

Males are easy to approach in the field and sing well in the laboratory. Because of a similar dominant frequency and long, uninterrupted trills, we have confused this *Gryllus*, in the field, with sympatric trilling *Oecanthus* tree crickets.

Male *G. regularis* parasitized by tachinid *Ormia ochracea* at Agua Fria (Sakaguchi & Gray 2011).

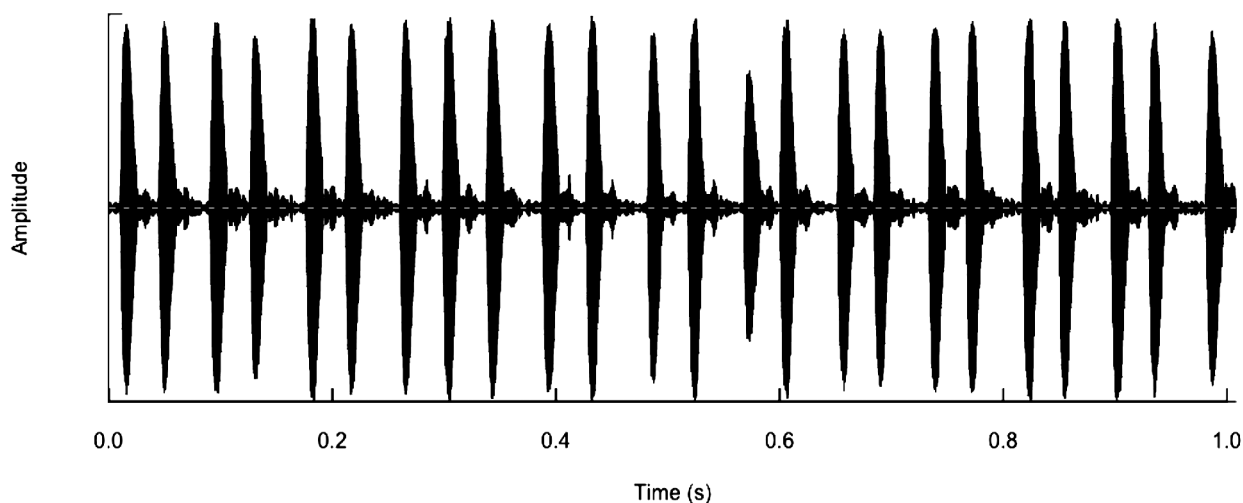


FIGURE 95. *G. regularis* with subtle pairing of pulses (R11-167), from Yavapai Co., AZ (S11-105), at 21°C.

The Integer Group

G. integer Scudder and *G. armatus* Scudder.

Sister species with a series of very fast 2-3 pulse chirps concatenated together (Fig. 96) such that they can sound like an irregular ‘stutter-trill’ despite not being a true trill as defined here (p. 25). Separated by geography (Fig. 100), DNA (Fig. 98), and song differences (Fig. 96).

Gryllus integer Scudder

Mud Crack Field Cricket

Figs 96–104, 106, Table 1

1901 *Gryllus integer* Scudder. Psyche 9: p. 268. Lectotype male (Fig. 99) designated by Weissman *et al.* 1980: “W. Berkeley, Calif., Aug 20, 1897. S.H. Scudder coll. *Gr. integer*; Scudder’s type 1901. Red label, type 14065.” Specimen labeled Weissman and Rentz cotype #1). Type in ANSP.

‘*Gryllus* VI’ of Weissman & Rentz (1977a) and Rentz & Weissman (1981).

G. integer (in part) of Weissman *et al.* (1980).

‘*Gryllus* #6’ of DBW notebooks.

Distribution. California (except for southeastern deserts) north into Washington, east into Idaho and Wyoming and south into western Colorado, northern and central Utah, and Nevada (Fig. 100). Also known from 5 California Channel Islands.

Recognition characters and song. A medium sized, short hind femur, always solid black headed, long and narrow tegmina, long hind winged cricket. Song usually with intermittent bursts of 3 (range 2–4) p/c, usually without an introductory, short trill (Figs 101, 102; R16-60, S16-21), 1000 c/m, PR usually >70. But these general patterns are not fixed in that many populations are a composite of calls including individuals with a pure trill (discussed below), a short introductory trill that changes to 3p/c, and a 2p/c song. Morphologically indistinguishable from sister species *G. armatus* but separated by habitat and geography, slight song differences, and consistent DNA differences, as follows: (1) *G. armatus* is from hotter, more southern desert US locations (see Fig. 100); (2) Most, but not all *G. armatus*,

