

The Field Cricket *Gryllus assimilis* and Two New Sister Species (Orthoptera: Gryllidae)

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ABSTRACT In preparation for revisionary studies of western U.S. *Gryllus* field crickets, some eastern U.S. names for species with supposed transcontinental distributions must be resolved. One such species, *Gryllus assimilis* (F.), as currently characterized, occurs in the West Indies, Brazil, Central America, and Mexico, and in five of the southernmost U.S. states. Our studies of calling songs and morphology indicate that at least three species exist among these populations. The type locality of *G. assimilis* is Jamaica, but the type specimen is lost and two similar species of *Gryllus* occur there. One of these species occurs widely outside of Jamaica, and we assign it to *G. assimilis* and designate a neotype. The other occurs only in Jamaica and is assigned to *Gryllus jamaicensis* T. J. Walker n. sp. Nearly all populations formerly known as *G. assimilis* from southern California, southern Arizona, southern Nevada, and Mexico west of the continental divide are assigned to *Gryllus multipulsator* Weissman n. sp. Populations located elsewhere (with one exception) are deemed conspecific with Jamaican *G. assimilis*, although *G. assimilis* from islands east and south of Hispaniola have calling songs with dominant frequencies higher than is characteristic of the species elsewhere. Studies of mitochondrial DNA of *assimilis*-type *Gryllus* from widespread localities are compatible with the above species classification. Hybridization trials between *G. assimilis* and *G. multipulsator* demonstrated high interfertility. *Gryllus contingens* F. Walker and *Gryllus mundus* F. Walker are removed from synonymy with *G. assimilis*.

KEY WORDS *Gryllus*, cryptic species, introduced species, sister species

Gryllus field crickets have made significant contributions to studies on insect communication and speciation, predator–parasitoid–prey interactions, and behavioral and sexual selection questions (see Walker 2009 for references). Unlike eastern U.S. field crickets, whose taxonomy was settled by 1974 (Alexander 1957, Alexander and Bigelow 1960, Walker 1974) with techniques still used today, the taxonomy of western U.S. field crickets remains unresolved. They were last comprehensively examined >100 yr ago (Scudder 1901, 1902), and modern investigative techniques have been applied to only a small geographically limited area (Weissman et al. 1980). This lack of further publication on the western U.S. fauna containing >40 species (D.B.W., unpublished data) has been a major deterrent to studies by scientists who require names for their study organisms. This article is the first of several that deals with western U.S. field crickets with the goal of enabling identification of all U.S. *Gryllus* species and many from Latin America, especially Mexico.

Although most *Gryllus* species found in the western United States are restricted to areas west of the Mississippi River, some taxa, such as *Gryllus assimilis* (F. 1775), have more widespread distributions (Walker 2009) and thus present extra difficulties. This is not a trivial problem because *assimilis* is the oldest of all American *Gryllus* names, and Rehn and Hebard (1915) synonymized all 47 *Gryllus* names in the literature from North, Central, and South America; the Caribbean; and Galapagos Islands under the name *G. assimilis*. Walker (2009) notes that *G. assimilis* is found in the United States in southern Florida (where it is apparently introduced; Alexander and Walker 1962), southern California (where it is apparently native; Weissman et al. 1980), and the Brownsville, TX, area, despite reservations discussed by Weissman et al. (1980) as to whether Florida and California populations were conspecific. Additionally, Huang et al. (2000) showed Florida and California *assimilis* as nearest relatives based on mitochondrial DNA (mtDNA). Complicating a situation already demanding attention, T.J.W. (unpublished data) recorded calling songs indicating that Jamaican *Gryllus*, although morphologically similar, are two species.

U.S. *Gryllus* was first revised by Scudder (1901, 1902) who recognized 10 species, one of which is now placed in *Acheta*. Subsequently, in works more regionally restricted, new species were added and old names

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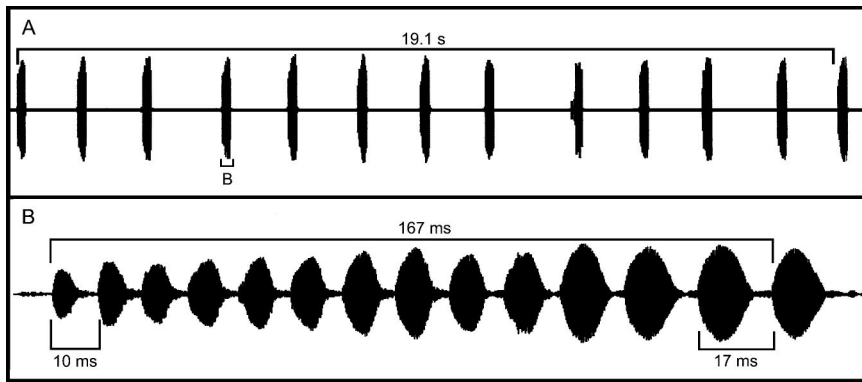


Fig. 1. Song structure of species of the *G. assimilis* complex as illustrated by waveforms of a song of *G. multipulsator* at 25.6°C. (A) Series of chirps produced during 20 s at 0.63 C/S (C/S calculated from the indicated 19.1 s measurement). (B) Expansion of 200ms of A, showing the fine structure of the fourth chirp. The whole-chirp PR, based on the indicated 167 ms measurement is 77.8 (13/0.167 s). The method of measuring PP for pulse-by-pulse analysis is indicated for the first and 13th pulse.

resurrected, such that 16 *Gryllus* species are now recognized in the United States (Blatchley 1920; Alexander 1957; Alexander and Bigelow 1960; Walker 1974, 2001; Weissman et al. 1980; Cade and Otte 2000).

Since an earlier publication (Weissman et al. 1980), D.B.W. has recorded calling songs from >6,000 male *Gryllus* from central and western United States, Mexico, and Central America. *Gryllus* producing an *assimilis*-type song (Fig. 1A and B), i.e., a song whose chirps are delivered at 1–2.5 per second at 25°C and contain six to 17 pulses, with the pulses coming significantly slower at the end, are now known from southern California, Arizona, Nevada, Texas, Florida, the West Indies; throughout Mexico, including much of Baja California (Weissman et al. 1980); Honduras; Costa Rica; and Brazil (David et al. 2003). These crickets with *assimilis*-type songs also share the following morphological characters: long flight (rear) wings, head more narrow than pronotum, and pubescent pronota. All populations apparently lack any diapausing stage (Weissman et al. 1980).

