

## Morsei Group

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

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

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

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

### *Aglaothorax morsei* (Caudell, 1907)

*Neduba morsei*—Caudell, 1907: 301.

*Neduba (Aglaothorax) morsei*—Rentz & Birchim, 1968: 61 (A change in status).

Fig. 15 (distribution), Fig. 16 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 5 (male terminalia), Plate 8 (female subgenital plate), Plate 11 (male titillators), Plate 14 (male calling song).

#### **Common name.** Morse's Shieldback

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

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

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

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

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

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

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

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

**Karyotype.** (n=2)  $2n\text{♂}=24$  (22t+Xty t), toptype T82-115 (S82-58).

TABLE 3. Comparative chaetotaxy of the Morsei Group.

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

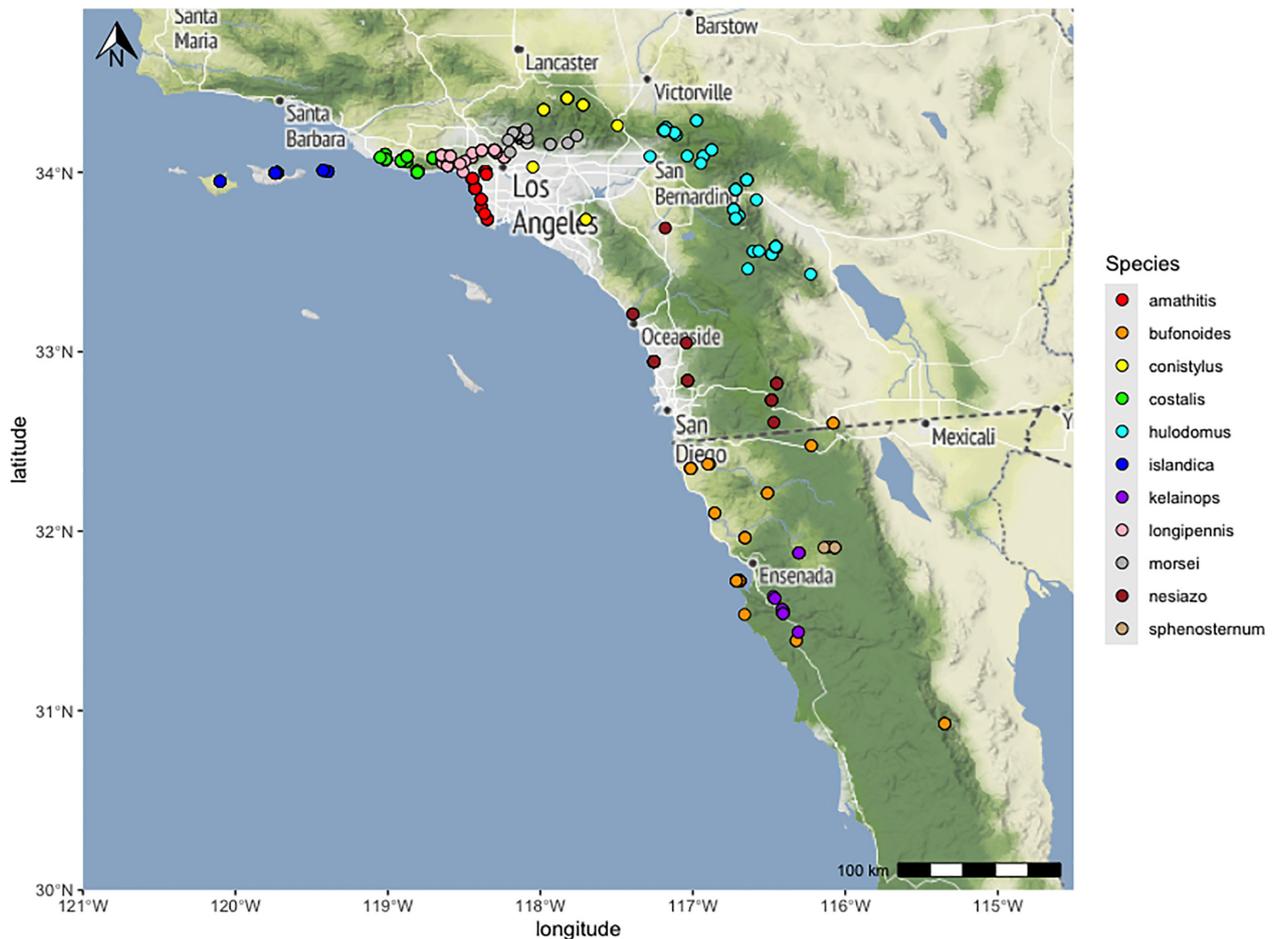


FIGURE 15. Distribution of Morsei Group species.