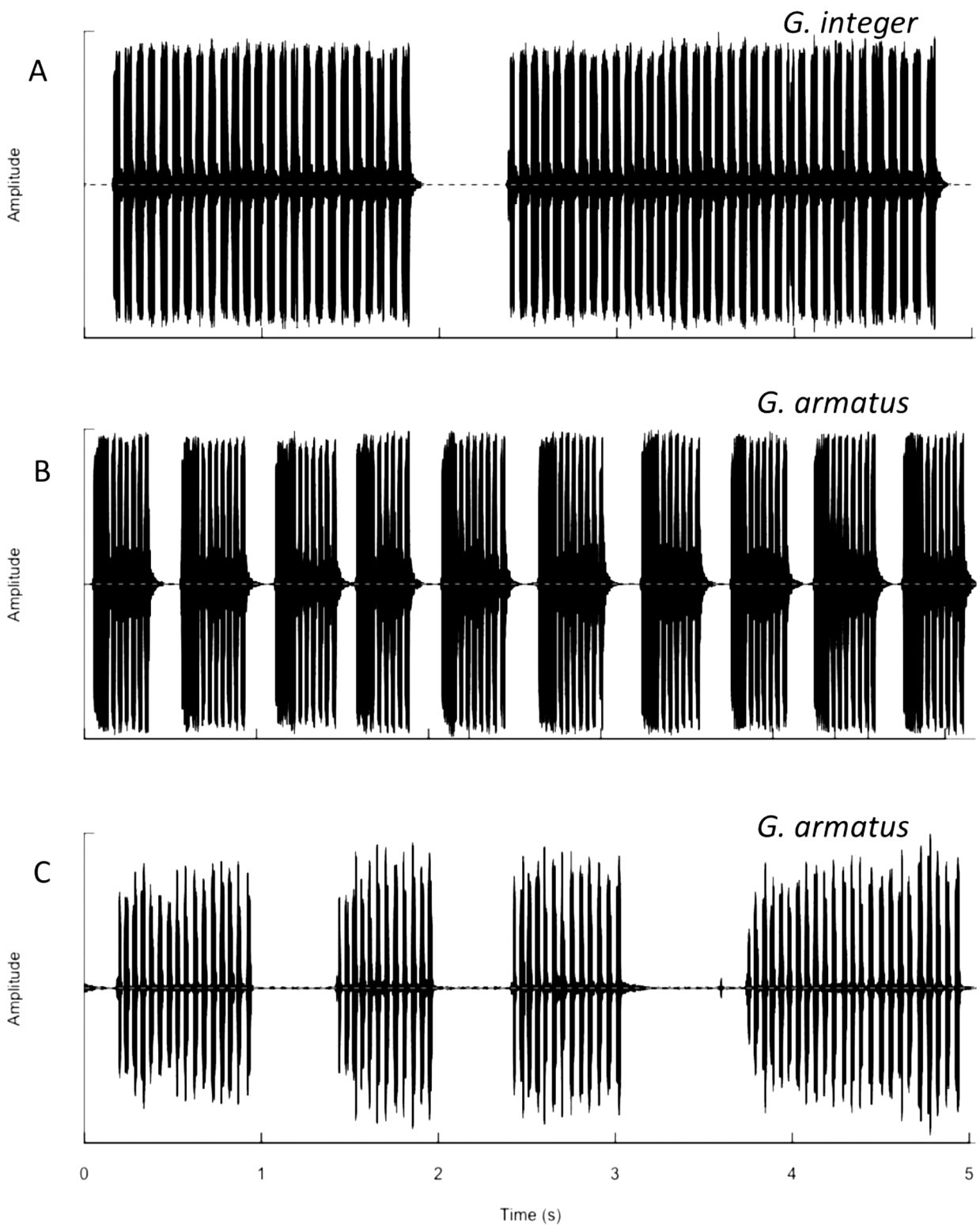


FIGURE 96. Five second waveforms of typical calling songs of (A) *G. integer*, (B) *G. armatus* with introductory trill, and (C) *G. armatus* without introductory trill. (A) *G. integer*: (R16-60) Tulare Co., CA (S16-21), at 24.2°C; (B) *G. armatus*: (R15-177) Artesia, NM (S15-58), at 25.1°C; (C) *G. armatus* (2003-170) Bernalillo Co., NM, at 20.6°C.

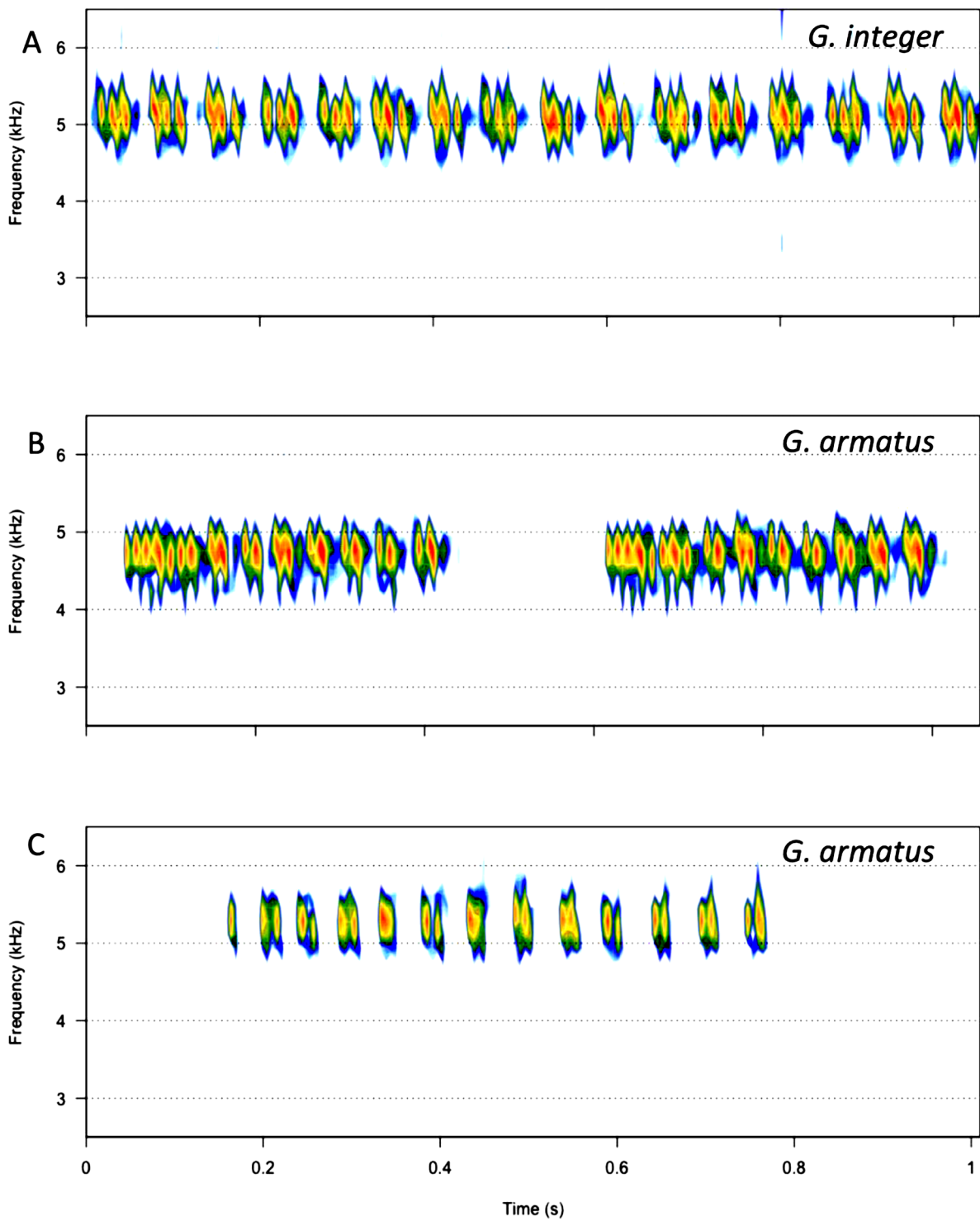


FIGURE 97. One second spectrograms of (A) *G. integer*, (B) *G. armatus*, and (C) *G. armatus*; same male recordings as in Fig. 96.