To resolve the status of *G. assimilis* in the United States, these questions must be addressed: Which Jamaican species should bear the name *G. assimilis*? From where did Florida populations come? And are western U.S. populations conspecific with those in Florida? We apply a combination of morphological, calling song, mtDNA analysis, and hybridization studies to answer these questions.

Materials and Methods

Specimens. Jamaican *Gryllus* were collected by T.J.W. during trips in 1968, 1970, and 1985 and by Delano Lewis in 2004. Florida *assimilis*-type crickets were from cultures maintained by A. Zera originally started with crickets collected by T.J.W. from Homestead, Dade Co., in 1992. All other specimens, unless noted, were collected by D.B.W. Recording techniques have changed over the years with equipment

improvements and have been described previously (Weissman et al. 1980, Walker 2004).

D.B.W. captured adult crickets of both sexes, and rarely late instars if adults were scarce, by using a clear plastic tube to minimize contact with and possible damage to cerci. Cercal length was measured for the longest intact cercus immediately after killing by using model CD-6[™] CS Absolute Digimatic calipers (Mitutoyo, Tokyo, Japan). A cercus broken several molts before the adult stage can seem undamaged on capture because of regeneration during subsequent molts. Damaged cerci were not measured.

Stridulatory files were examined by D.B.W. as described by Rentz and Weissman (1981), namely, the right tegmen was removed and placed upside down under a cover slip. File teeth were counted at 500 \times magnification with a compound microscope, and an ocular micrometer was used to measure file length across its curve. The tegmen was stored in a gelatin capsule on the same pin as held the male. Tegminal width was measured as maximal distance from medial edge to forewing angle by using Cu₁ vein as landmark. Body length was not generally measured because it is not a reliable character. D.B.W. found that adults, upon dying and drying, shrank anywhere from 2.4 to 7.6 mm in length, most notably in gravid females.

Song Analysis. T.J.W. digitized tape-recorded songs at a sampling rate of 44,100 per s and used CoolEdit 2000 (Syntrillium Software, Phoenix, AZ) to analyze the resulting wave files. Pulse period was measured (Fig. 1B) from the start of one pulse in a chirp to the start of the next. Pulse-start to pulse-start was used rather than pulse-end to pulse-end because a pulse's beginning is easier to determine than its end (Fig. 1B). This convention made the period of the last pulse within a chirp indeterminate, because there is no next pulse within the chirp.

The rate at which pulses are produced in *assimilis*-type songs drops significantly within each chirp, making it difficult to characterize these songs by pulse rate

(PR). To document the changes in PR within chirps, pulse rates were calculated pulse-by-pulse as the reciprocal of the pulse period (PP), i.e., $1/PP$ when PP is measured in seconds. A single number indicative of PR within a chirp, a "whole-chirp PR," was calculated as $(n - 1)/\sum PP$, where n is number of pulses in the chirp, and $\sum PP$ is the sum of all PPs within a chirp. This is not quite the same as the average of the pulse-by-pulse PRs, but it is much easier to determine, because $\sum PP$ is simply the time from the beginning of the first pulse to the beginning of the last pulse in the chirp.

Calculating a single number indicative of PR within a recorded song is complicated by the fact that chirps within a song vary in pulse number and the number of pulses affects the whole-chirp pulse rate. Determination of the average whole-chirp pulse rate for a song was made easier and more repeatable by disqualifying chirps that deviated from the modal pulse number of a song by >1 and by using only the first 10 qualifying chirps. If fewer than 10 chirps qualified, all that qualified were used.

Ambient temperature has great but largely predictable effects on PR in the songs of ensiferan Orthoptera (Walker 1962, 1975; Walker and Weissman 2001). To compare PRs in *assimilis*-type songs produced at different temperatures, we used the formula in Walker (2000) to estimate what the PRs would have been had all songs been produced at 25°C.

DNA Extraction, Polymerase Chain Reaction (PCR) Amplification, and Sequencing. D.A.G. isolated total genomic DNA from leg muscle tissue of individual specimens using the DNEasy tissue kit (kit 69504, QIAGEN, Valencia, CA). All sampled individuals were male, except for one female (DAG 04-100) from which we had obtained eggs and reared and recorded the calling song of two sons (see Appendix 1 for sample information). Portions of two mitochondrial genes were amplified: cytochrome oxidase I (COI) and 16s rRNA (16s). For COI, 5'-to-3' primer sequences were CAACATTTATTTTGATTTTTTGG (forward) with TCCAATGCACTAATCTGCCAT-ATTA (reverse) (Simon et al. 1994); for 16s, they were CGCCTGTTTATCAAAAACAT (forward) with CCGGTTGAACTCAGATCA (reverse) (Palumbi et al. 1991). Both genes were amplified in 50- μ l reactions by using JumpStart REDTaq DNA polymerase (D-8187, Sigma, St. Louis, MO) with supplied buffer and dNTPs (D-7295, Sigma). Reagent concentrations were as suggested by the manufacturer. Initially, PCR reactions were heated to 94°C for 5 min, followed by 30 cycles of 94°C for 1 min, 52°C (for COI) or 49°C (for 16s) for 1 min, and 72°C for 1.5 min, followed by a further 94°C for 1 min, 52°C (for COI) or 49°C (for 16s) for 1 min, and 72°C for 5 min. Negative controls were performed with each reaction.

After agarose gel electrophoresis to verify successful PCR amplification and the absence of amplification in negative controls, amplification products were cleaned using the GenElute PCR clean-up kit (NA1020, Sigma). Cleaned reaction products were sequenced in both directions using the same primers used in PCR amplification. Sequencing was performed

at the California State University Northridge DNA sequencing facility (www.DNAsequencing.org) on an Applied Biosystems (Foster City, CA) ABI Prism 377 DNA Sequencer platform with BigDye version 3.1 chemistry. Consensus sequences for each sample were obtained by manual alignment of forward and reverse sequences using BioEdit (Hall 1999). The COI sequences were translated to amino acid sequences by using the invertebrate mitochondrial code to help ensure that the target mitochondrial genes were amplified rather than nuclear pseudo-genes; no indels were observed and all sequences translated. Representative sequences have been deposited with GenBank (accession nos. EF050741–050748).