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

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

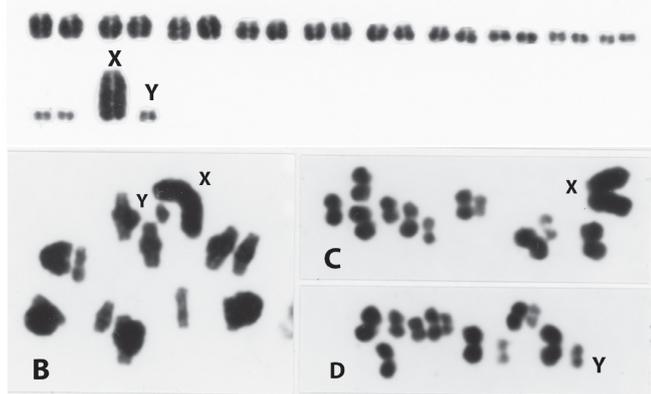
male TOPOTYPE USA. CA: Los Angeles Co. S82-57



calling song TOPOTYPE USA. CA: Los Angeles Co. 25.0°C R82-218



karyotype TOPOTYPE USA. CA: Los Angeles Co. S82-58, T82-115



female USA. CA: Los Angeles Co. JAC000002951



male terminalia USA. CA: Los Angeles Co. JAC000002949 R V



male USA. CA: Los Angeles Co. JAC000002930



titillators USA. CA: Los Angeles Co. JAC000002949 female subgenital plate USA. CA: Los Angeles Co. JAC000002948

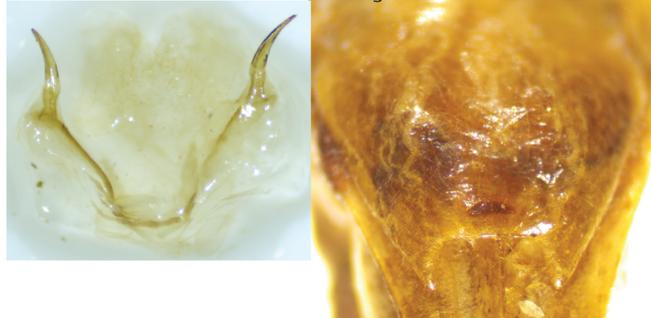


FIGURE 16. *A. morsei* male and female habitus, calling song, male and female terminalia, and karyotype. Idiogram top panel shows karyotype  $2n\sigma=24$ ; B. Metaphase I plate showing associated X and y chromosomes, which ensures proper segregation to opposite poles; C and D showing metaphase II cells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

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

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

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

*Neduba* (*Aglaothorax*) *morsei costalis*—Rentz & Weissman, 1981: 99.

*Aglaothorax costalis* stat. rev. (Revised to species level).

*Neduba* (*Aglaothorax*) *morsei curtatus*—Rentz & Weissman, 1981: 100 **New junior subjective synonym.**

*Neduba* (*Aglaothorax*) *morsei tectinota*—Rentz & Weissman, 1981: 104 **New junior subjective synonym.**

Fig. 15 (distribution), Figs. 17–18 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 5 (male terminalia), Plate 8 (female subgenital plate), Plate 11 (male titillators), Plate 14 (male calling song).

### **Common name.** Coastal Shieldback

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

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

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

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

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

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

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

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

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

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

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

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

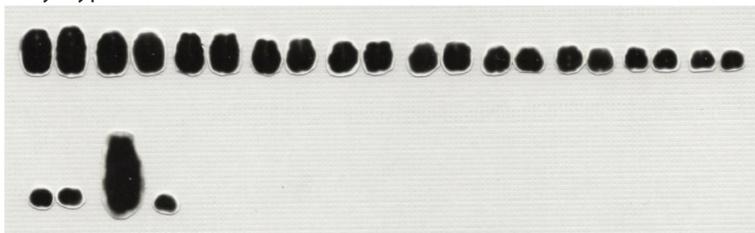
male PARATYPE USA. CA:Ventura Co.



