of the Kaweah River in the Sequoia National Forest.

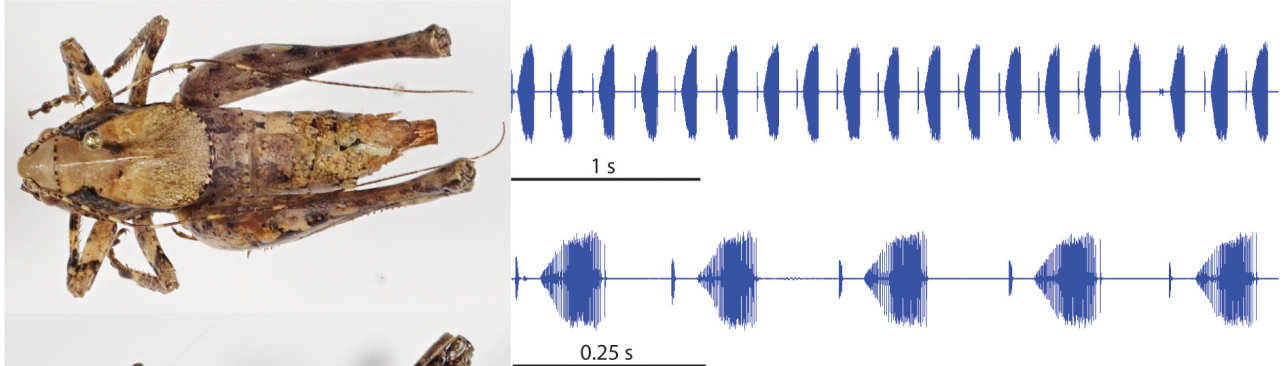
Habitat. Found in tangles and among grass along a stream flowing out of a side canyon. Also collected on bushes along the road paralleling the Kaweah River.

Seasonal occurrence. Males were active and females were a mixture of last instar nymphs, teneral adults, and mature adults in late June (25-VI-2017, JA Cole & W Chatfield-Taylor, LACM). By August this species was rare (12-VIII-2015, JA Cole, LACM). This species may be active earlier in the season than sympatric *N. sequoia*.

Stridulatory file. (n = 7) length 2.7–3.4 mm, 126–173 teeth, tooth density 51.0 ± 4.9 (45.8–60.7) teeth/mm.

Song. (n = 7) Unique. The PTR of 5.1 ± 0.3 s⁻¹ is much faster than any other Sequoia or Sierranus Group species, and twice as fast as sympatric *N. sequoia*. The MPTL is brief at 72.3 9.1 ms. The short MPTL contributes to a low PTdc of $35.8 \pm 4.9\%$. PTF of 17.0 ± 1.0 kHz is higher than other Sequoia Group species and is difficult to hear except at short range.

male HOLOTYPE CA: Tulare Co. JAC000002143 calling song PARATOPOTYPE CA: Tulare Co. 24.9°C JCR170625_06



male terminalia PARATOPOTYPE CA: Tulare Co. JAC000002142



female PARATYPE CA: Tulare Co. JAC000002149



karyotype PARATOPOTYPE CA: Tulare Co. S15-43 JCT15-12



female terminalia PARATOPOTYPE
CA: Tulare Co. JAC000002150



FIGURE 30. *N. duplocantans* male and female habitus, calling song, male and female terminalia, karyotype.

Karyotype. (n = 3) $2n\♂ = 21$ (18t + XtXtYm), shared with *N. sierranus*, JCT15-12, paratopotype.

Recognition. Male *N. duplocantans* are separated from sympatric *N. sequoia* by stridulatory file tooth density (47–52 teeth/mm vs. 55–59 teeth/mm, respectively). To the north, *N. inversa* has a similarly constricted pronotum but that species also has a higher tooth density (64–68 teeth/mm). Male *N. prorocantans* to the south have similar stridulatory files but have a weakly constricted pronotum. The fast song PTR is unique, and readily separates this species by ear from syntopic *N. sequoia* as well as from neighboring *N. prorocantans* to the south, as well as *N. inversa* to the north due to the multiple OPT in that species. Adult activity apparently commences earlier in the season than *N. sequoia* in areas where they co-occur, but the two species may be found together in midsummer.

Etymology. *l. duplo* “twice as much, double” + *cantans* “singing,” referring to the rate of PT production that is twice as fast as a sympatric congener.

Notes. This species was discovered by song while collecting a series of *N. sequoia*, and its distinctiveness was appreciated further when cytogenetic analysis revealed a distinct karyotype. The discovery of two morphologically cryptic Sequoia Group species (*N. duplocantans* and *N. sequoia*) that are both sympatric and syntopic is of considerable evolutionary interest. The species pair has diverged in several aspects: calling song, karyotype, and phenology. The calling song PTR differed by a factor of two. Considering the remarkably different songs and distinct karyotypes, stasipatric and secondary contact hypotheses should be tested in the Sequoia Group. With *N. duplocantans* adult activity commencing before *N. sequoia* have matured, allochronic isolation may also be evolving between the two species. Two females among the paratype series were identified through rDNA sequence (Figs. 4-5). Introgression of mtDNA among the Sequoia Group species (Fig. 4) is expected if young, geographically proximal species have a history of hybridization as observed in *Aglaothorax* (Cole 2016).

Material examined. (n = 2) **Tulare Co.**, in addition to Type material (above), 1♀, Hammond, Kaweah Powerhouse 3 Forebay, 36.48618N, 118.83553W, 853 m, 17-VIII-2010, W Chatfield-Taylor, LACM; 1♀, Ash Mountain, Kaweah Power Station 3, 36.48606N, 118.83586W, 7-VI-1986, DJ Burdick, CAS.

Discussion

Morphology. Crypsis and masquerade (Skelhorn *et al.* 2010) are common defensive strategies in katydids (Gwynne 2001), yet even among the camouflage-adept Tettigoniidae *Neduba* stands out by virtue of the bewildering array of color patterns found within and among species. As cryptic coloration may evolve quickly and involve simple genetic mechanisms (Steiner *et al.* 2007), the observation that multiple species share the same color patterns attests to their survival value and the maintenance of diversity by natural selection. Apostatic selection (Clarke 1962) will be a fascinating hypothesis to test. Visual predators encounter color morphs in proportion to their frequency, thus a cycle ensues whereupon predation reduces the frequency of the most common color morphs over time while simultaneously, previously rare color morphs enjoy greater reproductive success and increase in frequency (Bond & Kamil 1998).

Although the use of species-specific genitalic characters is routine in systematics, the relationship between genitalic morphology and reproductive isolation is unclear. The “lock and key” hypothesis has been supported via mating trials in katydids (*Idiostatus*; Rentz 1972). Across a diversity of animals, however, this hypothesis has received little support; rather, tactile reproductive isolation may be more common than mechanical isolation (reviewed in Masly 2012). We found in *Neduba* that morphology of the titillator arms is correlated with major clades but not species, and that the ventral sclerites of the titillators are informative at the species level only in the Carinata Group. The titillators of the internal sclerotized genitalia of *Aglaothorax* apparently have a tactile function in copulation (Rentz & Birchim 1968; JAC pers. obs) and this is probably the case in *Neduba* as well. Non species-specific genitalia may be explained if behaviors, such as movements and/or sequences of titillator deployment during copulation, are more important to mate recognition than the morphology of those structures. Future behavioral research that investigates titillator function in *Neduba* courtship and copulation should be rewarding.