DNA Analysis. PAUP* version 4.0b10 (Swofford 2002) running on a Macintosh G4 computer (Apple Computer, Cupertino, CA), and MrBayes version 3.1.2 (Huelsenbeck and Ronquist 2001) running in parallel on the Cornell Computational Biology Service Unit (<http://cbsuapps.tc.cornell.edu/mrbayes.aspx>) were used to generate gene-trees for successfully sequenced samples (41 samples; 516 bp of 16s, 732 bp of COI). In all, we examined gene-tree structure using four analytic methods: maximum parsimony (MP), maximum likelihood (ML; under two different data partitions and evolutionary models), and Bayesian analysis. MrModeltest version 2.2 (Nylander 2004) was used to determine the best evolutionary models for ML and Bayesian analyses. Before MP analysis, we used the Partition Homogeneity test as implemented in PAUP* to test for significant differences between the COI and 16s genes. No difference was found ($p \gg 0.05$). Thus, the MP analysis was performed on both genes simultaneously. ML analyses used the MP tree as a starting point. MrModeltest indicated different evolutionary models for different ML data partitions. The Bayesian analysis and one of the ML analyses had four data partitions (16s, and separate first, second, and third codon positions for COI) analyzed using the GTR + SS model. A second ML analysis used non-partitioned data and the HKY + G model; estimates of the transition/transversion ratio parameter and the gamma shape parameter were obtained using the MP tree already in memory. The Bayesian analysis was run for one million generations, with trees sampled every 1,000 generations. A majority rule consensus tree was obtained from 900 sampled trees after convergence of LnL values.

Divergence between taxa was assessed using analysis of molecular variance (AMOVA) as implemented in Arlequin version 2.000 (Schneider et al. 2000). Significance of the AMOVA was based on 1,023 permutations. Measures of nucleotide diversity and average pairwise distance between taxa were likewise calculated in Arlequin.

Hybridization Trials. D.B.W. crossed Baja California first generation *G. multipulsator* n. sp. with Florida 39th generation *G. assimilis*. Females were isolated as last instars in pint containers with 19-mm-deep plastic dishes filled with sterilized, moist sand for oviposition. The appropriate male was introduced 7 d after the female molted to adult. They were fed ad libitum

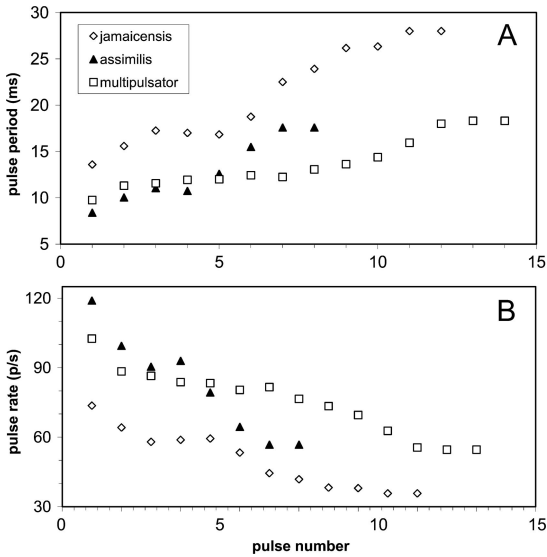


Fig. 2. (A) Pulse-by-pulse changes in average PP within n chirps in recordings of males of three species of the *G. assimilis* complex: *G. assimilis*, Jamaica, WTL68-545, eight-pulse chirps ($n = 20$); *G. jamaicensis*, WTL68-698, 12-pulse chirps ($n = 12$); *G. multipulsator*, WTL03-27, Baja California, 14-pulse chirps ($n = 16$). The last pulse in *assimilis*-type songs is similar to the penultimate pulse, so we estimate its indeterminate PP as equal to the PP of the penultimate pulse. (B) Pulse-by-pulse variation in average PR (same data set as in A).

organic romaine lettuce, dry cat and rabbit food, and uncooked oatmeal. The pair was kept together for 14 d at room temperature. Hatching success was recorded as none, fair, or excellent. Results of all attempted crosses are presented.

The following abbreviations are used in the text: C/S, chirps per second; DF, dominant (carrier) frequency; P/C, pulses per chirp; PP, pulse period; PR, pulse rate (per second); CAS, California Academy of Sciences, San Francisco, CA; FSCA, Florida State Collection of Arthropods, University of Florida, Gainesville, FL; MLNS, Macaulay Library of Natural Sounds, Cornell University, Ithaca, NY; WTL, Walker Tape Library; and S, collecting Stop number of D.B.W.

D.B.W. retains his recordings, whereas most of those in WTL have been digitized and archived by the

Macaulay Library of Natural Sounds, Cornell University. Walker (2009) includes an online database with detailed data for all WTL recordings as well as field notes describing where recorded individuals were found. D.B.W. specimens are deposited at CAS; T.J.W. specimens are deposited at FSCA, unless otherwise noted.

Results

As formally set forth in the descriptions at the end of this section, we distinguished three species among populations currently known as *Gryllus assimilis*, namely, *G. assimilis* (Jamaica, Grand Cayman, Hispaniola, Florida, Texas, eastern Mexico, Central America), *G. jamaicensis* (Jamaica), and *G. multipulsator* (western Mexico, western United States). The evidence for this classification is laid out below.

Analysis of Calling Songs. Species of crickets that are reproductively active at the same time and place can nearly always be distinguished by the calling songs of males. When populations are allopatric, differences in calling songs may be indicative of species status or be attributed to geographic variation.

In Jamaica, T.J.W. heard, recorded, and distinguished only two *Gryllus* calling songs. Both were of the *assimilis* type (Fig. 2), but one song had fewer pulses per chirp (Fig. 3), a faster average pulse rate (Fig. 4), and a lower dominant frequency (Fig. 5). This became the primary basis for describing a new species of *Gryllus* from Jamaica. Because the Fabricius' type specimen of *G. assimilis* is lost (Alexander 1957), and his description gives no clue as to which Jamaican *Gryllus* he had, either might be assigned the name. We chose to assign *assimilis* to the Jamaican species that occurs widely outside of Jamaica and to name the species known only from Jamaica *G. jamaicensis*.

In Central America, eastern Mexico, and southern Texas (Fig. 6), the calling songs of *assimilis*-type *Gryllus* are indistinguishable from the songs of Jamaican *G. assimilis*. In contrast, in Mexico west of the continental divide and in California, Nevada, and Arizona, calling songs of *assimilis*-type *Gryllus* have more pulses per chirp (Fig. 3) and a higher dominant frequency (Fig. 5). These differences in calling song are as great as

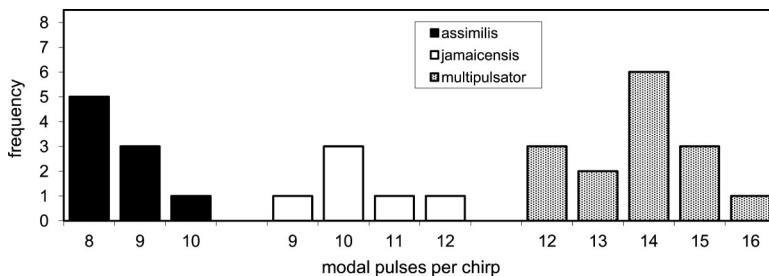


Fig. 3. Frequency distribution of modal pulses per chirp for songs of nine individuals of *G. assimilis* from Jamaica, six of *G. jamaicensis*, and 15 of *G. multipulsator* from Baja California, Mexico.