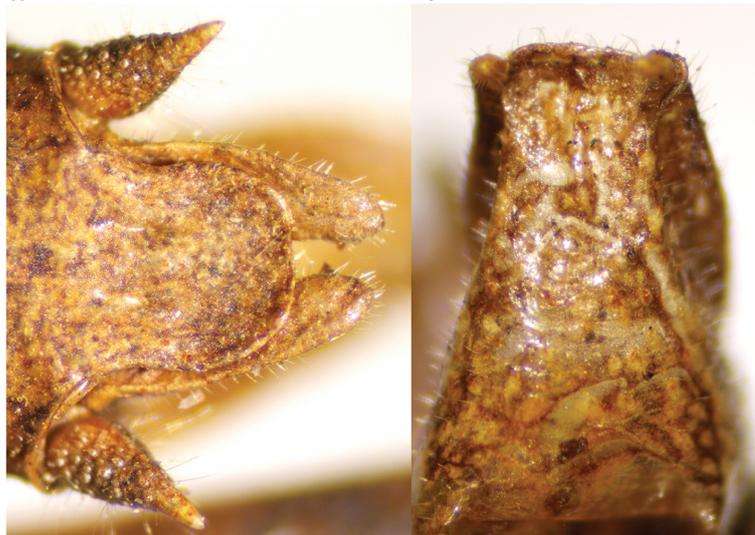
calling song TOPOTYPE USA. CA:Ventura Co. 24.9°C JCR05MU04-1



karyotype TOPOTYPE USA. CA:Ventura Co. S82-33 T82-21



male PARATOPOTYPE USA. CA:Ventura Co.  
R V



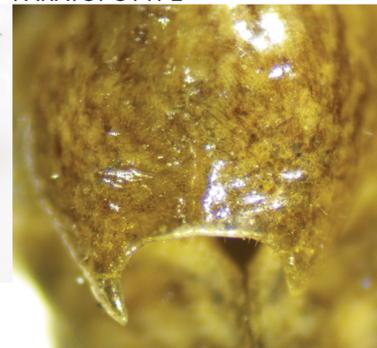
female PARATYPE USA. CA:Ventura Co.



titillator PARATOPOTYPE  
USA. CA:Ventura Co.



female subgenital plate  
PARATOPOTYPE



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

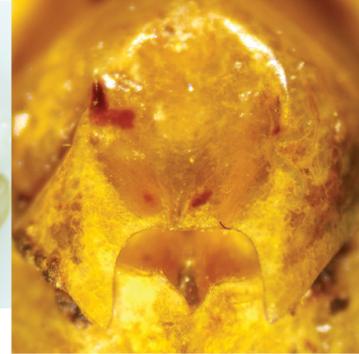
male *curtatus* TOPOTYPE  
USA. CA: Los Angeles Co. JAC000002869



male *curtatus* USA. CA: Los Angeles Co. JAC000002872  
R V



titillators *curtatus* USA. CA: Los Angeles Co. JAC000002912 female subgenital plate *curtatus* USA. CA: Los Angeles Co. JAC000002908



female *curtatus* USA. CA: Los Angeles Co. JAC000002892



male *tectinota* PARATOPOTYPE USA. CA: Los Angeles Co.  
R V



male *tectinota* PARATOPOTYPE  
USA. CA: Los Angeles Co.



titillators *tectinota* TOPOTYPE JAC000002836 female subgenital plate *tectinota* USA. CA: Los Angeles Co. JAC000002845



female *tectinota* PARATOPOTYPE  
USA. CA: Los Angeles Co.



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

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

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

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

### *Aglaothorax longipennis* (Rentz & Weissman, 1981)

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

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

**Common name.** Santa Monica Mountains Shieldback

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

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

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

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

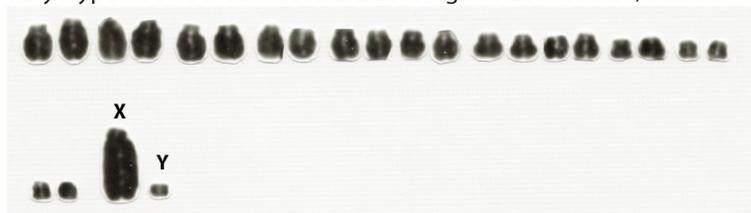
male TOPOTYPE USA. CA: Los Angeles Co. S82-34, R82-85, T82-17



