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 $21^{\circ} \mathrm{C}$.

## 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 $2-4$ ) $\mathrm{p} / \mathrm{c}$, usually without an introductory, short trill (Figs 101, 102; R16-60, S16-21), $1000 \mathrm{c} / \mathrm{m}, \mathrm{PR}$ 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 $3 \mathrm{p} / \mathrm{c}$, and a $2 \mathrm{p} / \mathrm{c}$ 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 $24.2^{\circ} \mathrm{C}$; (B) G. armatus: (R15-177) Artesia, NM (S15-58), at $25.1^{\circ} \mathrm{C}$; (C) G. armatus (2003-170) Bernalillo Co., NM, at $20.6^{\circ} \mathrm{C}$.


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); S1236 (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 $1-3$ ) $\mathrm{p} / \mathrm{c}$ until that burst is over. In contrast, $G$. integer usually with no introductory trill and $3 \mathrm{p} / \mathrm{c}$, although some males sing with $2-4 \mathrm{p} / \mathrm{c}$ ); and (3) there is a congruent, and consistent association between those males with $2 \mathrm{p} / \mathrm{c}$ 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 1950 m (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 (range14.3-17.8 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 $2-4 \mathrm{p} / \mathrm{c}$ 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 Willows, 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 17819.4 m W Hwy 14, 3064', 21-vii-2015 (S15-95). Lake Co., Clearlake Oaks, 5-viii-2014, 1428' (S1463). Los Angeles Co., Santa Catalina Island, Toyon Canyon, 9-x-1983, S. Bennett. Madera Co., Hwy 416.2 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 1984.4 air miles E Lemon Cove, 725', 29-vi-2016 (S1621). 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, $4509^{\prime}, 42^{\circ} 34^{\prime} 24.0-119^{\circ} 53^{\prime} 03.3^{\prime \prime}$ (S14-26); 17 m NE Plush, 16 -vi2004, 4700’ (S04-55). Utah: Emery Co., Green River, 4350’, 21-vi-1987 (S87-55). Garfield Co., Hwy 2767.4 m N Bullfrog Marina, $37.6309^{\circ}-110.7211^{\circ}$, 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 242.5 m W Hanksville, 29 -viii-2017, $38.3737^{\circ}-110.751^{\circ}$. Washington: Grant Co., Lake Lenore, Hwy 17, mile post 84.8, 9 m 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 $24.2^{\circ} \mathrm{C}$.


FIGURE 102. One second waveform of typical calling song of $G$. integer (R16-60) Tulare Co., CA (S16-21), at $24.2^{\circ} \mathrm{C}$ revealing the typical fast 3 pulse/chirp structure.


FIGURE 103. Anomalous song (top) of G. integer (R98-123) Churchill Co., NV (S98-95), at $25^{\circ} \mathrm{C}$, 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). 16 S also shows a clear separation between G. integer and G. armatus, with two 16 S 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 16 S 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 16 S 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 $3 \mathrm{p} / \mathrm{c}$ and the second male had an introductory trill usually followed by $3 \mathrm{p} / \mathrm{c}$ but occasionally by 2 or $4 \mathrm{p} / \mathrm{c}$. 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 $2 \mathrm{p} / \mathrm{c}$ and 8 males had a short ( $1-4$ pulses) introductory trill followed by $2 \mathrm{p} / \mathrm{c}$. 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 ( $=3.2 \mathrm{~m} \mathrm{~S} \mathrm{Ticaboo):} 17$ males had no introductory trill and 2 (rarely 3) p/c while 7 males had introductory trills followed by 2 (rarely 3 ) $\mathrm{p} / \mathrm{c}$; one male had zero or one introductory pulse and then $2-3 \mathrm{p} / \mathrm{c}$. The ITS2 sequence of 4 males all mapped with G. integer. (4) Of 101992 males recorded from Hanksville, UT (S92-109), 9 sang with $2-3 \mathrm{p} / \mathrm{c}$, without an introductory trill, and the tenth male sang an introductory trill followed by $2-3 \mathrm{p} / \mathrm{c}$. 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 $2 \mathrm{p} / \mathrm{c}$.