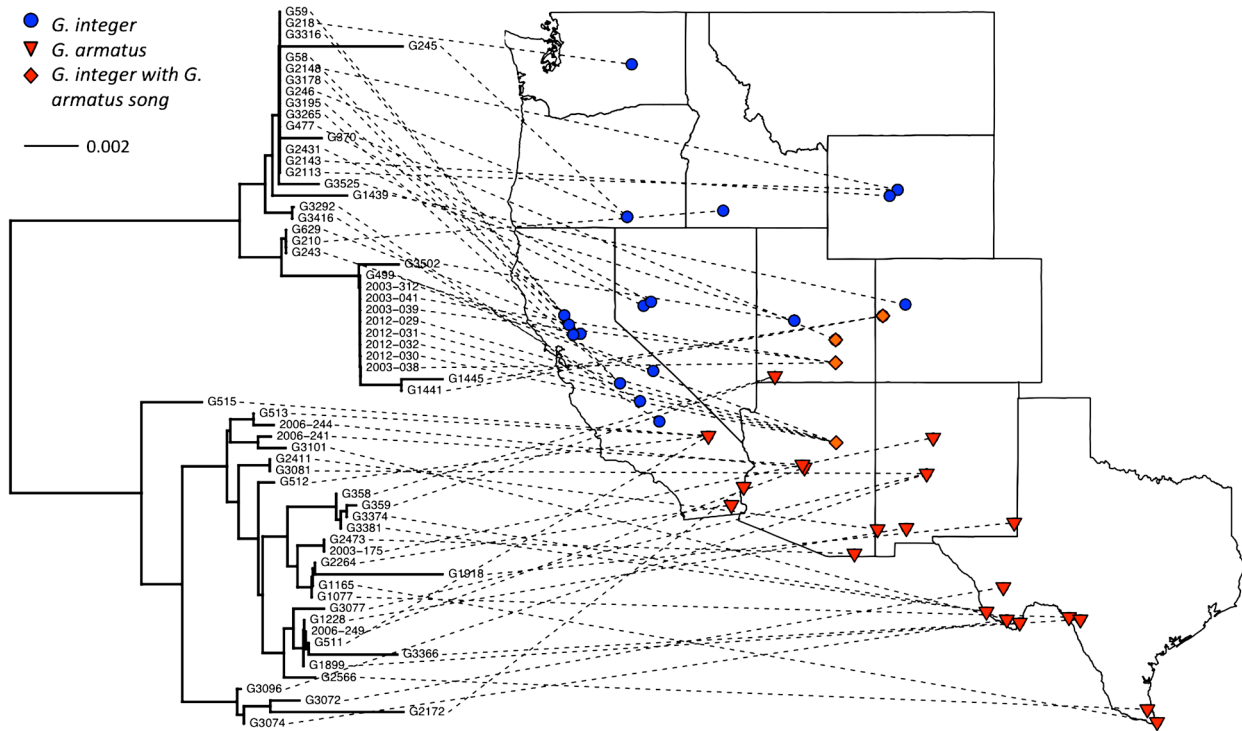


FIGURE 98. ITS2 gene tree and distribution map for both *G. armatus* and *G. integer* showing both geographic separation and zone of possible hybridization. Collection stop numbers for ***G. armatus***: S04-121 (G358, G359); S05-110 (G511, G512, G513, G515); S07-26 (G1165); S07-33 (G1077); S07-79 (G1228); S10-62 (G1918); S10-63 (G1899); S11-90 (G2172); S12-36 (G2264); S12-104 (G2411); S13-18 (G2473); S13-46 (G2566); S15-54 (G3096, G3077, G3081); S15-71 (G3101, G3074); S15-73 (G3072); Albuquerque, NM (2003-175); Cordes Junction, AZ (2006-241); Agua Fria, AZ (2006-244). Collection stop numbers for ***G. integer***: S03-100 (G58, G59); S04-36 (G243); S04-40 (G210); S0455 (G245, G246); S04-60 (G218); S04-128 (G370); S05-23 (G477); S05-99 (G499); S06-77 (G629); S09-109 (G1439); S09-114 (G1441, G1445); S11-72 (G2113, G2148); S11-73 (G2143); S12-116 (G2431); S15-80 (G3195, G3316); S15-91 (G3178, G3265); S15-95 (G3292); S16-21 (G3416); S17-6 (G3502, G3525); S16-5 (G3374, G3381); S16-12 (G3366); Hwy 276 mile 30 Sinclair Gas, Garfield Co., UT (2003-038, 2003-039, 2003-041); Winslow, AZ (2003-312, 2012-029, 2012-030, 2012-031, 2012-032).

have an “introductory trill” of 2–8 evenly spaced pulses at the beginning of each burst of chirps (see Fig. 108, p. 114), usually followed by 2 (range 1–3) p/c until that burst is over. In contrast, *G. integer* usually with no introductory trill and 3 p/c, although some males sing with 2–4p/c); and (3) there is a congruent, and consistent association between those males with 2p/c and parallel differences in the ITS2 gene sequences when compared with *G. integer* (see Fig. 98). In distribution map (Fig. 100), note a possible area of hybridization in the Four Corners area of southeastern Utah, west-central Colorado, and north-eastern Arizona where males sing more like *G. armatus* but possess *G. integer* DNA. In this paper, we arbitrarily give priority to the DNA and consider such populations to be *G. integer*. Nevertheless, it is the extensive DNA/song correspondence that ultimately convinced us to consider these two taxa as different and preserve both of Scudder’s names.

Derivation of name. “integer” in Latin means whole, entire, sound (Brown 1956). From Scudder’s original description, we have no indication why he chose this name. While the common name “western stutter-trilling field cricket” has been used for many years (Weissman *et al.* 1980; Walker 2019), the song, except for in a few rare individuals, is not a trill but consists of 2 to 4 closely group pulses. In the field, especially at warm temperatures, the song can resemble an uneven trill. The common name “stutter triller” is more appropriate for *G. cohni* from Arizona, which has an irregular trill song. We thus adopt a new common name for *G. integer* in this paper.

Geographic range. (Fig. 100). Usually sporadically distributed but can be locally common. Not known from the hot Southwestern Sonoran and Chihuahuan Deserts where it is replaced by *G. armatus*, but does occupy the Great Basin Desert and the western part of the Mohave Desert. DC Lightfoot has kindly allowed us to examine some 25

specimens he collected in the Oregon Counties of Harney, Malheur, and Wasco during the early 1980s. While these are morphologically highly suggestive of *G. integer*, none have associated recordings. We believe his specimens indicate a more widespread distribution of this taxon east of the Cascades in Oregon.

Habitat. From sea level to 1950m (Mono Lake, CA, S78-123 & S78-125). Usually in towns but associated with a variety of microhabitats: watered lawns, dry grassy fields, garbage dump areas, cracks in concrete and dry ground, around florescent lights at gas stations, and mud-soil cracks in dry lake beds (Mono Lake, CA, S78-123 & S78-125; Washoe Co., NV, S83-49; Lake Lenore, WA, S04-60).