calling song TOPOTYPE USA. CA: Los Angeles Co. 25.5°C R82-100



karyotype TOPOTYPE USA. CA: Los Angeles Co. S82-34, T82-14



male terminalia USA. CA: Los Angeles Co. JAC000002697  
R V



female USA. CA: Los Angeles Co. JAC000002672



male USA. CA: Los Angeles Co. JAC000002724



titillator TOPOTYPE



female subgenital plate PARATYPE



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

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

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

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

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

**Karyotype.** (n=1)  $2n \text{♂} = 24$  (22t+Xty t), topotype T82-14 (S82-34).

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

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

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

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

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

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

**Common Name.** Bluffs Shieldback.

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

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

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

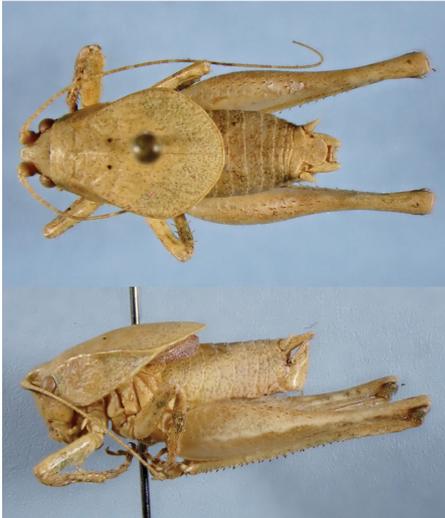
**Distribution.** Palos Verdes Peninsula and Los Angeles Basin, Los Angeles County, California.

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

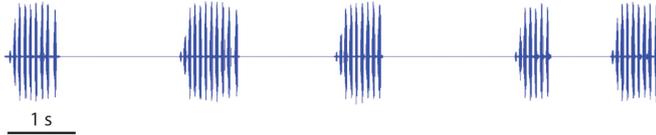
**Seasonal occurrence.** Wide adult activity season across spring and summer, from 12-V-1946 (no collector, LACM) to 27-IX-1980 (C. Nagano & E. Birdsall, LACM).

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

male HOLOTYPE USA. CA: Los Angeles Co. S92-58, R92-75, T92-27



calling song PARATYPE USA. CA: Los Angeles Co. 24.5°C JCR08KH01



karyotype PARATOPOTYPE USA. CA: Los Angeles Co. S92-58, T92-28



male terminalia HOLOTYPE USA. CA: Los Angeles Co. S92-58  
R V



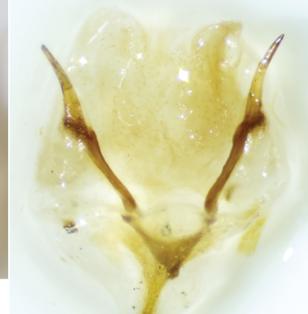
female PARATOPOTYPE USA. CA: Los Angeles Co. S92-58



titillator PARATYPE USA. CA: Los Angeles Co. JAC000002758



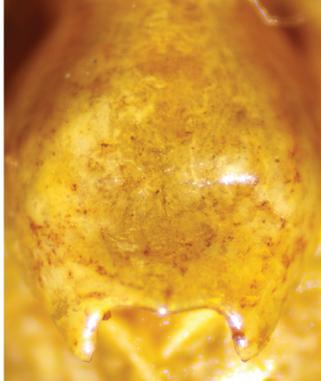
titillator PARATYPE USA. CA: Los Angeles Co. JAC000002741



male PARATYPE USA. CA: Los Angeles Co. JAC000002764



female subgenital plate PARATOPOTYPE USA. CA: Los Angeles Co. S92-58



female subgenital plate PARATYPE USA. CA: Los Angeles Co. JAC000002745



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

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

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

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

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

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

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

### ***Aglaothorax islandica* (Rentz & Weissman, 1981)**

*Neduba (Aglaothorax) morsei islandica*—Rentz & Weissman, 1981: 101.

*Aglaothorax islandica* **stat. rev.** (Revised to species level).

*Neduba (Aglaothorax) morsei santacruzae*—Rentz & Weissman 1981: 103 **New junior subjective synonym.**

Fig. 15 (distribution), Fig. 21 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 5 (male terminalia), Plate 8 (female subgenital plate), Plate 12 (male titillators), Plate 15 (male calling song).

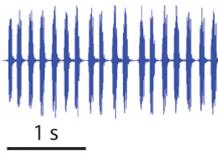
**Common name.** Northern Channel Islands Shieldback.

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

male PARATOPOTYPE  
USA. CA: Ventura Co.