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 $2 \mathrm{p} / \mathrm{c}$ ). 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 $2 \mathrm{p} / \mathrm{c}$ ), 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 $\mathrm{F}_{1}$ G. integer, Lake Co., CA (S14-63) x $\mathrm{F}_{1}$ G. armatus, Dona Ana Co., NM (collected in 2014), and all four crosses yielded good hatches while incubated at $27^{\circ} \mathrm{C}$ and $12 \mathrm{~L} / 12 \mathrm{D}$. The adults were paired from 17-xi-2014 to 19xi 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 $2 \mathrm{p} / \mathrm{c}$ ) 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 $\mathrm{p} / \mathrm{c}$, although some males sing with $2-4 \mathrm{p} / \mathrm{c}$ ); and (3) there is a congruent, and consistent association between those males with $2 \mathrm{p} / \mathrm{c}$ 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-
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 congruity that ultimately convinced us to consider these two taxa as different and retain both of Scudder's names.


FIGURE 105. Lectotype male, G. armatus, specimen and labels.

Scudder (1902) notes that, in G. armatus, the "Pronotum rather more than half as broad again as long..." While this condition exists in some individuals of G. armatus, it is not universal nor diagnostic of any Gryllus species.

Song easily distinguished from other Southwestern crickets, except $G$. integer, because none have a combination of $2-3 \mathrm{p} / \mathrm{c}, 700-1000 \mathrm{c} / \mathrm{m}$, and a PR $>70$. Most easily separated from G. integer, as discussed above, and by the distribution map (Fig. 106). Because different males within the same population have variable songs, we emphasize the significance of, and need for, multiple male song analysis. A couple of examples of song variation in G. armatus, within the same population, are here provided: (1) All 7 males from Deming, NM (S07-79) had introductory trills and $2 \mathrm{p} / \mathrm{c}$. (2) In contrast to the "clean and uniform" situation at Deming, of 7 males collected in Baker, CA (S05110), 5 males had introductory trills and then 2 (occasionally 3 ) $\mathrm{p} / \mathrm{c}$; 1 male had no introductory trill but 2 (rarely 3 ) $\mathrm{p} / \mathrm{c}$; and the $7^{\text {th }}$ male sang with an irregular trill (Fig. 109, R05-43). The latter male also had a red pronotum (see Fig. 111b) and a low PR of 38.5, yet his ITS2 DNA mapped with the other 6 males from this stop (Fig. 98), and consistent with G. armatus. Morphologically, this long-winged male agreed with typical G. armatus. (3) In Big Bend National Park, TX (S91-43 \& S16-12), 3 of 6 males had introductory trills followed by $2 \mathrm{p} / \mathrm{c}$ while the other 3 males had no introductory trills and $2 \mathrm{p} / \mathrm{c}$. (4) At Shoshone, CA (S92-60), some males sang with an introductory trill and then 2p/c while other males sang with no trill and 3p/c. (5) The only male heard in Bisbee, AZ (Fig. 110, R13-52, S13-18), had an introductory trill and then groups of 2 to 10 pulses/chirp.


FIGURE 106. Known US distribution, G. armatus, along with sister species G. integer, showing zone of possible hybridization in the Four Corners area.

Distinguished from G. texensis, with which it overlaps in the eastern part of G. armatus'Texas distribution, by G. armatus'generally higher number of file teeth vs. shorter hind femur length, and always long hind wings. Some $22 \%$ of $G$. texensis have short hind wings and are never as clearly two-toned as seen in G. armatus and G. integer. Very warm $\left(>35^{\circ} \mathrm{C}\right)$ field-singing individuals of $G$. vocalis can sound like $G$. armatus but are clearly identified when they sing in the laboratory, around $25^{\circ} \mathrm{C}$, because of their slower chirp and pulse rates.