Song Evolution. The paradigm that insects with acoustically mediated pair formation will have species-specific songs is not met across *Neduba*. Considering that diversification began in the middle Miocene (Cole & Chiang 2016), *Neduba* songs have evolved little overall: 12 of the 20 extant species share the same song structure: two alternating PT types, with one train longer than the other, delivered at a rate between 1 and 4 wingstroke cycles per second (Plate 4C, E–J, Plate 5A–C, H–I). Deviations from this shared song structure occur in two geographic

regions with sympatric and/or parapatric distributions of multiple *Neduba* lineages: the South Coast Ranges (Plate 4A–B, D, Plate 5C) and the Sierra Nevada of California (Plate 5D–G). The clustering of novel song types around regions of contact, together with genetic evidence for hybridization, suggests reinforcement of mate recognition as a driver of song evolution in *Neduba* as shown for the related genus *Aglaothorax* (Cole 2016). Colloquially speaking, *Neduba* songs do not evolve unless they have to. A paucity of song evolution is therefore not surprising if the limited dispersal ability of these flightless insects prevents contact between populations save those with adjacent ranges, limiting circumstances during which songs evolve.

Chromosome Evolution. Can chromosomal changes lead to speciation or do chromosome changes merely follow reproductive isolation? Chromosome rearrangements may be directly involved in postzygotic isolation by creating problems with meiosis in hybrids (Shaw *et al.* 1998; White 1978). Rearrangements that evolve within a population may theoretically drive rapid sympatric speciation (stasipatric speciation; White 1978). Alternatively, rearranged regions may prevent genes that are involved in reproductive isolation from recombining (Noor *et al.* 2001; Riesberg 2001), or chromosomal differences may exist among reproductively compatible races, as has been shown in orthopterans such as grasshoppers (*Vandiemenna*; Kawakami *et al.* 2009) and tree weta (*Hemideina*; Morgan-Richards 1997).

The microevolution of *Neduba* karyotypes may be described as sequences of Robertsonian changes (centric fusions; Ueshima & Rentz 1979) that may accumulate within populations with relatively little fitness cost. Between populations, however, different rearrangements may present a formidable barrier via reduced hybrid fitness or hybrid sterility (Hauffe & Searle 1998; we especially recommend the extensive review in King 1993), most readily if effective population size is small as heterozygotes for individual rearrangements do not suffer a great fitness cost (Barton 1980). Cycles of isolation and contact are the most likely explanation of observed karyotype differences at parapatric boundaries (see Speciation below). However, stasipatric speciation (White 1978) cannot be completely ruled out and may serve as an alternate hypothesis for *Neduba* chromosome evolution (but see extensive counter discussion in King 1993, p. 213). Stasipatric speciation predicts that a new species will evolve within the range of its sister species and that a parapatric boundary will form between the pair (White 1978). Furthermore, hybrid sterility that results when different karyotypes combine will impose strong natural selection; thus, mating signals are expected to evolve to enhance prezygotic isolation. These predictions are consistent with our observations of the Sequoia Group species pair *N. duplocantans* and *N. sequoia*. The former species occupies a fraction of the range of the latter, both overlap in adult activity and are completely syntopic when they co-occur, and the male songs differ in PTR by a factor of 2, which is the most extreme difference found within the Sequoia and Sierranus Groups. Contrary evidence is furnished by the observation that *N. duplocantans* and *N. sierranus* share the same karyotype. Given the controversy surrounding stasipatric speciation (Coyne & Orr 1989; Kawakami *et al.* 2009, 2011), this case deserves thorough investigation.

Concerning macroevolution, while there seems to be no general relationship between numbers of species in the genus and karyotype diversity, there is the intriguing possibility of selective cause and effect in which chromosomal changes facilitate speciation in certain groups but not in others. Karyotypes within genera of Orthoptera are, in general, conservative with reference to number of chromosomes, centromere positions, and sex chromosome systems. On one end, the grasshopper genus *Melanoplus* has hundreds of taxa with the same gross karyotype of 23 acrocentric or telocentric chromosomes in the male. In notable contrast are three katydid genera in the Tettigoniinae: the Australian *Nanodectes* where 12 species have 10 different karyotypes (Ueshima & Rentz 1991), the central North American *Pediodes* where some 18 species have 9 karyotypes (Ueshima *et al.*, unpublished), and, as discussed here, western North American *Neduba* where 20 taxa have 9 different karyotypes.

Demonstrating whether chromosome rearrangements or speciation came first may be impossible because this problem relates to origins, and events relating to origins may be unique, short lived, and/or near impossible to capture in nature. Acknowledging these limitations, *Neduba* offers a natural experiment in which the role of chromosome evolution in speciation may be tested via a macroevolutionary perspective. The genus is composed of two major clades: the Carinata Group, in which karyotype is invariable, and a clade that encompasses the remaining five species Groups in which eight karyotypes have evolved. Both clades possess similar diversity, facilitating controlled phylogenetic comparative testing (Felsenstein 1985; Garland *et al.* 1999; Martins & Hansen 1996).

Speciation. Combining the evidence above, we hypothesize that *Neduba* speciated via allopatric isolation, secondary contact, and reinforcement. Range shifts caused by climate change and reshaping of the coastline created episodic isolation and secondary contact (for another katydid example see Barendse 1990). During periods of

isolation, populations diverged by an unspecified combination of genetic drift and selection, which generated local variation amidst a background of polymorphic ancestral characters. In cases where lineages were not sufficiently diverged, gene flow homogenized those lineages after secondary contact (differential fusion; Templeton 1981). An example appears to be *N. carinata*, in which lineages that diverged (in part) due to the Monterey Bay geographic break (Hall 2002) now exchange genes in the absence of that barrier. In other cases of contact mate recognition via acoustic or tactile mating behavior evolved (reinforcement: Dobzhansky 1940), thereby reducing the frequency of hybridization in contact zones or preventing wasteful courtship of heterospecifics (see Cole 2016 for an example in the related nedubine *Aglaothorax*). Some cases of contact apparently involved populations that differed in karyotype, in which chromosome differences fixed in populations during periods of allopatric isolation. Again, reinforcement enhanced mate recognition to reduce the fitness consequences of hybridization that resulted from combining disparate karyotypes.

With increased understanding of their diversity, the affinity of *Neduba* taxa with biogeographic regions of California is evident. The *Neduba* distribution is remarkably similar to that of the salamander genus *Ensatina*, a classic example of a supposed ring species (Kuchta *et al.* 2009; Wake *et al.* 1986; Wake & Yanev 1986), which is a case of isolation by distance that is arranged in a circle rather than a line. In both groups, dispersal is limited and habitable zones are wooded mid-elevation mountain slopes around the seasonally arid Central Valley grassland (Wake *et al.* 1986). *Neduba* fails to qualify as a ring species for the same reasons that most other candidates, including *Ensatina*, have been falsified: it cannot be ruled out that populations have experienced a history of alternating periods of isolation and secondary contact rather than an uninterrupted expansion around a central barrier (Coyne & Orr 2004). *Neduba* species generally have abutting parapatric ranges and are sympatric in multiple regions (Figs. 8–9, 19), a pattern that is consistent with contact between separate clades rather than from contact between the ends of a ring of populations.