Life cycle and seasonal occurrence. No egg diapause: Stanford, CA (S92-45); Colusa Co., CA (S15-80); Sacramento River SRA, CA (S15-81). Two generations/year in southern populations but doubt such in more northern localities.



FIGURE 99. Lectotype male, *G. integer*, specimen and labels.

Variation. Color: Individual crickets, especially second-generation ones from hot climates like the California Central Valley, can have a distinctive two-tone contrasting appearance: black head and pronotum coupled with beige/straw colored tegmina (Fig. 99) and legs. In certain individuals, even the pronotum can be beige/straw colored. **Hind wing length:** Always with long hind wings although these have been occasionally shed in field-collected adult males (Weissman *et al.* 1980). Of 133 studied *G. integer* males, all but 9 had intact long hind wings. All those without long hind wings were, in fact, dealate, a condition discussed elsewhere for *Acheta domesticus* (Weissman & Rentz 1977b, Walker 1977) where both hind wings are shed. This condition is easily diagnosed in those males whose right tegmen has been removed for file analysis. Interestingly, in two populations found away from humans (Mono Lake, CA, S78-123 & S78-125, & Lake Lenore, WA, S04-60), where individuals were living in cracks in dry mud flats with short grass, 4 of 6 males (S78-123 & S78-125) and 1 of 5 males (S04-60) had lost their hind wings. In contrast 6 males from a similar habitat (Washoe Co., NV, S83-49) all had unshed, long hind wings. At some localities, female *G. integer* may be difficult to assign to species. In those situations where we can make such assignments, no female, of 83 collected, was dealate. **Ovipositor length:** The 3 females from Wyoming (S11-72) have the longest ovipositors (range 14.3–17.8 mm) of any population of this species, perhaps reflecting the cold winters there and the need to deposit eggs deep in the soil. **Pronotum dimensions:** Scudder (1901) noted that the pronotum is nearly twice as broad as long. While this condition exists in some individuals, it is not universal, and

certainly not diagnostic for this species. **Song:** Variable, but usually without an introductory trill and 3p/c. In other cases, *G. integer* can have a short introductory trill of 1-3 pulses followed by 2–4p/c and, rarely, a pure trill (Fallon, NV, S98-95, R98-123, Fig. 103). A male from Riverton, WY (S11-73) sang with 4 pulses in all chirps. In the face of such variation, multiple male analysis from the same population will usually give a definitive answer.

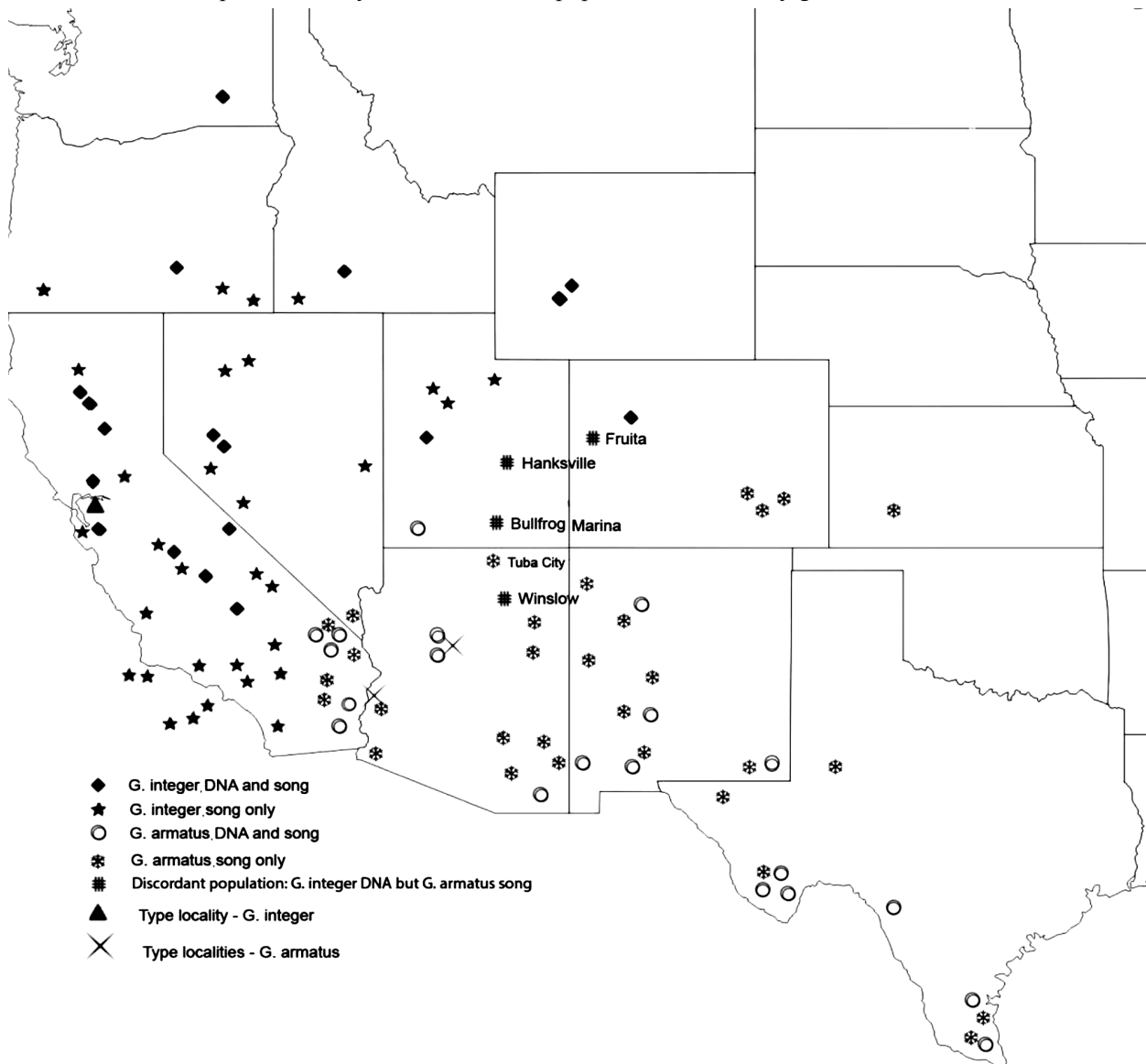


FIGURE 100. Known US distribution, *G. integer*, along with sister species *G. armatus*, showing zone of possible hybridization in the Four Corners area.