Derivation of name. "arma" is Latin meaning weapons, and "-atus" is Latin meaning provided with, having the nature of, pertaining to, apparently in reference to the increased number of spines on the outer side of the hind tibia (seven to eight) when compared with the three other Gryllus species that Scudder (1902) believed to occur in the "southern Rocky Mountain region (Colorado, Utah, New Mexico and Arizona)." Scudder (1902) notes that in the southern US, both G. firmus and G. rubens have $7-8$ spines on the hind tibia. In fact, since the type series of G. armatus is comprised of at least two, and possibly three species, his hind tibia spine distinction is useless. Plus, a quick comparison of our extensive, song-associated series, shows variation of between 5 to 7 spines in both $G$. armatus and $G$. integer within many populations.

Geographic range. (Fig. 106). Southwestern US deserts including the eastern Mohave, Sonoran, and Chihuahuan Deserts with other non-desert populations in southwestern Utah on the edge of the Great Basin Desert,
northeastern Arizona, northern New Mexico, eastern Colorado east of the Rocky Mts., southern Texas, and western Kansas.

Habitat. From near sea level to 2190 m (El Malpais National Monument, NM, S96-68). Often in towns and associated with a variety of microhabitats: watered lawns, garbage dump areas, cracks in concrete and dry ground, around florescent lights at gas stations, soil cracks in dry pond and lake beds (El Malpais National Monument, NM, S96-68).

Life cycle and seasonal occurrence. No egg diapause: Cottonwood Cove, NV (S90-44); Arizona Western College (S90-54); Van Horn, TX (S91-48); near Goffs, CA (S16-32). Probably two generations/year but not sure if drought conditions at certain times of year, can limit populations to one generation/year.

Variation. Color: Second generation adults frequently contrasting two toned with black head and (usually) black pronotum but beige/straw tegmina and legs. Male G513 from Baker, CA (S05-110), with a reddish pronotum (Fig. 111b). A male from Cornudas, TX (Fig. 112, S01-65, R01-177) darker than those Baker, California specimens. Hind wing length: Always with long hind wings although these are occasionally shed in field collected adult males (Weissman et al. 1980). Of 268 song-confirmed G. armatus males, all but 4 had intact long hind wings. Those without long hind wings were, in fact, dealate, a condition discussed elsewhere for Acheta domesticus (Weissman \& Rentz 1977b, Walker 1977). Ninety-nine field collected females all had long hind wings. Song: See discussion above under Recognition characters and song.


FIGURE 107. Five second waveforms of typical calling songs G. armatus with (top) an introductory trill (R15-177) Artesia, NM (S15-58), at $25.1^{\circ} \mathrm{C}$, and without (bottom) (2003-170) Bernalillo Co., NM, at $20.6^{\circ} \mathrm{C}$.


FIGURE 108. One second waveforms of typical calling song of G. armatus, same males as in Fig. 107, showing presence (top) and absence (bottom) of an introductory trill in a burst.