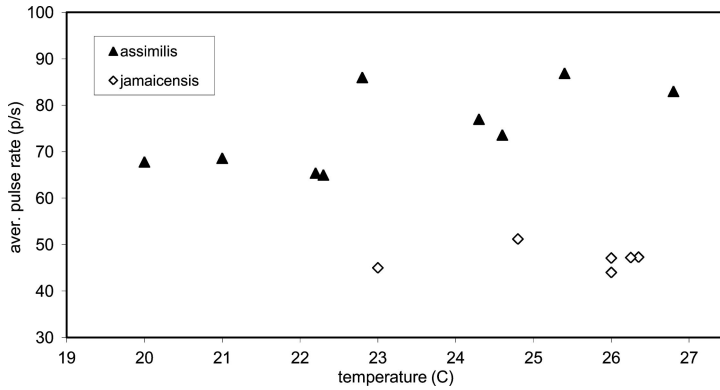


Fig. 4. Average PRs for songs of nine individuals of *G. assimilis* and six of *G. jamaicensis*.

those separating many sympatric pairs of crickets that are congeneric (Walker 2009).

T.J.W. has recorded *assimilis*-type *Gryllus* calling songs from six West Indian islands other than Jamaica (Appendix 2). The songs from Hispaniola and Grand Cayman are indistinguishable from those of *G. assimilis* from Jamaica, but those from Puerto Rico, St. Croix, Montserrat, and Trinidad are to some degree intermediate between *G. assimilis* and *G. jamaicensis* in dominant frequency, pulse rate, or both (Fig. 7).

Males of the *assimilis*-type *Gryllus* established in Florida call like Jamaican *G. assimilis* (Fig. 5), but the parent stock probably came from elsewhere in the range of *G. assimilis*. If *G. assimilis* occurs in Cuba, which seems likely considering its occurrence on Grand Cayman and Hispaniola, it would need travel <100 miles across the Florida Straits to reach Florida by storm (adults can fly), raft, or human transport.

Morphological Comparisons. For Jamaican specimens of known song type, *G. assimilis* males had longer and wider tegmina and longer files with fewer teeth/mm than *G. jamaicensis* males. Furthermore, a sample of 98 non-Jamaican *G. assimilis* males failed to have a teeth/mm value as great as the lowest value for two *G. jamaicensis* (Table 1). None of the measurements in Table 1 separate all *G. assimilis* from all of *G. multipulsator*.

DNA Analyses. The MP and both ML analysis methods gave virtually identical results. Trees produced by both ML methods and one of two equally parsimonious MP trees were identical (Fig. 8). The other MP tree differed only in that it placed the sub-clades (G21, G578, G577, G576, G251, G248) and (G115, 04-100) together, rather than sharing a polytomy with the lineage leading to the larger group of mostly *assimilis*-type sequences. The Bayesian analysis showed overall similar separation of the *assimilis* and *multipulsator* sequences but was so poorly resolved within these groups as to be of little added value. AMOVA showed significant divergence ($F_{st} = 0.264, P < 0.0001$) between *G. assimilis* and *G. multipulsator* sequences. Intraspecific nucleotide diversities were similar (*G. multipulsator* 0.003759 ± 0.002167 , *G. assimilis* 0.003641 ± 0.002067). The corrected average pairwise distance was 0.0165.

Hybridization Trials. In the laboratory *G. assimilis* and *G. multipulsator* readily mate and produce viable offspring (Table 2).

Species Diagnoses and Descriptions
Gryllus assimilis (F.)

1775 *Acheta assimilis* F., Syst. Ent. 280. Type locality: "Jamaica". There is no mention of Montego Bay as

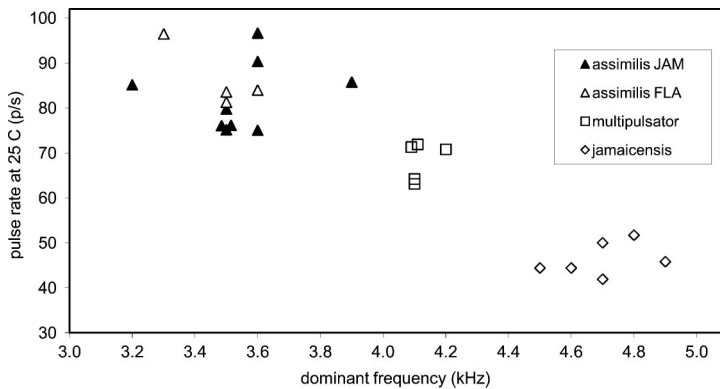


Fig. 5. Scatter plot of average PR at 25°C and dominant frequency of songs of 13 *G. assimilis* from Jamaica and Florida, five *G. multipulsator* from Baja California, and six *G. jamaicensis*.