Specimens examined. California: Colusa Co., Sacramento River SRA, 96', 18-vii-2015 (S15-81). 13m S Wil-lows, 29-viii-2003, 120' (S03-87). I5 overpass area at Hwy 20, 19m, 18-vii-2015 (S15-80). Fresno Co., Coalinga, 29-viii-1998 (S98-86). Jacalitos Canyon, 29-viii-1998, 820' (S98-83); 4-v-2003 (S03-31). Inyo Co., Bishop, 28-viii-2005, 4450' (S05-99). Lone Pine, 3500', 5-viii-1978 (S78-117), Mono Lake, 3 m S Lee Vining off Test Station Road, 6400', 6-viii-1978 (S78-123 & 125). Kern Co., Sand Ridge 3-5.8 m E Edison, 1000', 22-xii-1983 (S83-163); Hwy 178 19.4 m W Hwy 14, 3064', 21-vii-2015 (S15-95). Lake Co., Clearlake Oaks, 5-viii-2014, 1428' (S14-63). Los Angeles Co., Santa Catalina Island, Toyon Canyon, 9-x-1983, S. Bennett. Madera Co., Hwy 41 6.2 m E Fresno Co. line, 457', 20-vii-2015 (S15-91). Mendocino Co., Willets, 1300', 2-viii-1980 (S80-58). Monterey Co., King City, 23-viii-1978. Sacramento Co., Folsom, 174', 19-vii-2015 (S15-87). San Luis Obispo Co., Montana de Oro State Park, 24-viii-2006 (S06-97). Santa Barbara Co., San Miguel Island, Cuyler Harbor, 31-viii-1978, S.E. Miller; Santa Barbara Island, widespread, iv-1979, SBMNH; Santa Cruz Island, Stanton Ranch. Santa Clara Co., Los Gatos, 12-viii-2006 (S06-72). Stanford University, Lake Lagunita, 2-v-1992 (S92-45). Shasta Co. Lake Shasta

Dam area, 4-viii-1980 (S80-66 & 67). *Tulare Co.*, Hwy 198 4.4 air miles E Lemon Cove, 725', 29-vi-2016 (S16-21). *Ventura Co.*, San Nicolas Island, Navy Barracks area, 16-viii-1978. *Yolo Co.*, University of California, Davis, 1-ix-2003 (S03-101). I5 near intersection Hwy 505. 18-viii-2006, 130' (S06-77). *Shasta Co.*, Redding, 29-vi-1992. **Colorado:** *Garfield Co.*, Rifle, 15-viii-2009, 5140' (S09-109). *Mesa Co.*, Fruita, 16-viii-2009, 4420' (S09-114). **Idaho:** *Owyhee Co.*, 2m N Bruneau, 12-vi-2004, 2900' (S04-40). 2m S Bruneau, 7-vi-1996, 2600' (S96-37). Mt. Home, 3260', 7-vi-1996 (S96-41); 26-vi-2014 (S14-31). 13m SE Mt. Home, 7-vi-1996, 2780' (S96-40). **Nevada:** *Churchill Co.*, Fallon, 16-ix-1998, 4000' (S98-95); 14-ix-2012 (S12-116). Stillwater National Wildlife Refuge, 1-iii-2005, 3940' (S05-23). *Humboldt Co.*, Paradise Valley, 8-vi-1996, 4600' (S96-42). *Lyon Co.*, Weeks, 19-iv-1998, 4320' (S98-32). *Mineral Co.*, Hawthorne, 26-vi-1992, 4320' (S92-65). Schurz, 27-vi-1992, 4000' (S92-66). *Pershing Co.*, Rye Patch State Rec Area, 27-vi-1992, 4050' (S92-67). *Washoe Co.*, Hwy 447 18m NW Gerlach, 3-vi-1983, 4700' (S83-49). *White Pine Co.*, Baker, 9-vi-1996, 5380' (S96-49). **Oregon:** *Harney Co.*, Burns, 2-vi-1997, 4020' (S97-51). Fields, 28-vi-1992, 4300' (S92-69). Hwy 205 16.6m NW Fields, 2-vi-1997, 4720' (S97-52). *Jackson Co.*, Emigrant Lake Recreational Area, 27-vii-1992, 1800' (S92-82). *Lake Co.*, Lakeview, 4700' (S92-71), 28-vi-1992. Warner Valley, 12 m N Plush, 24-vi-2014, 4509', 42° 34' 24.0 -119° 53' 03.3" (S14-26); 17m NE Plush, 16-vi-2004, 4700' (S04-55). **Utah:** *Emery Co.*, Green River, 4350', 21-vi-1987 (S87-55). *Garfield Co.*, Hwy 276 7.4 m N Bullfrog Marina, 37.6309° -110.7211°, 27-vii-2003, 3900'. *Millard Co.*, 2.05 m NW Flowell, 20-v-2017, 4653' (S17-6). *Tooele Co.*, Tooele, 30-vii-1992, 5100' (S92-94). 12m N Tooele, 20-vi-1987, 4500' (S87-51). *Wayne Co.*, Hanksville, 1-viii-1992, 4500' (S92-109); 19-v-2001 (S01-37); 12-ix-2004 (S04-128); Hwy 24 2.5m W Hanksville, 29-viii-2017, 38.3737° -110.751°. **Washington:** *Grant Co.*, Lake Lenore, Hwy 17, mile post 84.8, 9m N Soap Lake, 19-vi-2004, 1020' (S04-60). **Wyoming:** *Fremont Co.*, Riverton, 18-vii-2011 (S11-73). Shoshoni, 18-vii-2011, 4849' (S11-72).