Specimens examined. Arizona: Cochise Co., Bisbee, 5500', 1-vi-2013 (S13-18). 2m E Bowie, 30-vii-1981, (S81-39). Coconino Co., Tuba City area, 6-viii-1991, 4800' (S91-82). Hwy 996.85 m NW intersection with I40. 8-viii-1991 4900’ (S91-89). Gila Co., Coolidge Dam, 30-vii-1981, 2400' (S81-43). Globe, 30-vii-1981, 3548' (S8144); 10-vi-2012, (S12-21). Graham Co., Safford, 30-vii-1981, 2920' (S81-41); 16-vi-1990 (S90-51); 28-vii-2015 (S15-103). Prison Hwy 366 near junction Hwy 191, 3333', 28 -vii-2015 (S15-102). La Paz Co., Ehrenberg, 3-ii2008, 190' (S08-4). Quartzsite, 1000', 26-vi-1980 (S80-46); 27-vii-1981 (S81-33); 26-viii-1982 (S82-104). Wenden, 14-ix-2011, 1800' (S11-87). Maricopa Co., Aquila, 23-vii-1990, 2100' (S90-71). Buckeye, 18-ix-2011, 840’ (S11-102). Goodyear, 31-vii-1981 (S81-46). Mohave Co., Bullhead City, 14-vi-1990, 500’ (S90-47). Davis Dam, 14-vi-1990, 900’ (S90-46). Navajo Co., Holbrook, 8-ix-1999, 5080’ (S99-116); 2002-032, 9-viii-2002. Hwy 77 0-12m N I40, 7-viii-1991, 5400’ (S91-86). Pima Co., Catalina, 18-viii-1998, 2940’ (S98-65). Tucson, 28-vii-1981 (S81-35); 17-viii-1998, 1920' (S98-63). Yavapai Co., Camp Verde, 21-viii-2012, 3151’ (S12-107). Yuma Co., Arizona Western College, 10-viii-1988, 200’ (S88-89); 18-vi-1990 (S90-54). Telegraph Pass, 15-ix-2011, 676’ (S1192). Yuma, 31-vii-1981 (S81-48). California: Inyo Co., Death Valley National Park, Furnace Creek, 0', 23-vi-1980 (S80-32); 5-vi-1983 (S83-60); 25-vi-1992 (S92-61); Stovepipe Wells, 5', 5-vi-1983 (S83-59); 25-vi-1992 (S9262). Shoshone, 25-vi-1992, 1560' (S92-60). Riverside Co., Blythe, 400', 26-vi-1980 (S80-47); 14-ix-2011, 240’ (S11-90). Indio, 6-viii-1988 (S88-74). Palm Springs, 2-iv-1989 (S89-8). San Bernardino Co., Baker, 4-viii-1991, 1000' (S91-72); 30-viii-2005, (S05-110). Barstow, 16-viii-1998, 2420' (S98-58); 28-vi-2003 (S03-73); 22-vii-2016 (S16-28). Havasu Lake, 6-vi-1983 (S83-62); 13-ix-2011, 460’ (S11-84). Ludlow, 2060', 16-viii-1998 (S98-60); 23-vii-2016 (S16-30). Newberry Springs, 16-viii-1998, 2160' (S98-59). Truck stop at Goffs exit off I40, 2103', 23-vii-2016 (S16-32). San Diego Co., Borrego Springs, 8-viii-1988 (S88-83). Colorado: Crowley Co., Manzanola, 26-viii-1989, 4200' (S89-65). Otero Co., La Junta, 26-viii-1989 (S89-66). Pueblo Co., Baxter, 