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



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



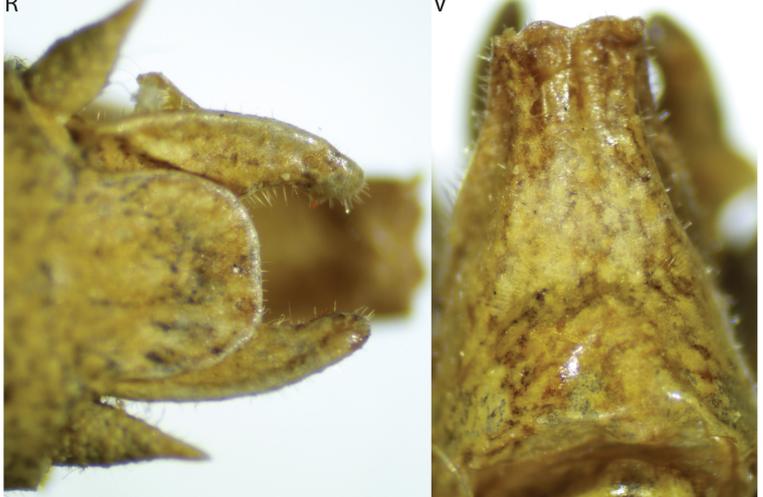
karyotype USA. CA: Santa Barbara Co. S18-30 T19-6



female PARATOPOTYPE  
USA. CA: Ventura Co.



male terminalia PARATOPOTYPE USA. CA: Ventura Co. DCR111  
R V



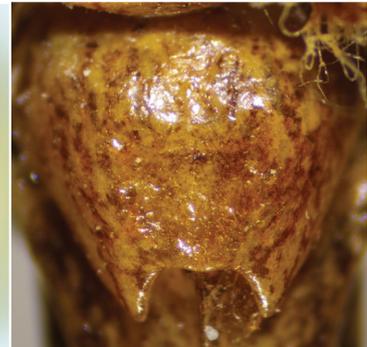
female *santacruzae* TOPOTYPE  
USA. CA: Santa Barbara Co.



titillator PARATOPOTYPE  
USA CA: Ventura Co.



female subgenital plate  
PARATOPOTYPE



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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

**Common name.** Forest Home Shieldback.

**History of recognition.** None.

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

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

male HOLOTYPE USA. CA: San Bernardino Co. S89-56, R89-64, T89-39



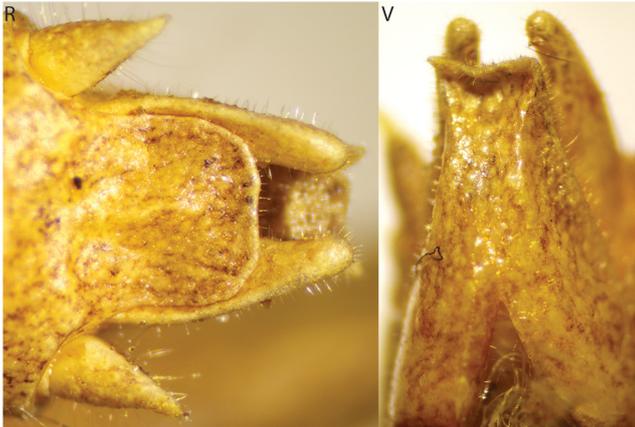
calling song TOPOTYPE USA. CA: San Bernardino Co. 22.8°C JCR130731\_02



karyotype PARATYPE USA. CA: San Bernardino Co. S82-65, T82-136



male terminalia HOLOTYPE USA. CA: San Bernardino Co. S89-56



female PARATYPE USA. CA: San Bernardino Co. S92-77



female PARATOPOTYPE USA. CA: San Bernardino Co. S92-77



female PARATYPE USA. CA: Riverside Co.



male PARATYPE USA. CA: Riverside Co. S82-61, R82-307



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



female PARATYPE USA. CA: Riverside Co. S82-61

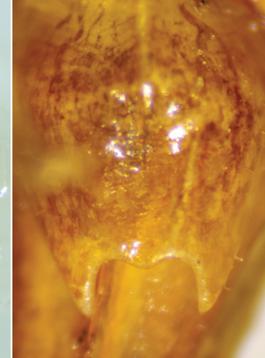


FIGURE 22. *A. hulodomus* male and female habitus, calling song, male and female terminalia, and idiogram of karyotype  $2n_{\text{♂}}=24$ .

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

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

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

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

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

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

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

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

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

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

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

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

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

**Common name.** Alluvial Shieldback.

**History of recognition.** None.

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

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

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

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

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

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

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

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

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

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

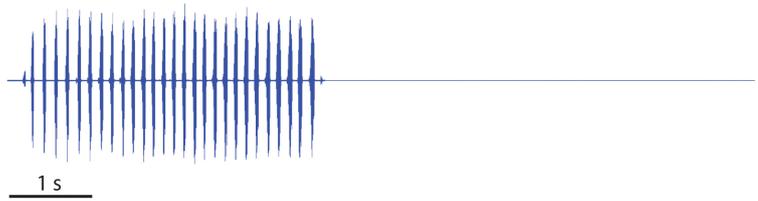
**Etymology.** Gr. *coni* a cone + *stylus* a pillar, stake. Refers to the cone shaped styli on the male subgenital plate.