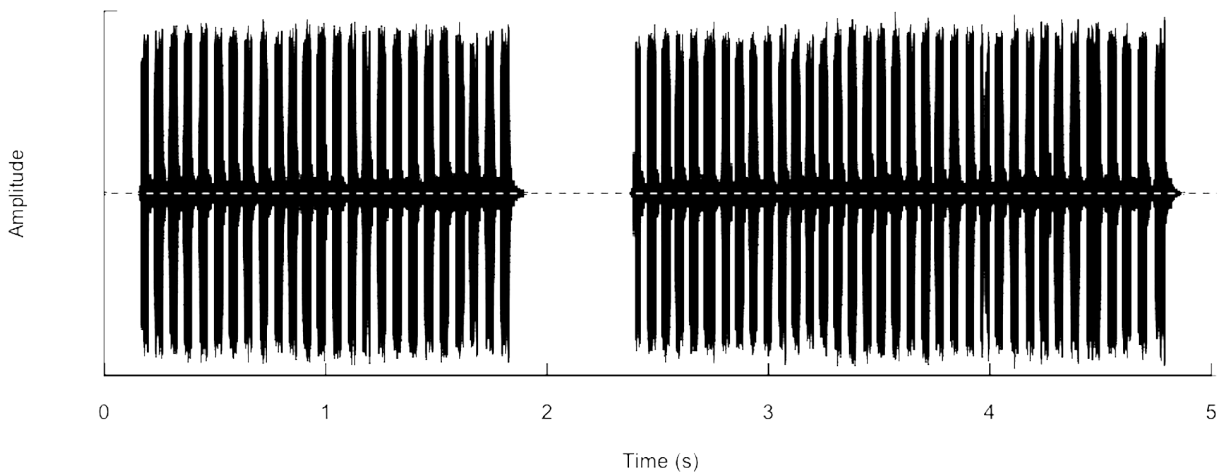


FIGURE 101. Five second waveform of typical calling song of *G. integer* (R16-60) Tulare Co., CA (S16-21), at 24.2°C.

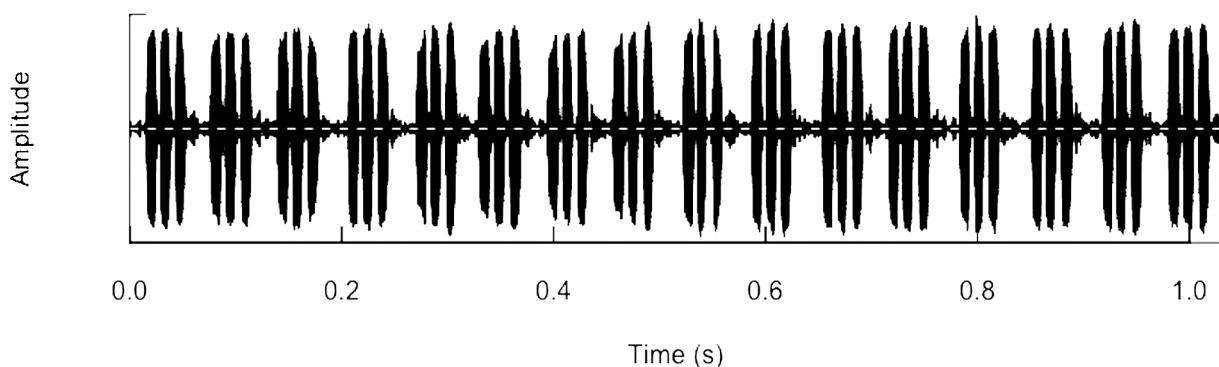


FIGURE 102. One second waveform of typical calling song of *G. integer* (R16-60) Tulare Co., CA (S16-21), at 24.2°C revealing the typical fast 3 pulse/chirp structure.

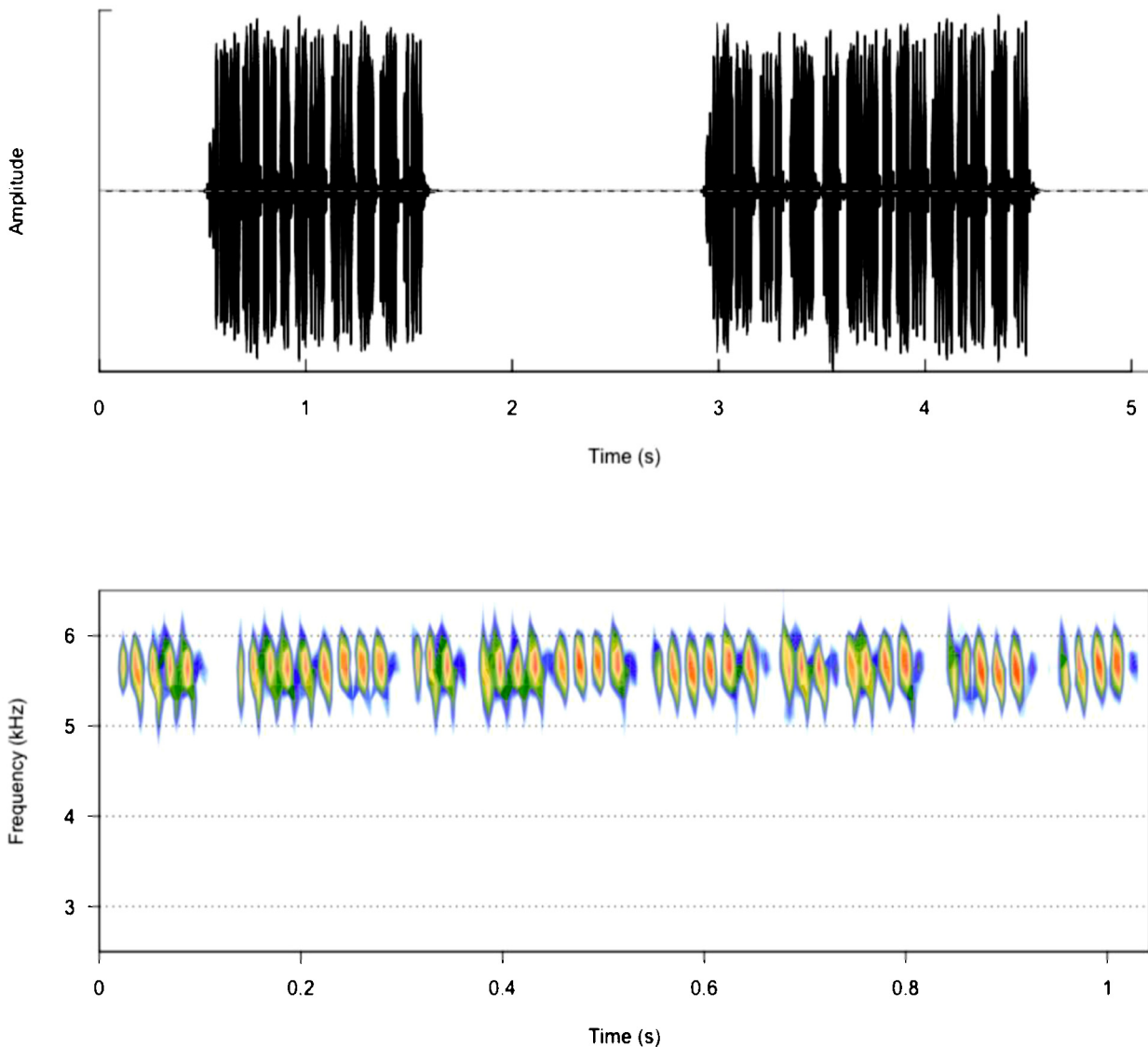


FIGURE 103. Anomalous song (top) of *G. integer* (R98-123) Churchill Co., NV (S98-95), at 25°C, without distinctive 3 pulse chirp structure. Spectrogram (bottom) of same male, but note different time scale.