26-viii-1989 (S8963). Boone, 26-viii-1989, 4350' (S89-64). Kansas: Ford Co., Dodge City, 27-viii-1989, 2400’ (S89-71). Nevada: Clark Co., Cottonwood Cove, 800', 24-vi-1980 (S80-36); 26-vii-1981 (S81-31); 14-vi-1990 (S90-44). Searchlight, 3512', 26-vii-1981 (S81-30); 23-vii-2016 (S16-32). New Mexico: Bernalillo Co., Albuquerque, 22-viii-1982 (S8289); 1-vii-1994 (S94-33). Catron Co., Reserve, 3-vii-1994, 5770' (S94-50). Cibola Co., El Malpais National Monu-
ment, Hwy 117, 31m S Hwy 40, 14-vi-1996, 7200’ (S96-68). Dona Ana Co., Las Cruces, 23-viii-1982 (S82-99); 26-vi-1983 (S83-103); 16-vi-1986 (S86-40); 5-vii-1986 (S86-78); 26-iv-1990 (S90-35); 26-ix-1992 (S92-127); 1-vi-2004 (S04-37). Eddy Co., Artesia, 3428', 30-vi-2015 (S15-58). Hope, 4095', 30-vi-2015 (S15-57). Hidalgo Co., Roadforks, 29-vii-1981, 4195' (S81-38); 19-viii-2012 (S12-104). Lea Co., Eunice, 6-ix-2010, 3420' (S10-62). Luna Co., Deming, 21-vii-2007, (S07-79). Socorro Co., Socorro, 4420', 29-vi-2015 (S15-54). Hwy 25 1m S La Joya, 15-viii-1993, 4850' (S93-68). Socorro, 13-vi-2007, 4460’ (S07-50). Texas: Brewster Co., Alpine, 5-vi-1991, 4200' (S91-44); 12-vi-2007 (S07-41); 2-vii-2015 (S15-73). Big Bend National Park, Rio Grande Village, 5-vi-1991, 1860' (S91-43); 28-v-2016 (S16-12). Hwy 118 near Terlingua, 2566', 2-vii-2015 (S15-72). Cameron Co., Rio Hondo, 8’, 10-vii-2013 (S13-44); Hwy 4 3.1m W Boca Chica State Park, 10-vi-2007, 10’ (S07-26). Culberson Co., Van Horn, 6-vi-1991, 4100’ (S91-48). Hidalgo Co., Bentsen-Rio Grande State Park, 110', 3-viii-2002 (S02-34), 10-vi-2007 (S07-27). Howard Co., Big Springs VA hospital grounds, 30-vi-2009, (S09-72). Hudspeth Co., Cornudas, 13-vii2001, 4420' (S01-65). Jeff Davis Co., Ft. Davis, 4852', 1-vii-2015 (S15-67). Kinney Co., Brackettville, 4-vi-1991, $1100^{\prime}$ (S91-40); 11-vi-2007 (S07-32); 7-ix-2010 (S10-63). Presidio Co., Presidio, 2580', 27-v-2016 (S16-5). Hwy 67 just S Shafter, 3920', 27-v-2016 (S16-3). Val Verde Co., Del Rio, 11-vi-2007, 1000' (S07-33). Ward Co., Monahans, 2-vii-1986 (S86-69). Willacy Co., Raymondville, 10-vii-2013 (S13-47); Farm Road 14203.1 m N Farm Road 1018, 10-vii-2013, $15^{\prime}$ (S13-46). Utah: Washington Co., La Verkin, 11-ix-2004, 3420' (S04-121). 1m NE La Verkin, 9-viii-1991, 3700' (S91-95).