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

male PARATOPOTYPE USA. CA: Los Angeles Co.  
JAC000002971



calling song PARATOPOTYPE USA. CA: Los Angeles Co. 25.5°C  
JCR045F03



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



female PARATOPOTYPE USA. CA:  
Los Angeles Co. JAC000002980



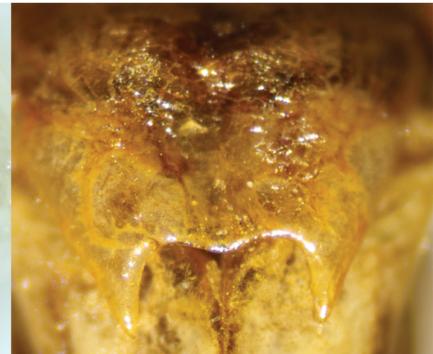
male terminalia HOLOTYPE USA. CA: Los Angeles Co. JAC000002979



titillators HOLOTYPE  
JAC000002979



female subgenital plate PARATOPOTYPE  
JAC000002980



female PARATYPE USA. CA: Los Angeles Co.  
JAC000005723



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

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

***Aglaothorax nesiaz* Cole, Weissman, and Lightfoot, sp. nov.**

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

**Common name.** Peninsular Shieldback.

**History of recognition.** None.

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

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

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

**Distribution.** Southern Peninsular Ranges of Southern California.

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

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

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

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

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

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

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

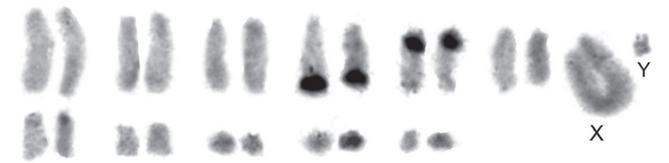
male HOLOTYPE USA. CA: San Diego Co. S21-21, R22-10, F1



calling song HOLOTYPE USA. CA: San Diego Co. 21.0°C R22-10



karyotype PARATOPOTYPE USA. CA: San Diego Co. S21-21, T21-23



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

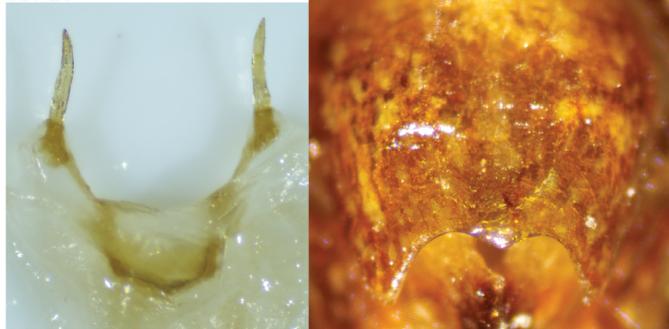


male terminalia HOLOTYPE USA. CA: San Diego Co. S21-21 R V



female subgenital plate PARATOPOTYPE S21-21

titillators PARATOPOTYPE S21-21



male PARATYPE USA. CA: San Diego Co. JAC000005726



male PARATYPE USA. CA: San Diego Co. R V

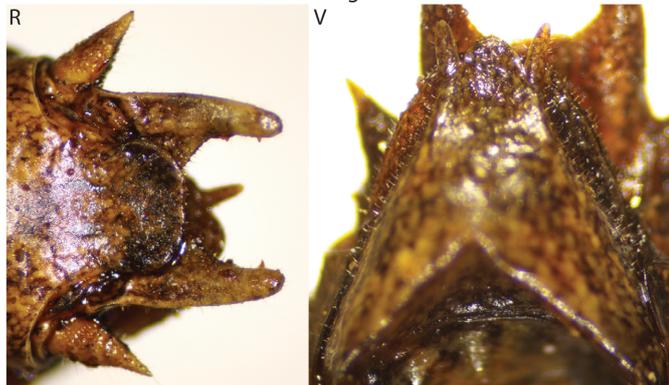


FIGURE 24. *A. nesiazo* male and female habitus, calling song, male and female terminalia, and karyotype. Idiogram shows karyotype  $2n\♂=24$ .