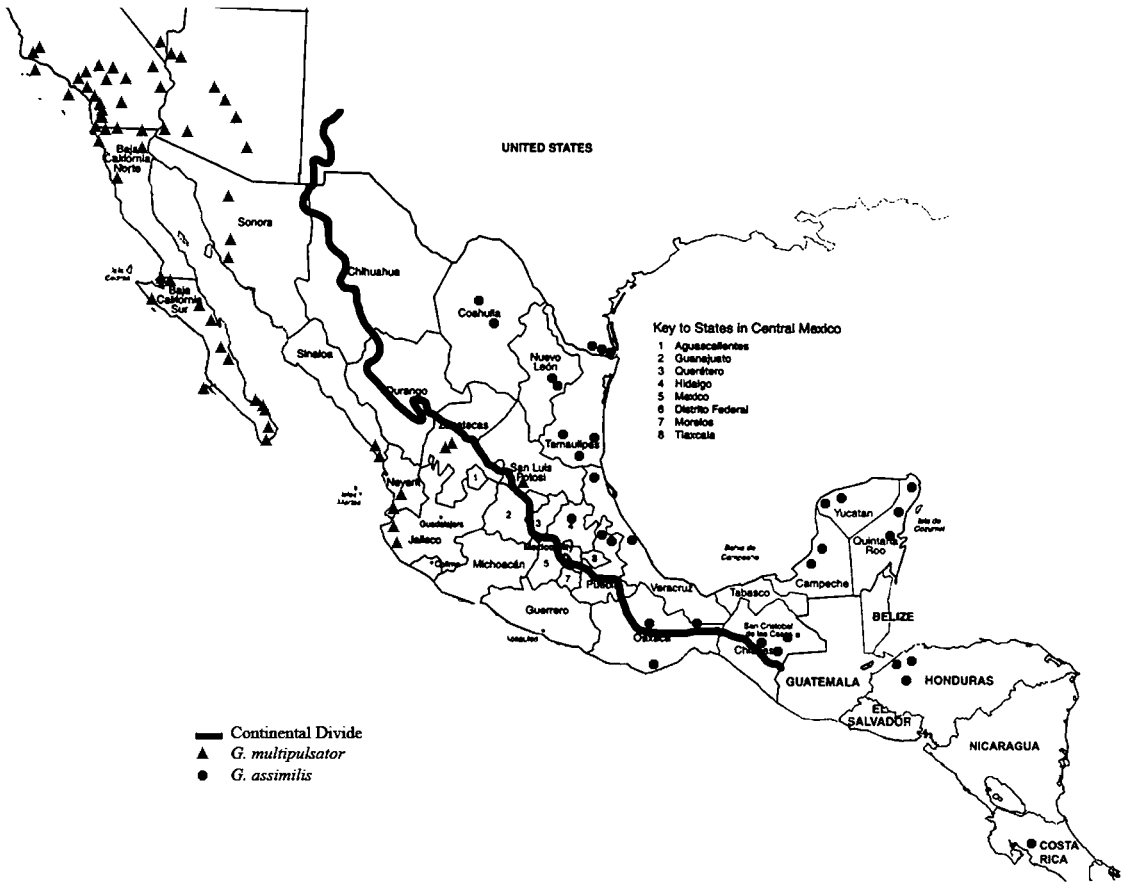


Fig. 6. Distribution map for *G. assimilis* (not shown are islands off the U.S. eastern coast) and *G. multipulsator*. Their distributions are almost perfectly separated by the Great Continental Divide that runs through Mexico's Sierra Madre Occidental.

indicated by Eades and Otte (2008). Type lost, according to Alexander (1957) (p. 585) and Eades and Otte (2008).

1869 *Gryllus determinatus* F. Walker, Cat. Dermapt. Salt. Br. Mus. 1:19. Type localities: Jamaica, St. Vin-

cent, San Domingo. Synonymized by Weissman et al. (1980).

Recognition Characters. Always macropterous, although rare individuals shed their flight wings (as in

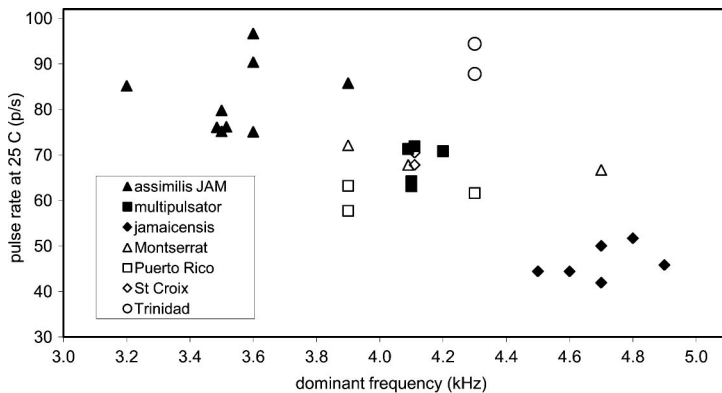


Fig. 7. Scatter plot of average PR at 25°C and dominant frequency of songs of *assimilis*-like crickets from four West Indian islands compared with those of the three species recognized in this paper and graphed in Fig. 5. Data points for Haiti and Dominican Republic individuals (from Appendix 2) are not shown because they are indistinguishable from Jamaica *assimilis*.

Table 1. Measurements of *Gryllus* species showing ranges of values

	<i>G. assimilis</i> (Jamaica)	<i>G. assimilis</i> (other localities)	<i>G. jamaicensis</i> (Jamaica)	<i>G. multipulsator</i> (all localities)
Specimens measured	4 ♂♂	98 ♂♂, 14 ♀♀	2 ♂♂	177 ♂♂, 67 ♀♀
No. teeth	108–125	94–125	120–127	98–143
File length (mm)	3.2–3.55	2.7–4.1	2.95–3.1	2.8–4.6
Teeth/mm	30.9–35.7	26.4–38.0	40.7–41.0	26.7–44.0
Length tegmen (mm)	13.4–16.2	12.6–17.2	11.6–12.8	13.1–16.8
Width tegmen (mm)	4.4–5.2	4.0–5.7	3.9–4.15	4.3–5.7
Length cercus (mm)	NA	10.0–15.0	11.7	8.7–15.2
Length hind femur (mm)	11.2–13.4	10.6–15.0	11.5–13.1	10.5–15.6
Length body male-fresh (mm)	NA	NA	NA	21.3–29.4
Length body male-dried (mm)	18.1–22.8	18.4–25.9	19.5–20.6	16.6–26.8
Length body female-fresh (mm)	NA	NA	NA	21.3–29.4
Length body female-dried (mm)	NA	19.9–23.1	NA	16.0–27.3
Length ovipositor (mm)	NA	12.1–17.6	NA	12.0–17.1

^a NA, not applicable.

Walker 1977, Weissman and Rentz 1977), medium to large size (Table 1), pronotum covered with short, fine hairs resulting in dull appearance; song 6–9 (rarely 10) P/C, PR (Fig. 2) for first pulse pair ranges from 50 to 111, PR of last pair ranges from 40 to 83. C/S variable but usually <2.5 at 25°C, which distinguishes *assimilis* from several other sympatric unnamed and unrelated species in Mexico and Central America that have songs with similar P/C. DF, 4.2 kHz. From *G. jamaicensis* n. sp., which also occurs on Jamaica, the latter often has more P/C (Fig. 3) and always has a lower average PR (Fig. 4) and higher dominant frequency (Fig. 5). From *G. multipulsator* n. sp., no overlap in P/C (Fig. 3) and no where sympatric (Fig. 6).