Conservation. This revision adds 12 species of katydids to the biodiverse California Floristic Province (Mittermeier *et al.* 2011), where a high number of endemic Orthoptera are already known (Harrison 2013). Conservation is clearly warranted for the geographic region and for the taxa we studied in particular: a *Neduba* species (*N. extincta*) is already extinct in the San Francisco Bay Area apparently due to human disturbance (Rentz 1977), yet the only federally listed endangered species of Orthoptera in California is the grasshopper *Trimerotropis infantilis* Rentz & Weissman (Hoekstra 1998). Insect conservation is challenging due to many factors including the difficulty of identifying species, sparse information on distribution and ecology (Hoekstra 1998), and a negative public image. It is our hope that the improved systematic and distributional knowledge in this revision will meet those challenges and thereby aid conservation efforts.

In the long term, beyond the local and direct adverse impacts of human agriculture, modification and destruction of natural habitats, and urban development, the adverse effects of climate change are already causing environmental declines of California regional ecosystems (Thorne *et al.* 2018; USGCRP 2017, 2018). Warmer temperatures, reduced water availability, and increased wildfire size and severity are all adversely impacting the conifer and oak woodland communities where most *Neduba* reside. Such impacts are predicted to increase for the foreseeable future. As California and Oregon woodlands decline from drought-induced tree mortality and more severe wildfire, *Neduba* population fragmentation and decline will be concomitant.

The response of *Neduba* populations to climate change may broadly mirror the changes observed in California butterfly communities: reduced diversity in lowland areas, stable diversity in moderate to high mountain elevations, and reduced diversity at the highest elevations (Forister *et al.* 2010). Lowland populations suffer from development and mountain populations displace upwards with climate change. As long as there is habitat at higher elevations to colonize, mountain populations are stable, but at the highest elevations no more suitable habitat remains to colonize. A key difference is that butterflies have flight capability and *Neduba* do not: any *Neduba* population movements in response to climate change will be slow. *Neduba* adaptation to climate change may be similar to that of other dispersal-limited endemic California taxa, such as *Ensatina* salamanders (Kuchta *et al.* 2009; Wake & Yanev 1986) and *Antrodiaetus* turret spiders (Starrett & Hedin 2007). The most sensitive species will be those in which have restricted ranges and that experience increased disturbance. Candidates are the Santa Catalina Island endemic *N. propsti* and *N. arborea* inhabiting a limited range in the east slope of the North Coast Ranges that now experiences increased fire frequency.

Conservation is accomplished when organisms are allowed to continue reproductive (tokogenetic) events into the future (Fitzhugh 2013). In the short term, conservation priorities that are already established in California for

more charismatic taxa may also be effective for many *Neduba* species. The highest concentration of threatened California plant and animal species occur in the Bay Area (Harrison 2013) and in the California Coast Ranges, where we have revealed much *Neduba* diversity and have suggested evolutionary processes that have shaped this diversity. Coast Range populations are protected in part by California State Parks and several regional parks, especially in the Bay Area, but with much private land and agriculture, conservation in this region of the state could be improved. The greatest *Neduba* diversity is found in the Sierra Nevada, where at the present time many populations are protected by National Forests and the National Parks system. Extensive contiguous land area preserved by these jurisdictions allows evolutionary processes and tokogeny to play out over long distances. We have given common names and one scientific name to highlight the association of these katydid with California National Parks.

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A. *Neduba carinata* male. CA: Santa Clara Co.



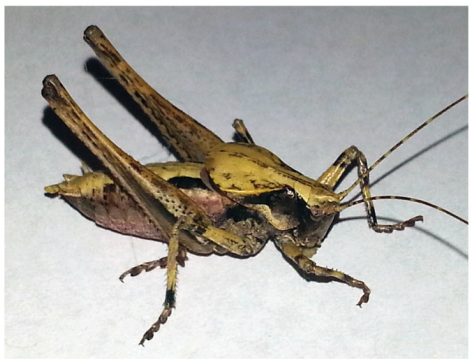
B. *Neduba ambagiosa* female phonotaxing to male. PARATOPOTYPES CA: Mendocino Co.



C. *Neduba ambagiosa* male. CA: Mendocino Co. Photo: Jim Hogue.



D. *Neduba radicata* male. PARATYPE CA: El Dorado Co.



E. *Neduba steindachneri* male. WA: Kitsap Co.



F. *Neduba cascadia* male. PARATOPOTYPE OR: Jackson Co.



G. *Neduba cascadia* male singing. PARATOPOTYPE OR: Jackson Co.



H. *Neduba cascadia* male. PARATOPOTYPE OR: Jackson Co.

PLATE 1. Live habitus of Carinata Group. A. *N. carinata* male, B. *N. ambagiosa* paratypes in phonotaxis, C. *N. ambagiosa* male (photo credit Jim Hogue), D. *N. radicata* paratype male, E. *N. steindachneri* male, F. *N. cascadia* paratopotype male showing mottled color form, G. *N. cascadia* paratopotype male singing (note elevated pronotal shield to give tegmina room to move, and perhaps, also create a parabola effect), H. *N. cascadia* paratyopotype male showing striped color form.



A. *Neduba propsti* male. CA: Los Angeles Co.



B. *Neduba castanea* male.
TOPOTYPE CA: Los Angeles Co.



C. *Neduba castanea* female. CA: Ventura Co.



D. *Neduba macneilli* male.
CA: Inyo Co. Photo: James Bailey.



E. *Neduba lucubrata* male.
PARATYPE CA: San Benito Co.



F. *Neduba sierranus* female.
CA: Mariposa Co.



G. *Neduba sierranus* male singing.
CA: Mariposa Co.

PLATE 2. Live habitus of the Propsti, Castanea, Lucubrata, and Sierranus Groups. A. *N. propsti* male, B. *N. castanea* topotype male, C. *N. castanea* female, D. *N. macneilli* male (photo credit James Bailey), E. *N. lucubrata* paratype male, F. *N. sierranus* female, G. *N. sierranus* male singing (note visible tegmina under pronotal shield).



A. *Neduba radocantans* male.
PARATYPE CA: El Dorado Co.



B. *Neduba arborea* male.
PARATOPOTYPE CA: Colusa Co.



C. *Neduba inversa* male.
PARATYPE CA: Fresno Co.



D. *Neduba prorocantans* male.
PARATYPE CA: Kern Co.



E. *Neduba prorocantans* female.
PARATYPE CA: Kern Co.



F. *Neduba sequoia* male.
PARATYPE CA: Tulare Co.



G. *Neduba sequoia* female.
PARATOPOTYPE CA: Tulare Co.



H. *Neduba duplocantans* male singing.
PARATOPOTYPE CA: Tulare Co.

PLATE 3. Live habitus of the Sequoia Group. A. *N. radocantans* paratype male, B. *N. arborea* paratopotype male, C. *N. inversa* paratype male, D. *N. prorocantans* paratype male, E. *N. prorocantans* paratype female, F. *N. sequoia* paratype male, G. *N. sequoia* paratype female, H. *N. duplocantans* paratopotype male singing.