DNA. Multilocus G3416 (Tulare Co., CA, S16-21) and 2003-039 (7.4 m N Bullfrog Marina, UT—site of specimens with *G. integer* DNA and *G. armatus* song), closest in tree to sister species *G. armatus* (Gray *et al.* 2019). ITS2 genetic distances (Fig. 98) within and between *G. integer* and *G. armatus* are described under *G. armatus* (p. 116). 16S also shows a clear separation between *G. integer* and *G. armatus*, with two 16S clades within *G. armatus* (Fig. 104).

Discussion. Our initial 16S genetic data showed clear separation between *G. integer* and *G. armatus*, but given our previous documentation of 16S clades in other species, such as *G. vernalis*, *G. veletis*, and *G. lightfooti*, we were unsure of its significance with these two taxa. With the subsequent analysis of the ITS2 gene, such separation was again confirmed (see Fig. 98): that is, individual *G. integer* and *G. armatus* are similarly and consistently different from each other for both 16S and ITS2 sequences. Nevertheless, we found four populations along the song-boundary suture zone between *G. integer* and *G. armatus*, that have both *G. integer* 16S and ITS2 DNA and a mostly *G. armatus* song: (1) Of 2 males recorded from Fruita, CO (S09-114), both had *G. integer* DNA. One male had an introductory trill followed by 3p/c and the second male had an introductory trill usually followed by 3p/c but occasionally by 2 or 4 p/c. A male from nearby Rifle, CO (S09-109) had typical *G. integer* DNA and a *G. integer* song with no introductory trill and 3p/c. (2) At Winslow, Arizona, the ITS2 DNA is definitely *G. integer* but of 11 males

recorded from there during 2003 (10-viii-2003), 2010 (10-viii-2010), and 2012 (27-vii-2012), we found the following: 3 males had no introductory trill and 2p/c and 8 males had a short (1-4 pulses) introductory trill followed by 2p/c. Based only on song, we would classify this population as *G. armatus* but per our convention of giving priority to the DNA results, we label this population as *G. integer*. (3) Of 25 males recorded in 2003 (collected 27-vii-2003) from Garfield Co., UT, Hwy 276 some 7.4 m N Bullfrog Marina (= 3.2 m S Ticaboo): 17 males had no introductory trill and 2 (rarely 3) p/c while 7 males had introductory trills followed by 2 (rarely 3) p/c; one male had zero or one introductory pulse and then 2–3 p/c. The ITS2 sequence of 4 males all mapped with *G. integer*. (4) Of 10 1992 males recorded from Hanksville, UT (S92-109), 9 sang with 2–3p/c, without an introductory trill, and the tenth male sang an introductory trill followed by 2–3p/c. In 2004 (S04-128), all 3 recorded Hanksville males had introductory trills usually followed by 3 (range 2–4) p/c. The latter's DNA (G370) mapped with *G. integer* as did a male (EC3035) from 4 km W Hanksville on Hwy 24, who had an introductory trill and then 2p/c.

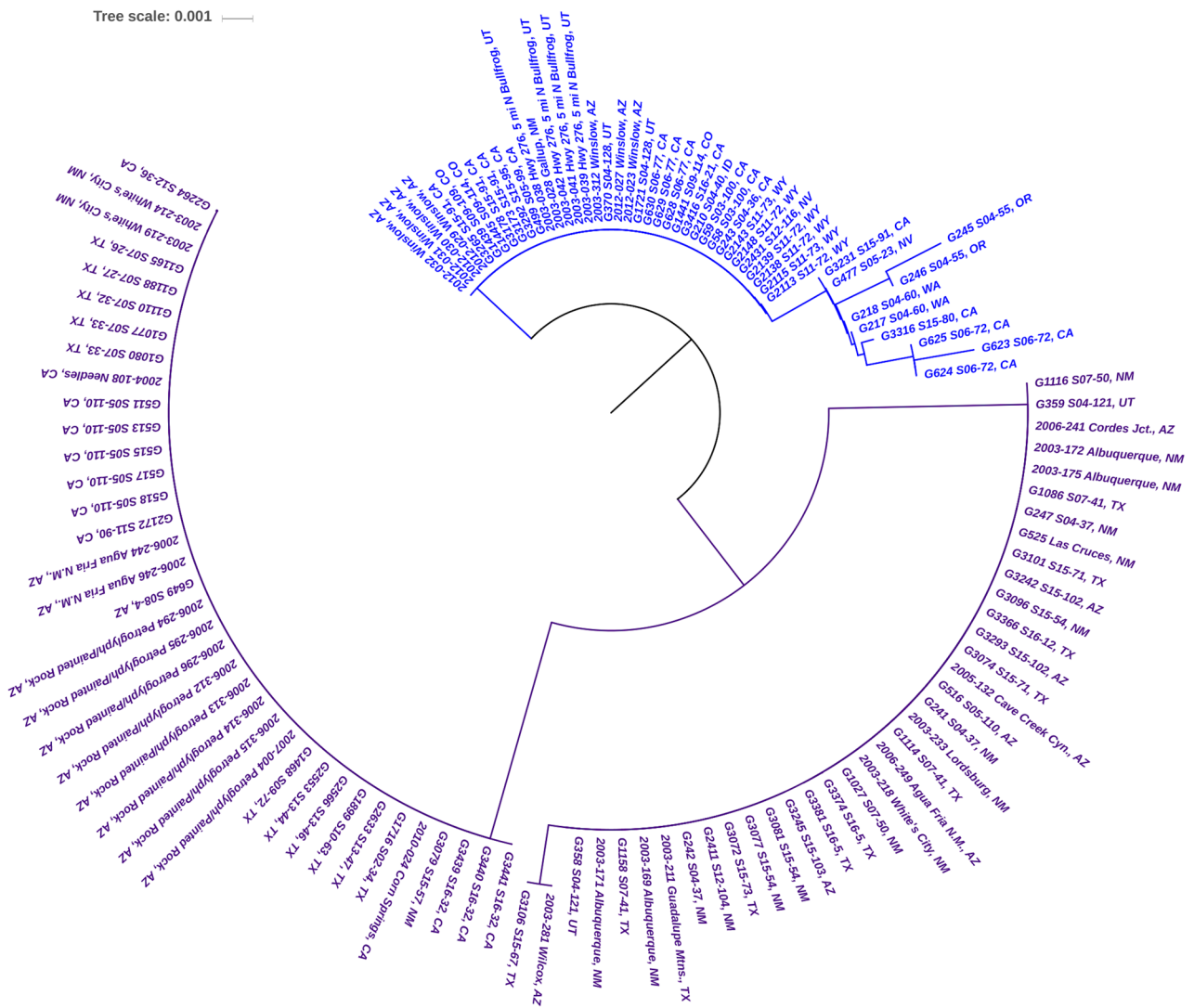


FIGURE 104. 16S gene tree with *G. integer* samples in blue and *G. armatus* samples in purple. Locality information follows all ID numbers. Note the two 16S clades within *G. armatus*.