NEOTYPE. Male: Jamaica, St. Catharine Parish, Worthy Park, 27-XI-1968, T. J. Walker #2, 1,200 feet, T.J.W. recording (blue label) 68-654 and 68-656. Type deposited in CAS, #18172. Right tegmen removed, in gelatin capsule on pin: 108 teeth, file 3.2 mm long, tegmen 4.4 mm wide and 13.4 mm long. Hind femur 11.2 mm. MLNS song recording #114558.

Song ($n = 11$ from Jamaica; $n = 118$ from elsewhere). 0.5–2.5 C/S at 25°C; 6–10 P/C, most often 8–9 (1 male from Mexico, Tamaulipas, Ciudad Mante, with five P/C); DF 3.2–3.9 kHz. Even though *assimilis* has the fewest P/C of the three species here recognized (Fig. 3), its pulse-by-pulse changes in PR have the greatest range (Fig. 2B). Its average whole-chirp pulse rate at 25°C is the highest and its dominant frequency is the lowest (Fig. 5).

Distribution Range. Other T.J.W. Jamaican collection localities include Worthy Park, Bath, near Negril, near Tire, near Milk River Bath. T.J.W. has recordings of songs that are indistinguishable from *G. assimilis* from Hispaniola and Grand Cayman (Appendix 2) and songs from Puerto Rico, St. Croix, Montserrat, and Trinidad that are similar (Fig. 7; Appendix 2). Also recorded and collected in Brownsville, TX, and Mexico east of longitude 102° and east of the Continental Divide (except for a population at Huatulco, Oaxaca, Mexico) (Fig. 6). Introduced into southern Florida.

Habitat. On Jamaica, most frequent in pastures, groves, cultivated fields, yards, and roadsides but sometimes in less disturbed areas, including a salt flat that also

had *G. jamaicensis*. In Mexico and Texas, frequently associated with people and their watered environs such as lawns, golf courses, and in towns.

Seasonal Occurrence. Adult males collected every month except March. Because there is no diapause at any stage, we believe that adults can be found year-round.

Variation. In different individuals, most body parts can range in color from reddish tan to black. Some individuals with light body color have noticeable longitudinal head stripes.

Discussion. Morphological characters listed by Nickle and Walker (1974) work to separate *assimilis* from other Florida *Gryllus* species but do not work throughout this study area where *assimilis* is frequently sympatric, as in Mexico, with other unnamed, unrelated (based on dissimilar songs) species of long winged *Gryllus* with hirsute pronota and heads more narrow than the pronotum. Males of *assimilis* can be separated from these other Mexican taxa by song, but females, in many instances, are morphologically inseparable. Field-captured female *assimilis* readily lay eggs that hatch without diapause. The nymphs mature without diapause and males that call allow maternal species determination.

Well into the night (e.g., 0300 hours) in many lowland Mexico localities, when one would expect equilibrated ground and air temperatures, D.B.W. frequently heard what sounded like two different *assimilis* songs: one stopwatch-timed at one C/S and the other at two C/S. Captured males were labeled and returned to the laboratory where, at uniform temperature, these differences vanished. In fact, some males singing in the field at two C/S at 20°C, sang in the laboratory at one C/S at 25°C, and vice versa. One male *assimilis* from Oaxaca, Mexico, was recorded in the laboratory at 23°C singing at one C/S. One month later, at 25.5°C, this same male was recording singing at three C/S.

Gryllus jamaicensis T. J. Walker n. sp.

Recognition Characters. Always macropterous, medium size, pronotum hirsute. Endemic and restricted

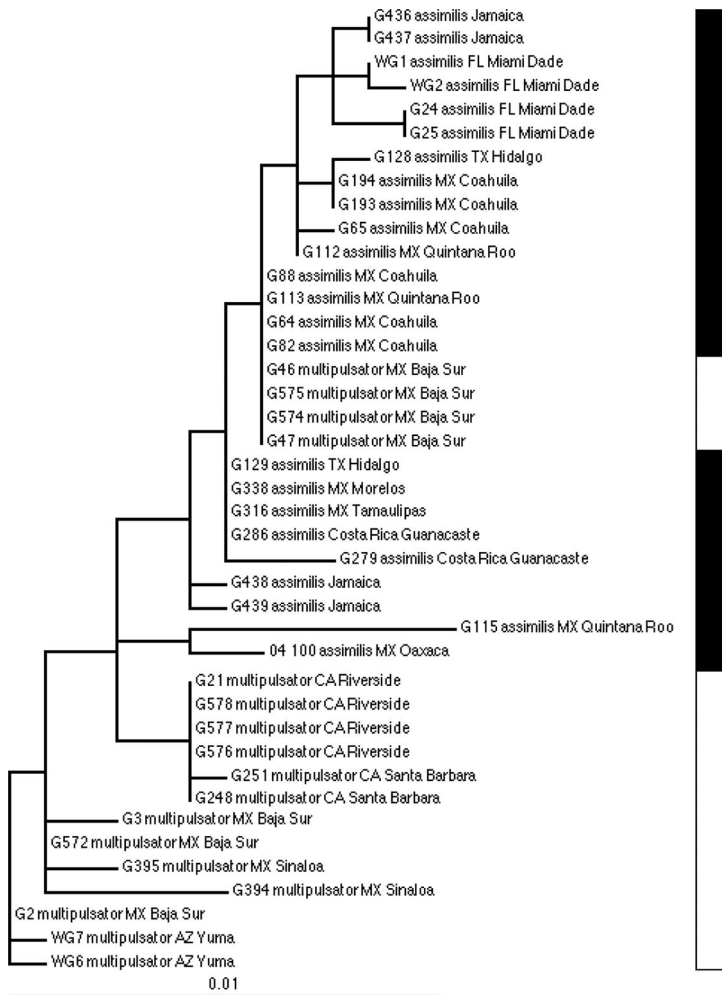


Fig. 8. Tree obtained from ML analysis by using the HKY + G model on unpartitioned data. The ML tree based on the GTR + SS model applied to four data partitions (16s, COI first position, COI second position, COI third position) was identical, as was one of two most parsimonious trees based on MP; the other MP tree was nearly identical (see text). Sample identity and collection locality information are given in Appendix 1; species identity is indicated by the black (*G. assimilis*) or white (*G. multipulsator*) bar at the right of the figure.

to Jamaica, where it differs from *G. assimilis* in file length, teeth/mm, and tegminal length and width (Table 1). Differs on basis of song in P/C (Fig. 3), average PR (Fig. 4), and DF (Fig. 5). Somewhat ecologically separated from *assimilis* through a preference for more xeric habitats. Nowhere sympatric with *multipulsator*.