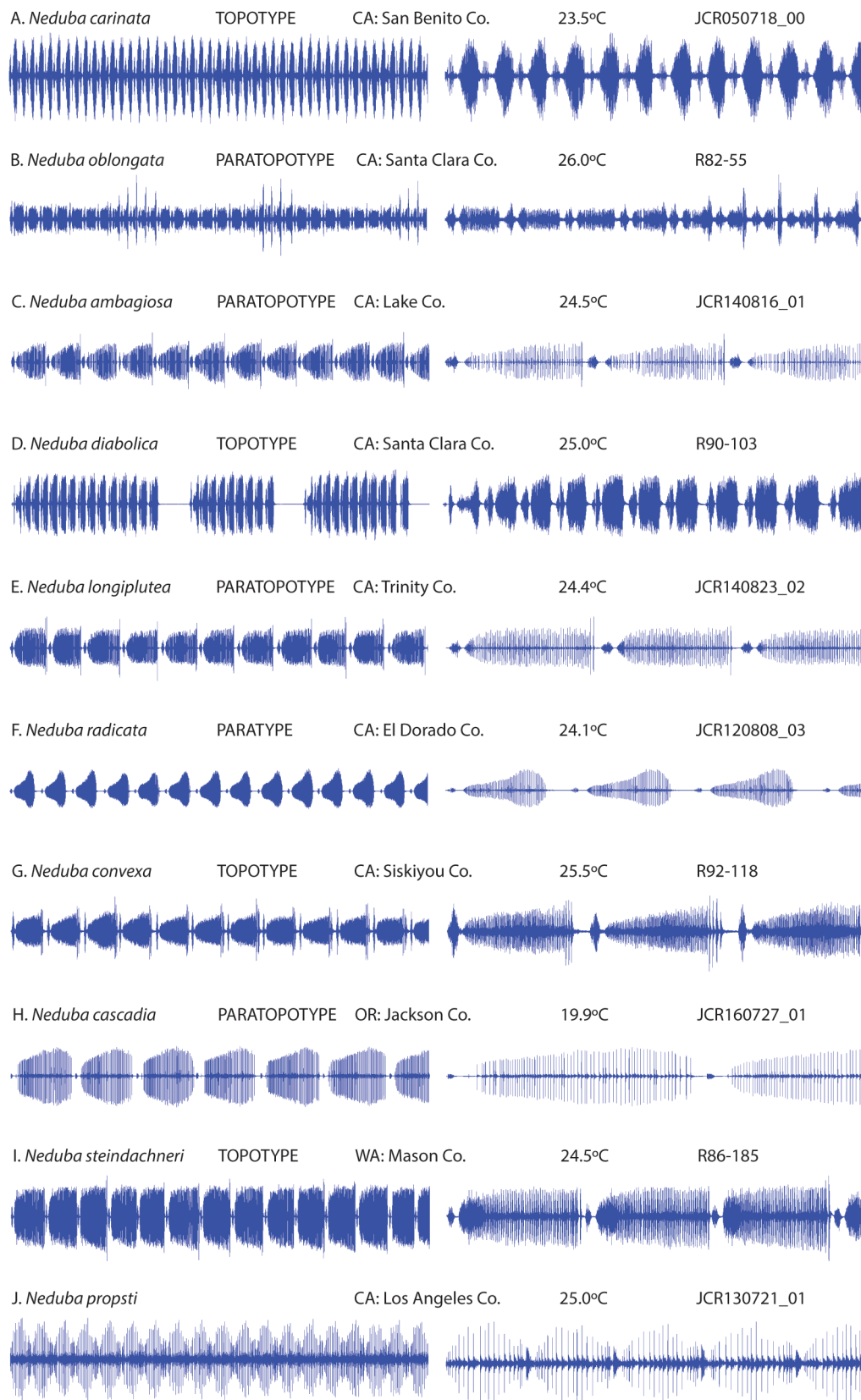


PLATE 4. Male calling songs of the Carinata and Propsti Groups. A. *N. carinata*, B. *N. oblongata*, C. *N. ambagiosa*, D. *N. diabolica*, E. *N. longiplutea*, F. *N. radicata*, G. *N. convexa*, H. *N. cascadia*, I. *N. steindachneri*, J. *N. propsti*. Left column shows 4 s oscillogram windows, right column are 1 s windows.