We have done some preliminary crossing trials between *G. integer* and *G. armatus*: (1) *G. integer* from Santa Clara Co., CA (S92-45, no introductory trill and all 3p/c) x *G. armatus* from Dona Ana Co., NM (S92-127, all with an introductory trill converting to 2p/c). Two of three crosses involving CA males x NM virgin females resulted in good egg hatches. One of four crosses involving CA virgin females x NM males resulted in a good egg hatch. (2) Two virgin *G. integer* females from Yolo Co., CA (S04-36, males with no introductory trill but all 3p/c) x Dona Ana Co., NM (S04-37, all males with an introductory trill converting to 2p/c), produced eggs. Only 2 eggs hatched in one cross and no eggs hatched in the second cross. (3) Four crosses (two reciprocals of each sex) were conducted

between F₁ *G. integer*, Lake Co., CA (S14-63) x F₁ *G. armatus*, Dona Ana Co., NM (collected in 2014), and all four crosses yielded good hatches while incubated at 27°C and 12L/12D. The adults were paired from 17-xi-2014 to 19-xi with eggs hatching 16-xii-2014, which is some 10 days longer than typical incubation periods seen in species with no egg diapause, although cooler ambient temperatures probably contributed to the delayed hatch. More controlled crosses could help clarify this situation, but these data certainly suggest compatibility between these two-sister taxa. On the other hand, laboratory hybridization is known in other sister pairs of *Gryllus* (e.g., Alexander 1957, Harrison 1986, Walker 2000).

Smith & Cade (1987) unsuccessfully tried crossing Davis, CA, *G. integer* (3p/c) with Austin, TX, *G. texensis*. Cade & Tyshenko (1990) reported that crosses of Las Cruces, NM, *G. armatus* (introductory trill to 2p/c) x Austin, TX, *G. texensis* resulted in limited offspring, and only when the female was *G. armatus*. Neither tried crossing California *G. integer* with New Mexico *G. armatus*.

Individuals, especially those at gas stations at night, can fly well. This vagility may also explain their presence on 5 of 8 California Channel Islands, although accidental introduction by human commerce can't be ruled out. We have no information as to whether or not sustaining populations exist on these islands.

Parasitic tachinids *Exoristoides johnsoni* emerged from 2 of 5 males from Fallon, NV (S98-95). O'Hara and Gray (2004) report this same tachinid emerging from a Holbrook, AZ cricket identified as *G. integer*; given the proximity of Holbrook to localities (e.g. Winslow, AZ) where crickets can be found with *G. integer* DNA and *G. armatus* song, and giving priority to DNA, the Holbrook host cricket likely is *G. integer* but we cannot completely rule out it being *G. armatus*.

This cricket has been used in studies on female response to male song (Hedrick & Weber 1998), olfactory discrimination (Kortet & Hedrick 2005, Leonard & Hedrick 2009), behavior (Hedrick *et al.* 2002; Hedrick & Kortet 2006, Niemelä *et al.* 2012a, b, Hedrick 2013, Hedrick & Bunting 2014), and life history parameters and immune response (Niemelä *et al.* 2012c).

***Gryllus armatus* Scudder**

Armed Field Cricket

Figs 87, 96–98, 100, 104–112, Table 1

1902 *Gryllus armatus* Scudder. Psyche 9: p. 293. Lectotype male here designated (Fig. 105, photos courtesy of J. Weintraub) “Palmer’s assorting no. 1072. Ari. Gr. armatus Scudder’s type, 1901. Red label, Type no. 14067.” Labeled cotype #7 by D.C. Rentz, 1979. Scudder’s lectotype and type series at ANSP, now consists of four males and one female (Scudder’s original series listed as 6 males and 1 female) representing at least two and possibility three species. While the lectotype is missing both hind legs and may be distorted due to past alcohol preservation, it clearly agrees with Scudder’s 1902 description as follows: (1) locality of Arizona (either Ehrenberg or Fort Whipple [the latter site near Prescott], Arizona); (2) head and pronotum shining black; (3) contrasting two toned black pronotum and beige tegmina; and (4) long hind wings. Lectotype measurements: body length 17.5, PW 5.9, PL 3.5. Right tegmen removed: 120 teeth, file length 3.1, TL 14.1, TW 4.15. Currently, Cigliano *et al.* (2019) list a male lectotype from “Arizona, Ehrenberg or Ft Whipple”, repeating an erroneous 2013 Orthoptera Species File iteration that discussed how Weissman *et al.* (1980) designated a lectotype for *G. armatus*. In fact, we made no such formal designation in 1980 but only discussed, on p. 345, Scudder’s original type series.

Gryllus integer (in part) of Weissman *et al.* (1980). ‘*Gryllus* #6’ of DBW notebooks.

Distribution. Southwest and southcentral US.

Recognition characters and song. A small to medium sized cricket with long, narrow tegmina, always long hind-winged (except in certain dealate individuals), probably 2 generations/year with the second summer generation frequently of contrasting solid black head and usually black pronotum coupled with beige/straw colored tegmina (see Fig. 105) and legs. Morphologically indistinguishable from sister species *G. integer* but separated by habitat and geography, slight song differences, and consistent DNA differences, as follows: (1) *G. armatus* is from hotter, more southern desert US locations (see Fig. 106); (2) Most, but not all *G. armatus*, have an “introductory trill” of 2–8 evenly spaced pulses at the beginning of each burst of chirps (see Figs 107, 108, S15-58, R15-177), usually followed by 2 (range 1–3) p/c until that burst is over. In contrast, *G. integer* usually with no introductory trill and 3 p/c, although some males sing with 2–4p/c); and (3) there is a congruent, and consistent association between those males with 2p/c and parallel differences in the ITS2 gene sequences when compared with *G. integer* (see Fig. 98). In distribution map Fig. 106, note a possible zone of hybridization in the Four Corners area of southeastern Utah, west-