Table 2. Results of crosses between Florida *G. assimilis* and Baja California, Mexico, *G. multipulsator*

		Males	
Females		<i>assimilis</i>	<i>multipulsator</i>
<i>assimilis</i>	■ ◆ ◆ ◆ □	■ ■ ■ ■ ■ ■ ■ ■ ■ ■	■ ◆
<i>multipulsator</i>	■ ■ ■ ■ ■ ■ ■ ■ ■ ■	■ ■ ■ ■ ■ ■ ■ ■ ■ ■	■

■, excellent or good egg hatch; ◆, fair egg hatch; and □, no egg hatch.

HOLOTYPE. Male: Jamaica, Hanover Parish, N. of Negril, Coll. #1. 22-VI-1970, T.J. Walker, J.J. Whitesell, P.C. Drummond. T.J.W. recording (blue label) 70-277 [=WTL1970-277]. Type deposited in CAS, #18173. Right tegmen not removed, right cercus 11.73 mm, hind femur 13.07 mm. MLNS song recording #131890.

PARATYPES. Jamaica, 1♂, St. Andrews Parish, The Palisadoes, 29-XI-68, recording 68-694, T.J.W.; 1♂, Clarendon Parish, near Portland Ridge, 0-5 feet, #2, 18-VI-1970, recording 70-236 and 289, T.J.W., J.J. Whitesell, P.C. Drummond.

Song ($n = 7$). 0.4-1.6 C/S at 25°C; 8-13 P/C, most often 10-12; DF 4.5-4.9 kHz. Pulse-by-pulse analysis of the song shows that PR drops sharply to a plateau and then more slowly to another (Fig. 2B). Of the three species here recognized, the average whole-

chirp pulse rate at 25°C of *jamaicensis* is the lowest and its dominant frequency is the highest (Fig. 5).

Distribution Range. Known only from Jamaica.

Habitat. *G. jamaicensis* occurs in drier, coastal areas of Jamaica and is not known in the inland, wetter areas. T.J.W. also recorded, but did not capture, *jamaicensis* as follows: type locality near Negril-white and red mangrove; Portland Ridge-rocky area between cactus-*Acacia* and black mangrove; near Kingston Airport-weedy area with cactus and mangrove; near Milk River Bath-cactus-*Acacia* salt flat.

Seasonal Occurrence. Adult males heard and recorded in June, August and November. Because we doubt there is diapause at any stage, we suspect that adults can be found year-round.

Variation. All three collected males light colored. See Table 1 for measurements.

Discussion. This species is less often encountered in Jamaica than *assimilis*. The sample of measured males is too small to ensure that males can always be distinguished morphologically from those of *assimilis* even in Jamaica (Table 1).

Gryllus multipulsator Weissman n. sp.

Gryllus assimilis (F.) Weissman et al. 1980. Trans. Am. Entomol. Soc. 106: 336.

Recognition Characters. Always macropterous (although some individuals dealate [see Walker 1977, Weissman and Rentz 1977]); size variable (Table 1) from medium to very large (♀ Mexico, Sonora, San Carlos Bay: 29.40 mm alive shrinking to 22.05 mm dead); head narrower than pronotum; pronotum covered with short, fine hairs resulting in dull appearance; song always with 11 or more P/C, which distinguishes it from *assimilis*. Restricted to southern California, southwestern Arizona, southernmost Nevada, and Mexico west of the Great Continental Divide (except for one population in the state of San Luis Potosi), geographically separated from both *assimilis* and *jamaicensis*.

Etymology. Named for producing chirps containing more pulses than any other *Gryllus* species.

HOLOTYPE. Male: USA: California, San Diego Co., Alpine, 1,900' 5-VI-1997. Stop 97-59. D.B.W. recording 97-18. D.B.W., VF Lee. Type deposited in CAS, #18174. Right tegmen removed, in gelatin capsule on pin. 125 teeth, file 4.05 mm long, tegmen 5.65 mm wide and 18.0 mm long. **PARATYPES.** 176♂ 67♀. **MEXICO:** Baja California Norte, Colonia Guerrero, 22-VII-1977, D.B.W., 1♂ 1♀; Descanso Dunes, km sign 49 Hwy 1 libre between Tijuana and Ensenada, 20-XII-1987, S87-128, 1♂; Guadalupe Canyon, 1-VIII-1981, S81-52, D.B.W., 1♂; Hotel Durado 2 m S Ensenada, 18-VII-1977, S77-3, D.B.W., 7♂ 5♀; 19-II-1978, D.B.W., 3♂; La Mision, 8-VII-1978, S78-22, D.B.W., DC Lightfoot, 1♂ 4♀; Maneadero, 260' 31-VIII-1995, S95-93, D.B.W., DC Lightfoot, 4♂ 1♀. Baja California Sur, Estero de San Jose 1.9 km W Guerrero Negro, 25-VII-1977, S77-31, D.B.W., C Mullinex, 1♂; Guerrero Negro, 25-VII-1977, S77-32, D.B.W., C Mullinex, 2♂; Loreto, 29-VIII-1995,