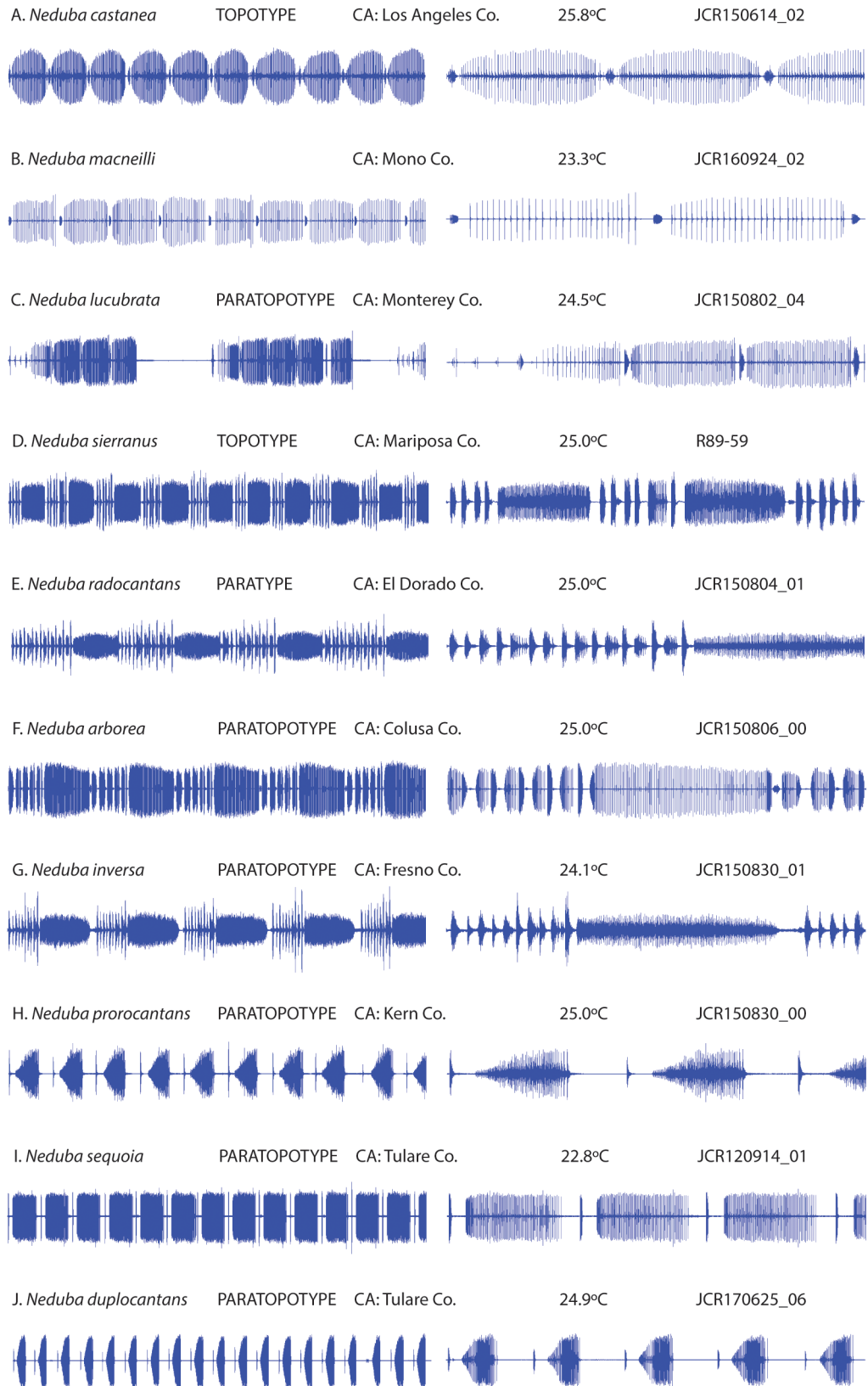


PLATE 5. Male calling songs of the Castanea, Lucubrata, Sierranus, and Sequoia Groups. A. *N. castanea*, B. *N. macneilli*, C. *N. lucubrata*, D. *N. sierranus*, E. *N. radocantans*, F. *N. arborea*, G. *N. inversa*, H. *N. prorocantans*, I. *N. sequoia*, J. *N. duplocantans*. Left column shows 4 s oscillogram windows, right column are 1 s windows.

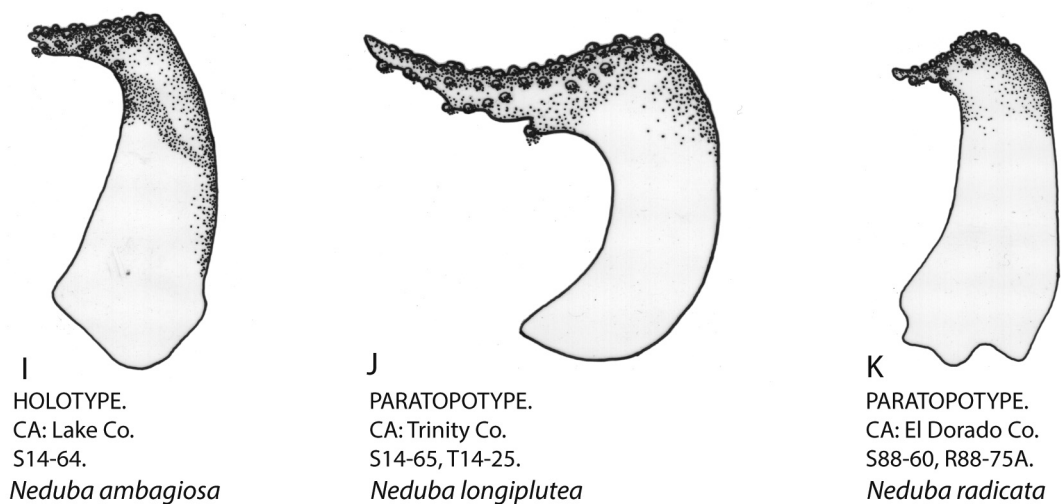
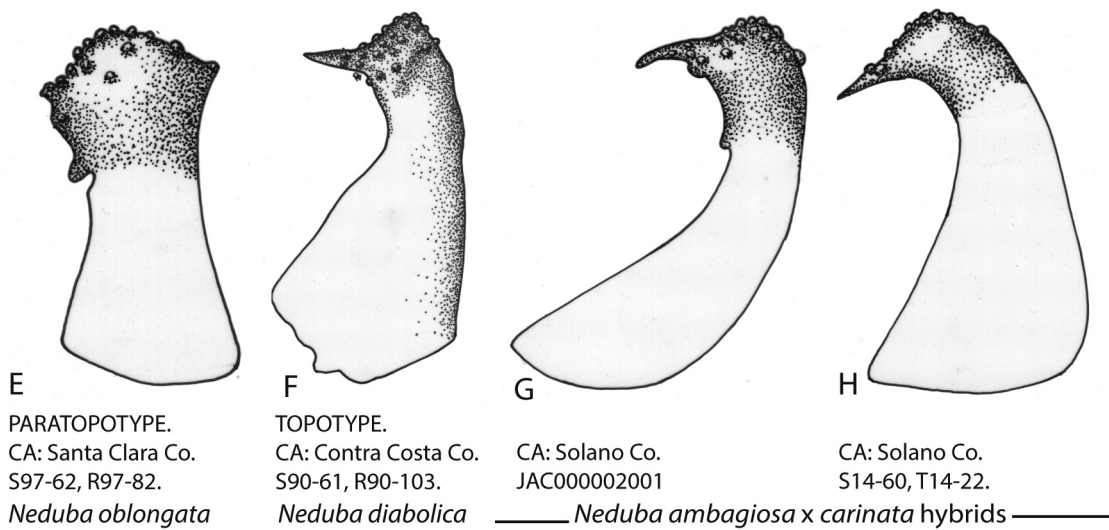
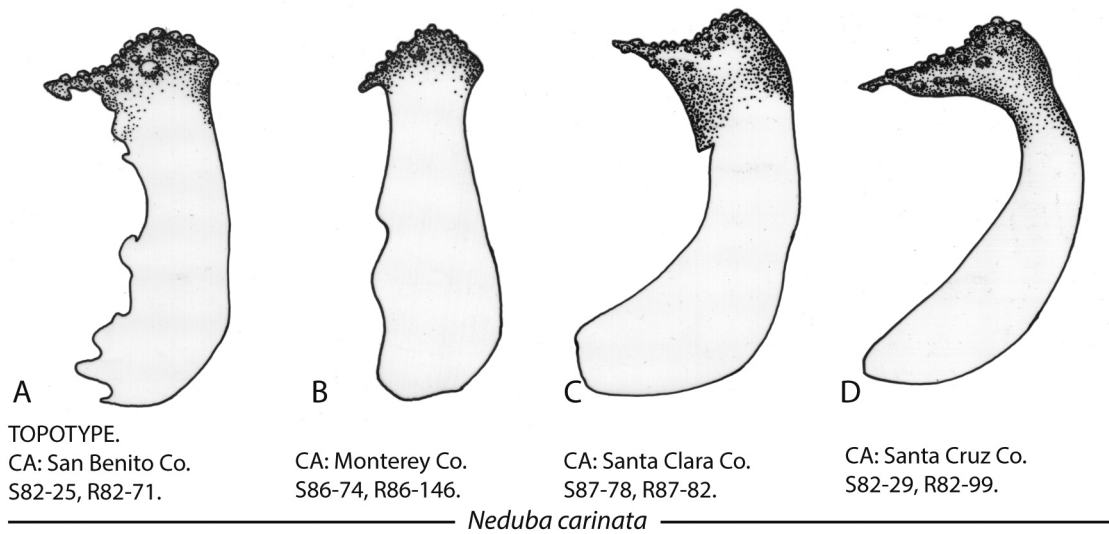


PLATE 6. Variation in the ventral sclerites of the titillators of the male genitalia: Carinata Group. A–D. *N. carinata*, E. *N. oblongata*, F. *N. diabolica*, G–H. *N. ambagiosa* × *carinata* hybrids, I. *N. ambagiosa*, J. *N. longiplutea*, K. *N. radicata*.



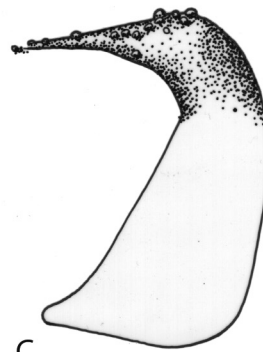
A

TOPOTYPE.
CA: Siskiyou Co.
S92-72, R92-118.