FIGURE 109. Atypical, irregular trill calling song of G. armatus (R05-43) Baker, CA (S05-110), at $21.5^{\circ} \mathrm{C}$. Top: 5 sec. waveform; Bottom: 1 sec . spectrogram.


FIGURE 110. Atypical calling song of G. armatus (R13-52) Bisbee, AZ, at $24^{\circ} \mathrm{C}$, with introductory trill followed by 2-10 pulse chirps. Top: 5 sec . waveform; Bottom: 1 sec . spectrogram.

DNA. Multilocus G3439 (Goffs, CA, S16-32) and G3374 (Presidio, TX, S16-5) map together and nearest to G. integer from Tulare Co., CA (Gray et al. 2019). Fig. 98 shows the distribution of ITS2 mapping done for both $G$. armatus and G. integer. Sequence identity of ITS2 sequences ( $\mathrm{N}=684$ aligned positions) was $98.5 \pm 0.87 \%$ within $\mathrm{N}=29$ G. armatus, $99.0 \pm 0.77 \%$ within $\mathrm{N}=34$ G. integer, and $95.7 \pm 0.78 \%$ between the two species.

Discussion. Scudder's series includes 3 males (our lectotype and D.C. Rentz's cotypes labeled \#4 and \#6) from "Arizona", but none are further labeled as to locality. We collected an Ehrenberg, AZ (S08-4) specimen, of G. arma$t u s$, that sang (R08-04 \& R08-06) with an introductory trill and 2p/c and maps with G. armatus for ITS2, confirming the ID of one AZ type locality. The other possible AZ type series locality, Fort Whipple, is located near Prescott. While we have no specimens of G. armatus from Prescott, that area is still within the geographic range of $G$. armatus (see Fig. 106). Other specimens in the type series include D.C. Rentz's labeled Utah cotypes \#5 (male) and \#8 (female). This male and female from Utah (Beaver Dam), are both well preserved, short hind winged specimens that may represent G. vocalis. While Scudder (1902) lists the Utah locality as Beaver Dam, this is probably not the unincorporated community of Beaver Dam in Box Elder Co., Utah, some 4 km E Fielding. Rather, Richard Baumann of BYU (pers. comm. to DBW, September, 2012) believes this original Beaver Dam locality is actually the Beaver Dam Wash, Washington Co., Utah, a seasonal stream near the southwestern Utah-Nevada border that occurs upstream from the unincorporated community of Beaver Dam, Mohave Co., Arizona. According to R. Baumann, BYU has many labeled specimens that say Beaver Dam, Utah, and they are from Beaver Dam Wash in Washington Co. This area is possibly near Lytle Ranch Preserve, a field station owned by BYU since 1986 (S. Clark, collection
manager BYU, pers. comm. to DBW, January, 2017). Vasco M. Tanner did much collecting there after his arrival at BYU in 1925. In any case, we have collected G. armatus from Washington Co., Utah (S91-95 \& S04-121). The Beaver Dam in Box Elder Co., Utah, is near Cutler Dam. The nearest Box Elder Co., Beaver Dam appropriatelysinging cricket that we collected was from S87-51, 19 km north Tooele in Tooele Co., and the one male there usually sang with $3 \mathrm{p} / \mathrm{c}$ (occasionally $2 \mathrm{p} / \mathrm{c}$ ) without an introductory trill. Given our absence of genetic data, he is tentatively identified as $G$. integer based on song.


FIGURE 111. Color variation seen in second generation (summer) G. armatus, with both pictured male individuals from Baker, CA (S05-110).

Our initial 16S genetic data showed clear separation between G. integer and G. armatus (see Fig. 104), but given our previous documentation of multiple 16 S clades, in species $G$. vernalis, veletis, and lightfooti, we were unsure of this significance. With our subsequent incorporation of the ITS2 gene, such separation was again confirmed. Nevertheless, several populations along the song-boundary between G. integer and G. armatus, have G. integer

ITS2 DNA and a mostly G. armatus song. These populations are discussed more completely under G. integer (see p. 104). We also entertained the thought that the G. integer-G. armatus complex could represent one widespread species with a west to east cline in song pattern. Again, subsequent DNA data corresponding with song differences and temperature regimes, persuaded us that two sister taxa were a better explanation.


FIGURE 112. Dark colored male G. armatus from Cornudas, TX (S01-65, R01-177).

We suggest that a minimum of 3-5 males per population be analyzed with sonograms, because of individual variation and because subtle song differences between G. integer, G. armatus, G. rubens, and G. texensis are not audible to most human ears. If the majority of males have an introductory trill followed by $2 \mathrm{p} / \mathrm{c}$, then they are probably G. armatus. Likewise, several males with no introductory trill and $3 \mathrm{p} / \mathrm{c}$ are likely $G$. integer. But select $G$. armatus-DNA males can also have no trill and $2 \mathrm{p} / \mathrm{c}$ and, rarely, no trill and $3 \mathrm{p} / \mathrm{c}$. And to complicate matters, males with $G$. integer DNA can have a short introductory trill of $1-3$ pulses followed by $2-4 \mathrm{p} / \mathrm{c}$ and, rarely, a pure trill. In the face of such variation, multiple male analysis from the same population has usually given us a definitive answer.

Additionally, it appears that the farther east one goes within the distribution of G. armatus, the higher percentage of males have introductory trills followed by $2 \mathrm{p} / \mathrm{c}$, although all 3 males from Texas, Bentsen-Rio Grande State Park (S02-34 and S07-27), where G. armatus occurs microsympatric with $G$. texensis, had $2 \mathrm{p} / \mathrm{c}$ without an introductory trill.

Interestingly, two males changed their song with time. One male recorded (R91-143) in the field from Tuba City, AZ (S91-82), had a short introductory trill at $22^{\circ} \mathrm{C}$ and then $2 \mathrm{p} / \mathrm{c}$, consistent with G. armatus. Five days later in the laboratory at $25^{\circ} \mathrm{C}$, this male sang (R91-155) without an introductory trill and with $2-3 \mathrm{p} / \mathrm{c}$, more consistent with $G$. integer song. He was not teneral upon capture. No DNA could be isolated more than 15 years later. A second male (2006-241) from Cordes Junction, AZ, was initially recorded at $20.8^{\circ} \mathrm{C}$, with no introductory trill and $2 \mathrm{p} / \mathrm{c}$. A subsequent recording, at $22.4^{\circ}$, showed an introductory trill and 2 (rarely 3 ) $\mathrm{p} / \mathrm{c}$.