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

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

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

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

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

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

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

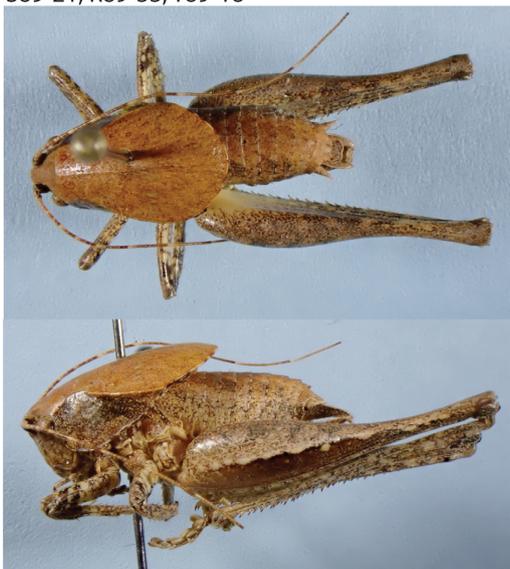
Fig. 15 (distribution), Fig. 25 (male and female habitus, calling song, male and female terminalia, karyotype), Plate 5 (male terminalia), Plate 8 (female subgenital plate), Plate 12 (male titillators), Plate 15 (male calling song).

**Common name.** Toad Shieldback.

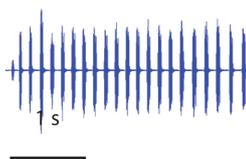
**History of recognition.** None.

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

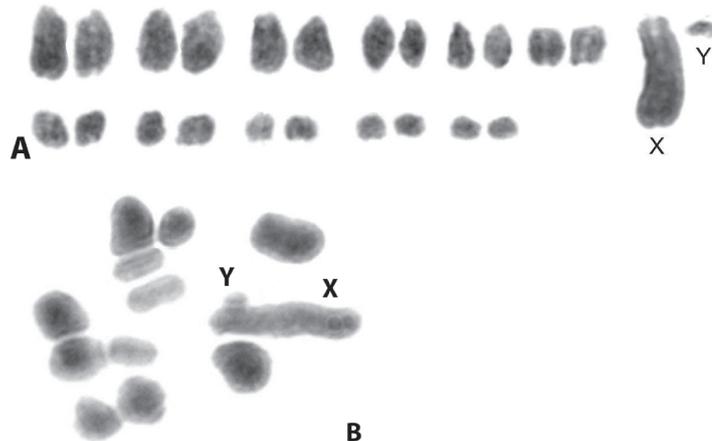
male HOLOTYPE México. Baja California.  
S89-21, R89-33, T89-18



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



karyotype PARATYPE México. Baja California. JCT19-6



female PARATYPE  
México. Baja California. S78-95



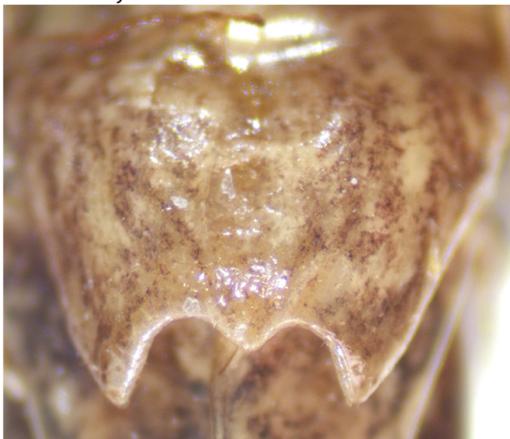
male terminalia HOLOTYPE  
R



titillators PARATOPOTYPE  
S89-21 R89-31



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



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



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

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

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

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

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

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

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

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

**Karyotype.** (n=13)  $2n \text{♂} = 24$  (22t+Xty t), paratype JCT19-6, paratopotype S89-21, T89-10. Type locality T89-10 (S89-21)  $2n \text{♂} = 24$ , metaphase I clearly showing associated Xy sex chromosomes and 11 pairs of autosomes.

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

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

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

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

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

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

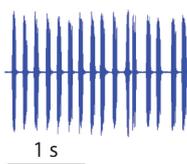
**Common name.** Ojos Negros Shieldback.