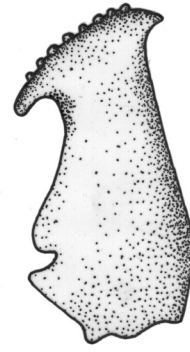
B

CA: Tehama Co.
JAC000002128.



C

CA: Lassen Co.
JAC000002085.

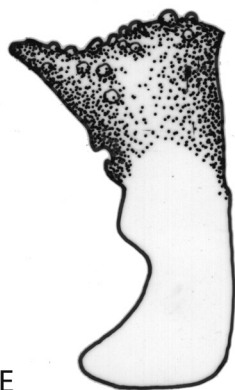


D

TOPOTYPE.
WA: Mason Co.
S86-95, R86-182.

Neduba convexa

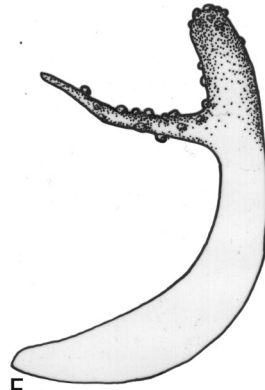
Neduba steindachneri



E

PARATOPOTYPE
OR: Jackson Co.
JAC000002025.

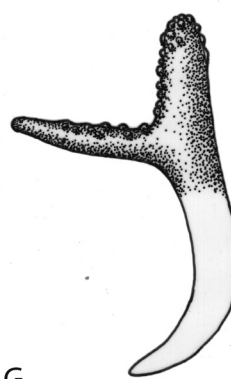
Neduba cascadia



F

CA: Los Angeles Co.
Avalon Canyon.

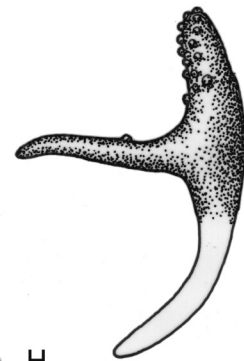
Neduba propsti



G

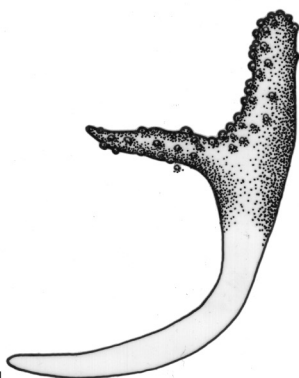
HOLOTYPE.
CA: Monterey Co.
JAC000002197.

Neduba lucubrata



H

PARATYPE.
CA: Monterey Co.
JAC000002199.



I

TOPOTYPE.
CA: Los Angeles Co.
S88-73, R88-120.

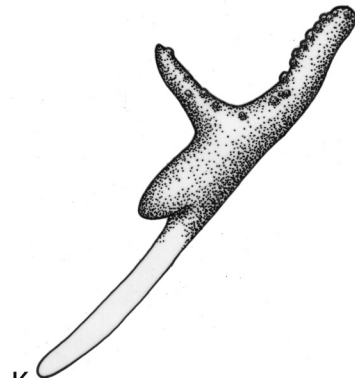
Neduba castanea



J

TOPOTYPE.
CA: Mono Co.
S86-98, R86-216.

Neduba macneilli



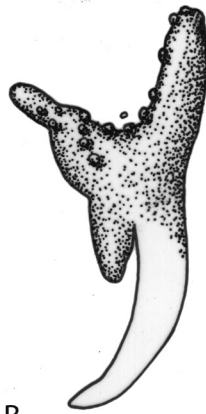
K

CA: Kern Co.
Walker Pass.

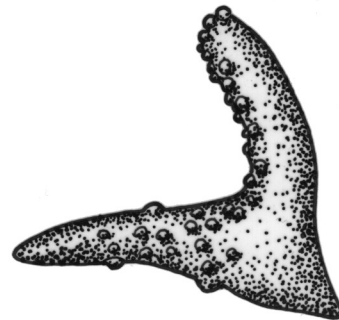
PLATE 7. Ventral sclerites: Carinata, Propsti, Lucubrata, and Castanea Groups. A–C. *N. convexa*, D. *N. steindachneri*, E. *N. cascadia*, F. *N. propsti*, G–H. *N. lucubrata*, I. *N. castanea*, J–K. *N. macneilli*.



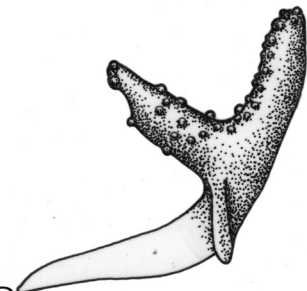
A
TOPOTYPE.
CA: Mariposa Co.
S89-47, R89-59.
Neduba sierranus



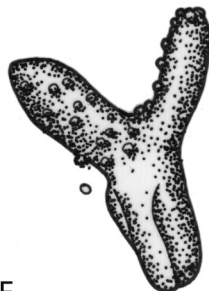
B
HOLOTYPE.
CA: El Dorado Co.
S95-62, R95-49.
Neduba radocantans



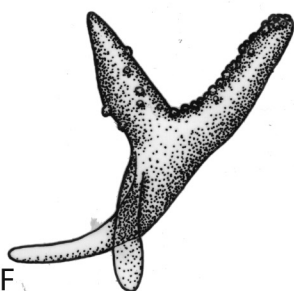
C
HOLOTYPE.
CA: Colusa Co.
JAC000001958.
Neduba arborea



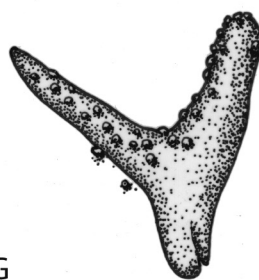
D
PARATOPOTYPE.
CA: Fresno Co.
JAC000002154.
Neduba inversa



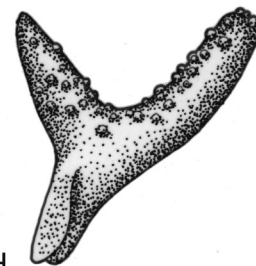
E
HOLOTYPE.
CA: Kern Co.
S83-115, R83-295.
Neduba prorocantans



F
HOLOTYPE.
CA: Tulare Co.
JAC000002314.



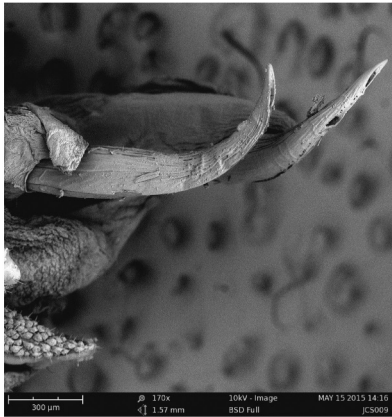
G
PARATOPOTYPE.
CA: Tulare Co.
JAC000002321.



H
PARATYPE.
CA: Tulare Co.
JAC000002329.

Neduba sequoia

PLATE 8. Ventral sclerites: Sierranus and Sequoia Groups. A. *N. sierranus*, B. *N. radocantans*, C. *N. arborea*, D. *N. inversa*, E. *N. prorocantans*, F–H. *N. sequoia*.