Rare field collected adult males of G. armatus sing a pure trill song of $1 \mathrm{p} / \mathrm{c}$ : Coolidge Dam (S81-43) and Buckeye (S11-102), AZ; Las Cruces, NM (S82-99); and Baker, CA (S05-110)], or predominantly so (Cottonwood Cove, NV [S90-44]; Globe, AZ [S82-103]; Las Cruces, NM [S83-103]; and Van Horn, TX [S91-48]) but, in all cases, the fast PR separates them from other trillers G. regularis and G. cohni in the Southwest, G. rubens in Texas, but not from G. texensis in Texas (see discussion in next paragraph).
G. armatus is sympatric with the Southeast fast trilling field cricket, G. texensis, at the Texas localities of Alpine (S91-44, S07-41, along with the slower triller G. regularis); Brackettville (S91-40, S07-32, S10-63); Rio Hondo (S13-44); town of Van Horn (S91-48); Big Springs (S09-72); Rio Grande Village in Big Bend National Park (S91-43, S02-34); and Bentsen-Rio Grande State Park (S02-34, S07-27); in Kansas at Dodge City (S89-71); and in New Mexico at Eunice (S10-62). When both G. armatus and G. texensis are singing adjacent to each other, and $G$. armatus is singing with 2 or $3 \mathrm{p} / \mathrm{c}$, differences in song, especially evenness and pitch, are apparent to "young" ears. When singing isolated from each other, we do not appreciate such song differences as easily. Because some $22 \%$ of adult $G$. texensis have short hind wings, the taxa can sometimes be separated in the field even though both have PR between $70-100$ at $25^{\circ} \mathrm{C}$

The population of crickets from Aguila, AZ, studied by Hedrick and Kortet (2006) under the name G. integer, is most likely G. armatus.

The tachinid Ormia ochracea recovered from G. armatus from single males collected at Havasu Lake, CA (S11-84) and Wenden, AZ (S11-87).

## The Vernalis Group

Gryllus vernalis Blatchley; Gryllus fultoni (Alexander); Gryllus cayensis Walker

Sister species of crickets that inhabit forest or forest edges in the central and southern US (G. vernalis and G. fultoni) and southern Florida (G. cayensis). G. cayensis does not normally produce a calling song. Separable by morphology (Table 1, p. 18), song (Figs 113, 114) and ITS2 DNA (Fig. 115); multilocus DNA (Gray et al. 2019) places $G$. cayensis closer to G. fultoni than to $G$. vernalis.

## Gryllus vernalis Blatchley

Northern Wood Cricket
Figs 57, 113-122, Table 1

1903 Gryllus americanus Blatchley. Blatchley 1903, p. 433.
1920 Gryllus assimilis vernalis Blatchley, nomen novum since G. americanus was preoccupied. Blatchley 1920, p. 704.
1930 Gryllus assimilis vernalis Blatchley. Blatchley 1930, p. 72. Lectotype female (Fig. 116, photos courtesy of Jennifer Zaspel and Gareth Powell, Purdue University Entomological Collection, where the types are deposited) chosen by Blatchley: Red label "Type". Crawford Co., Ind. W.S.B. 5-11-(18)99. Allolectotype male (Fig. 117) with the following data: White label "type" Crawford Co. Ind. W.S.B. 6/28/ (19)02. Blatchley chose a female as the lectotype because he thought the length of the ovipositor and shape and position of the female tegmina at rest [somewhat separated] were both good characters for separating G. vernalis from the sympatric G. pennsylvanicus (actually $=$ G. veletis) (Blatchley 1903, p. 434; repeated verbatim in Blatchley 1920, p. 706).
1957 Acheta vernalis (Blatchley). Alexander (1957).