**History of recognition.** None.

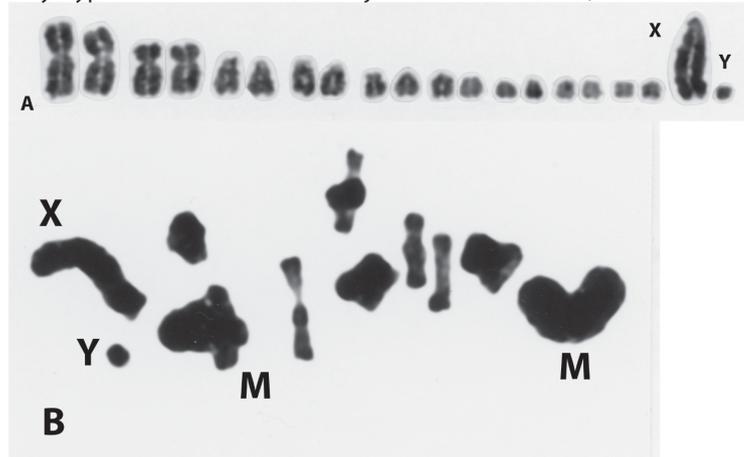
male HOLOTYPE México. Baja California. S88-84, R88-135, T88-52



calling song HOLOTYPE México. Baja California. 25.0°C R88-135



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



female PARATOPOTYPE México. Baja California. S88-84



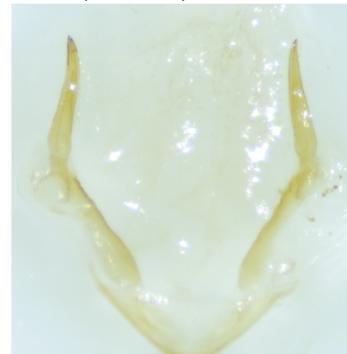
male terminalia HOLOTYPE México. Baja California. S88-84 R V



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



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



female subgenital plate PARATOPOTYPE S88-84



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

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

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

**Distribution.** Northern Baja California, México.

**Habitat.** Chaparral on laurel sumac.

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

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

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

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

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

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

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

**Material examined.** See Type Material above.

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

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

**Common name.** Wedge-breasted Shieldback.

**History of recognition.** None.

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

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

**Distribution.** Northern Baja California, México.

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

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

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

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

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

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

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

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

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

male HOLOTYPE S88-85, R88-124, T88-58  
México. Baja California.



calling song PARATYPE México. Baja California. 24.0°C R88-145



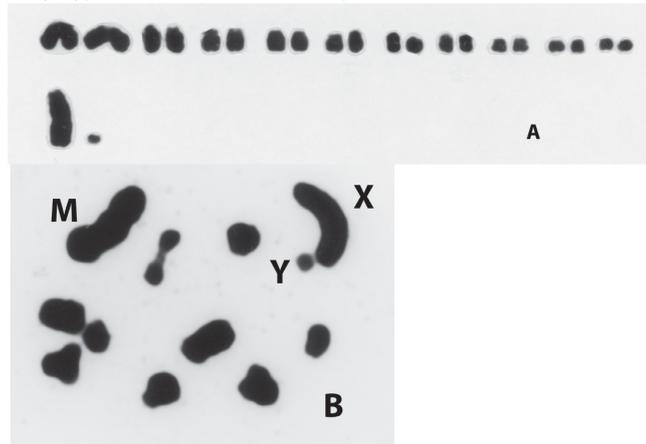
karyotype PARATYPE México. Baja California. JCT19-09



male PARATOPOTYPE México. Baja California.  
JAC000002999



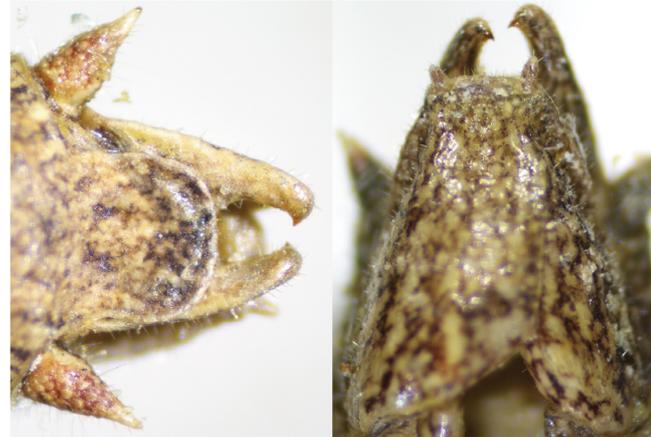
karyotype HOLOTYPE México. Baja California. T88-58



female PARATOPOTYPE S88-85  
México. Baja California.



male terminalia HOLOTYPE México. Baja California S88-85  
R V



female subgenital plate  
PARATOPOTYPE S88-85



titillators PARATOPOTYPE  
S88-85 R88-145



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