A. TOPOTYPE.
CA: San Benito Co.
JCS09, JAC000001964

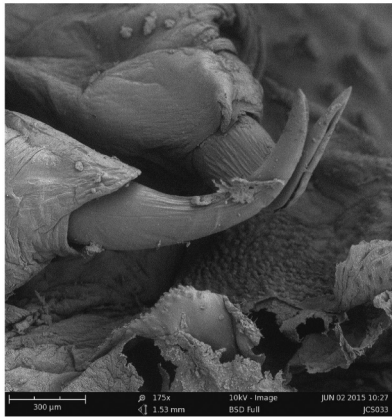


B.
CA: Monterey Co.
JCS08, JAC000001993

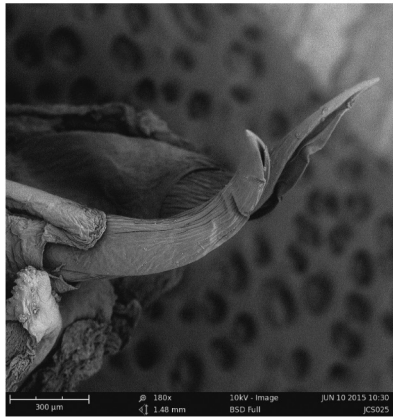


C.
CA: Santa Cruz Co.
JCS26, S82-29, R82-121

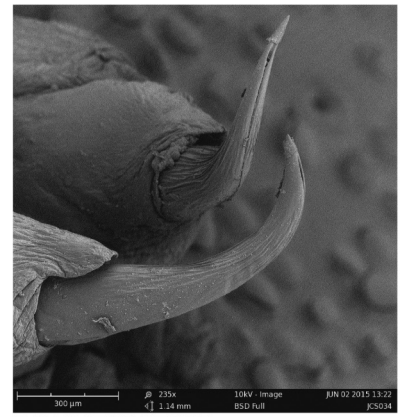
Neduba carinata



D. PARATOPOTYPE.
CA: El Dorado Co.
JCS33, JAC000001945
Neduba ambagiosa



E. TOPOTYPE.
CA: Contra Costa Co.
JCS25
Neduba diabolica



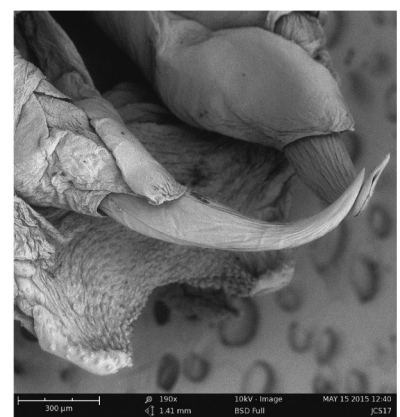
F. PARATOPOTYPE.
CA: Trinity Co.
JCS34, JAC000002181
Neduba longiplutea



G. PARATOPOTYPE.
CA: El Dorado Co.
JCS35, JAC000002295
Neduba radicata

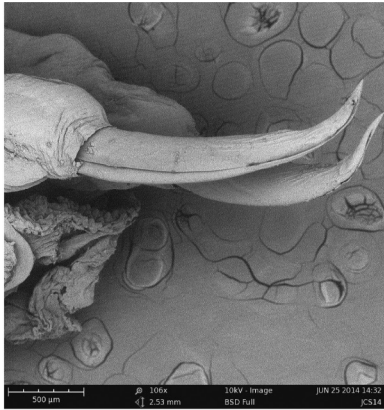


H. TOPOTYPE.
CA: Siskiyou Co.
JCS15, JAC000002106
Neduba convexa

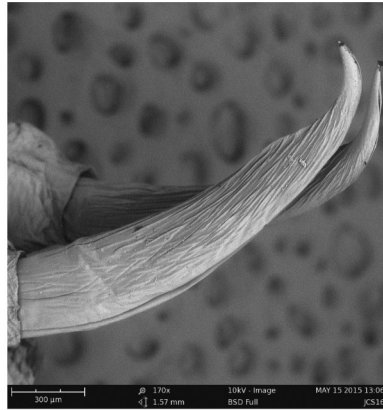


I.
WA: Kitsap Co.
JCS17, JAC000002391
Neduba steindachneri

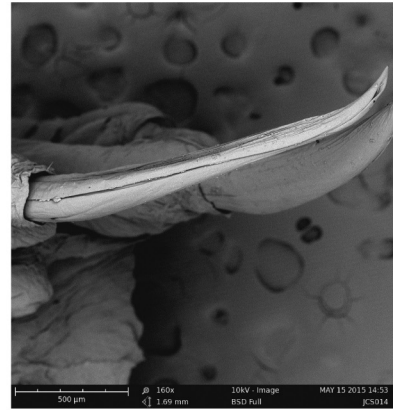
PLATE 9. Titllator arms of Carinata Group species.



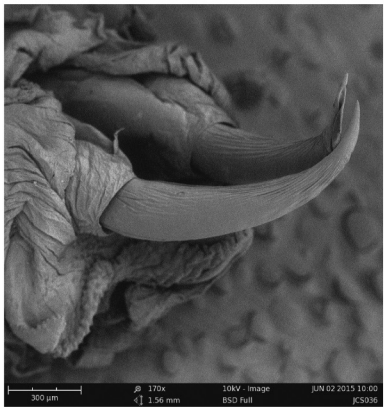
A.
CA: Los Angeles Co.
JCS13, JAC000002251
Neduba propsti



B. TOPOTYPE.
CA: Los Angeles Co.
JCS16, JAC000002045
Neduba castanea



C. TOPOTYPE.
CA: Mono Co.
JCS14, JAC000002242
Neduba macneilli



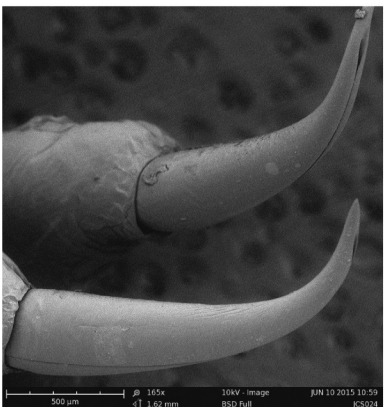
D. PARATYPE.
CA: Monterey Co.
JCS36, JAC000002202
Neduba lucubrata



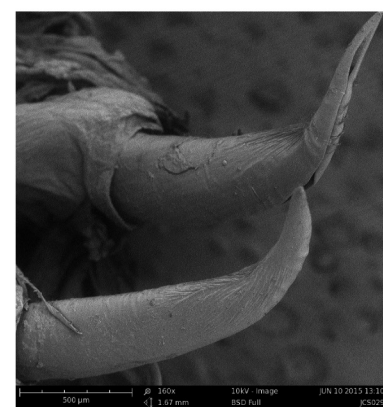
E. TOPOTYPE.
CA: Mariposa Co.
JCS23, S82-110, R82-241
Neduba sierranus



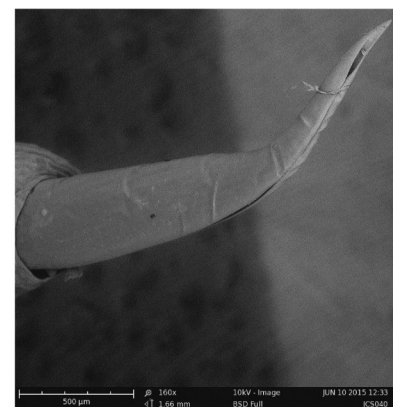
F. PARATOPOTYPE.
CA: El Dorado Co.
JCS39, JAC000002303
Neduba radocantans



G. PARATYPE.
CA: Fresno Co.
JCS41, JAC000002157
Neduba inversa

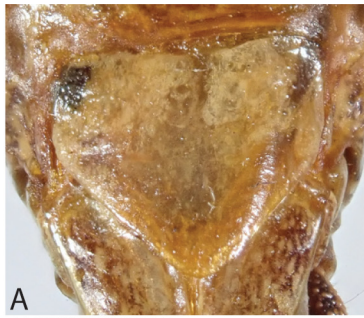


H. PARATOPOTYPE.
CA: Kern Co.
JCS29, S83-15, R83-306
Neduba prorocantans

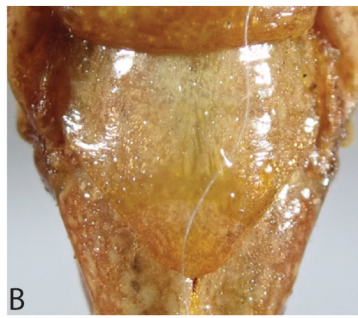


I. PARATOPOTYPE.
CA: Monterey Co.
JCS40, JAC000002319
Neduba sequoia

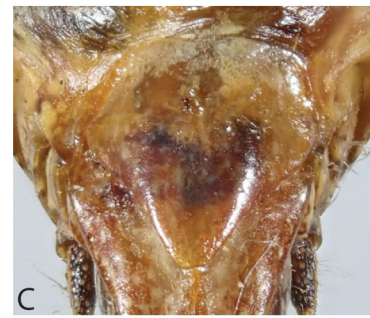
PLATE 10. Titillator arms of Propsti (A), Castanea (B–C), Lucubrata (D), Sierranus (E–F), and Sequoia (G–I) Group species.



A
JAC000001991
CA: Monterey Co.
Neduba carinata



B
JAC000002252 PARATOPOTYPE
CA: Santa Clara Co.
Neduba oblongata



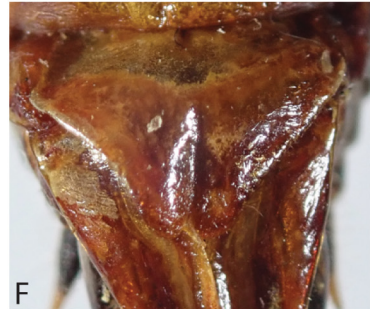
C
JAC000001950 PARATOPOTYPE
CA: Lake Co.
Neduba ambagiosa



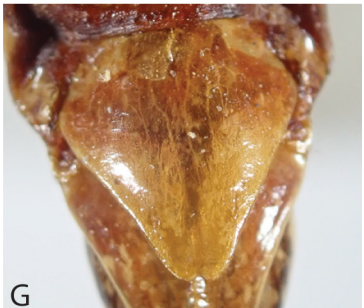
D
JAC000002135 TOPOTYPE
CA: Contra Costa Co.
Neduba diabolica



E
JAC000002189 PARATOPOTYPE
CA: Trinity Co.
Neduba longiplutea



F
JAC000002299 PARATYPE
CA: El Dorado Co.
Neduba radicata



G
JAC000002094
CA: Plumas Co.
Neduba convexa



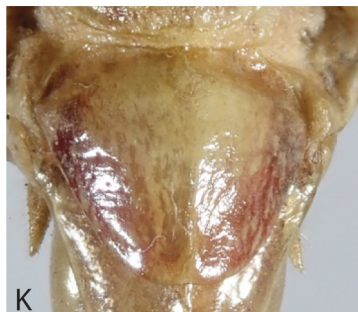
H
JAC000002032 PARATOPOTYPE
OR: Jackson Co.
Neduba cascadia



I
WA: Mason Co.
Neduba steindachneri



J
CA: Los Angeles Co.
Neduba propsti



K
JAC000002040 TOPOTYPE
CA: Los Angeles Co.
Neduba castanea

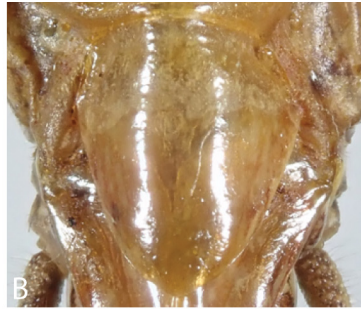


L
JAC000002231
CA: Kern Co.
Neduba macneilli

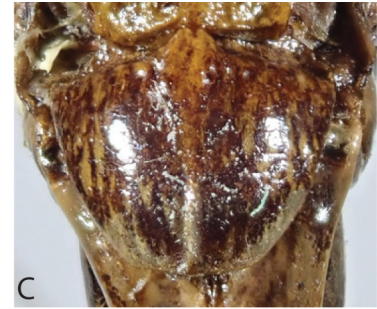
PLATE 11. Female subgenital plates of Carinata (A–I), Propsti (J), and Castanea (K–L) Group species.



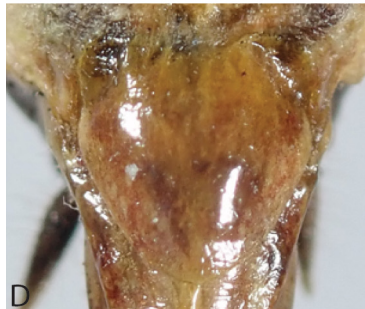
A
JAC000002198
CA: Monterey Co.
Neduba lucubrata



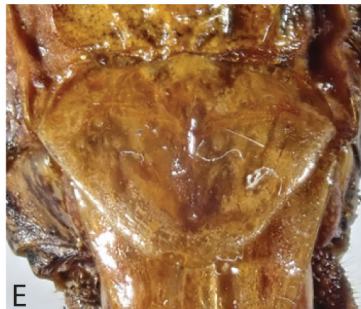
B
JAC000002360
CA: Madera Co.
Neduba sierranus



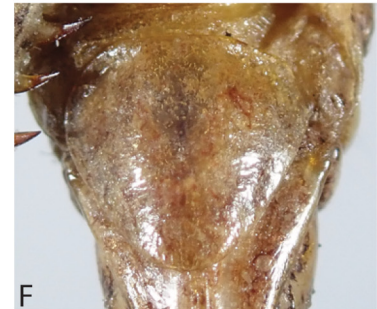
C
JAC000001954 PARATOPOTYPE
CA: Colusa Co.
Neduba arborea



D
JAC000002306 PARATOPOTYPE
CA: El Dorado Co.
Neduba radocantans



E
JAC000002160 PARATOPOTYPE
CA: Fresno Co.
Neduba inversa



F
S18-115 PARATOPOTYPE
CA: Kern Co.
Neduba prorocantans



G
JAC000002324 PARATOPOTYPE
CA: Tulare Co.
Neduba sequoia



H
JAC000002150 PARATOPOTYPE
CA: Tulare Co.
Neduba duplocantans

PLATE 12. Female subgenital plates of Lucubrata (A), Sierranus (B–D), and Sequoia (E–H) Group species.