S95-91, D.B.W., DC Lightfoot, 6♂; Magdalena Island, near Smart Peak, 9-VII-1983, S83-96, D.B.W., 2♂ 1♀; 8 km W La Paz at km sign 8, 7-VII-1985, S85-74, D.B.W., DC Lightfoot, 3♂; Miraflores, 800', 24-IV-1979, S79-93, D.B.W., 1♂; 18-III-2003, S03-5, D.B.W., DW Weissman, 7♂ 5♀; Puerto Escondido, 28-VII-1977, S77-45, D.B.W., C Mullinex, 1♂; San Bartolo 31-VII-1977, S77-62, D.B.W., C Mullinex, 2♂ 3♀; San Bruno, 27-VII-1977, S77-40, D.B.W., C Mullinex, 2♂ 1♀; San Ignacio, 25, 26-VII-1977, S77-36, D.B.W., C Mullinex, 6♂ 2♀; San Jose del Cabo, 1-VIII-1977, S77-70, D.B.W., C Mullinex, 2♂ 3♀; 19-VII-1978, D.B.W., 1♂; 2-I-1979, S79-22, D.B.W., 1♂; 18 km N Santa Anita, 3-I-1979, D.B.W., 1♂; Santa Monica 119.7 km NW Viscaino, 1,320', 21-VIII-1995, S95-74A,B, D.B.W., DC Lightfoot, 5♂ 3♀. Jalisco, Rincon de Careyes, 55 km N Manzanillo, Club Med Playa Blanca, sea level, 1-I-1985, S85-1, D.B.W., 7♂ 3♀; Puerto Vallarta, sea level, 29-III-1983, S83-13, D.B.W., 5♂ 1♀. Nayarit, Compostila, 2,700' 31-III-1983, S83-16, D.B.W., 1♂; Hwy. 200 4.5 km S Tepic, 3,200' 31-III-1983, S83-14, D.B.W., 1♂; Hwy 200 18 km S Tepic, 3,500' 31-III-1983, S83-15, D.B.W., 3♂; Hwy 15 libre at Sanleone 24 km SE Tepic, km sign 194.7, 3,540' 14-VIII-1999, S99-95, D.B.W., BI Weissman, 1♂. San Luis Potosi, Sanborn Hotel 13.5 km N San Luis Potosi, 5,820', 6-VIII-1994, S94-89, D.B.W., DC Lightfoot, VF Lee, 5♂ 4♀. Sinaloa, Concordia, Hwy. 40, 320' 11-VIII-1999, S99-85, D.B.W., BI Weissman, 7♂ 7♀; Mazatlan, sea level, 11-VIII-1099, S99-87, D.B.W., BI Weissman, 5♂ 3♀; Hwy 40 2 km NE intersection with Hwy 15 at km sign 295, sea level 11-VIII-1999, S99-86, D.B.W., BI Weissman, 1♂ 1♀. Sonora, Hermasillo, 750' 24-VII-1990, S90-77, D.B.W., DC Lightfoot, 1♂; Hwy 15 32.6 m S Santa Ana, km sign 115, 2,300' 24-VII-1990, S90-73, D.B.W., DC Lightfoot, 1♂ 1♀; San Carlos Bay, Club Med Guaymas, sea level, 22-III-1986, S86-15, D.B.W., 4♂ 1♀; 25-VII-1990, S90-78, D.B.W., DC Lightfoot, 5♂ 4♀. Zacatecas, Hwy 54 at El Fuerte km sign 290.5, 20 km SW Zacatecas, 6,800' 13-VIII-1999, S99-92, D.B.W., BI Weissman, 2♂; Hwy 54 km sign 286.2, 24 km SW Zacatecas, 6,640' 13-VIII-1999, S99-93, D.B.W., DC Lightfoot, 1♂; Hwy 54 at Villanueva, km sign 253, 5,920' 13-VIII-1999, S99-94, D.B.W., BI Weissman, 3♂ 2♀. **USA: ARIZONA.** Gila Co., Globe, 3,544' 25-VIII-1982, S82-103, D.B.W., 2♂. Maricopa Co., Hwy 85 just E Goodyear, 980' 31-VII-1981, S81-46, D.B.W., 1♂; Phoenix, 1,140' 16-V-1999, S99-25, D.B.W., 1♂ 1♀; Scottsdale, 22-IV-1985, S85-41, D.B.W., 3♂. Mohave Co., Davis Dam, 900' 14-VI-1990, S90-46, D.B.W., BI Weissman, 1♂; Kingman, 3,600' 19-VI-1990, S90-58, D.B.W., BI Weissman, 1♂. Pima Co., Ajo, 1,720' 20-VIII-1998, S98-72, D.B.W., 2♂; Saguero Rd near Tucson, 2,400' 28-VII-1981, S81-35, D.B.W., 1♂. Yuma Co., Western College, 300' 10-VIII-1988, S88-89, D.B.W., DC Lightfoot, 1♂. **CALIFORNIA.** Los Angeles Co., Santa Catalina Island, Middle Ranch, 28-IV-1970, D.B.W., 4♂ 4♀; 15-VI-1971, DC Rentz, D.B.W., 1♂; 2-VII-1972, D.B.W., 1♂; Santa Catalina Island, Isthmus, 4-VII-1973, D.B.W., 1♂; Santa Monica Mts., Transcas Reservoir, 18-VIII-1973, D.B.W., 1♀. Orange Co., Newport Beach, Backbay Dr., 7-VII-1976, D.B.W., 1♂; Irvine, on UC Irvine Campus, 7-VII-1976, D.B.W., 2♂.

Riverside Co., Blythe, 400' 26-VI-1980, S80-47, D.B.W., 2♂; Indio, 6-VIII-1988, S88-74, D.B.W., 1♂; Palm Springs, 2-IV-1989, S89-8, D.B.W., 2♂; 6-IV-1991, S91-14, D.B.W., 1♂; Riverside near UC Riverside campus, 6-VI-2003, S03-41, D.B.W., 3♂. San Diego Co., Alpine, 1,900' 5-VI-1997, S97-59, D.B.W., VF Lee, 3♂, including holotype; Borrego Springs, 8-VIII-1988, S88-83, D.B.W., DC Lightfoot, 1♂; Camp Pendleton, 10, 11-VII-1976, D.B.W., 7♂ 1♀; Cardiff by the Sea, sea level, 12 and 13-VII-1976, D.B.W., 2♂; 27-VI-1980, S80-48, D.B.W., 2♀; La Jolla, near Prospect and Beach Blvd., sea level, 11-VII-1976, D.B.W., 6♂; San Diego, Mission Bay, sea level, 18-VI-1994, S94-34, D.B.W., 1♂. San Bernardino Co., Essex, 2,000' 22-VII-1990, S90-69, D.B.W., DC Lightfoot, 1♂; Mentone, 2,000' 25-VII-1981, S81-28, D.B.W., 1♂; San Bernardino Mts., Sky Forest, 5,600' 17-VIII-1982, S82-64, D.B.W., 1♂. Santa Barbara Co., Gaviota State Park, 14-VII-1976, D.B.W., 1♂; Santa Cruz Island, Prisoner's Harbor, sea level 11-VII-2004, S04-65, D.B.W., BI Weissman, 2♂ 1♀; Santa Ynez Mts., Lake Cachuma, 600' 24-VII-1981, S81-20, D.B.W., 2♂ 1♀. NEVADA. Clark Co., Cottonwood Cove, 800' 14-VI-1990, S90-44, D.B.W., BI Weissman, 1♂.

Song ($n = 125$). DF 4.1–4.2 KHz for 5 ♂♂ from Baja California, Mexico, 11–17 P/C, frequently = 1 C/S especially when found in cool, damp, coastal habitats. This chirp rate is noticeably slower than what is usual for *assimilis* and results because *multipulsator* chirps contain almost twice as many pulses, which are delivered at a slower PR. Interchirp intervals have not been compared. In *multipulsator* the average whole-chirp pulse rate at 25°C and dominant frequency are intermediate with respect to *assimilis* and *jamaicensis* (Fig. 5). Pulse-by-pulse analysis of the song shows that PR gradually drops to one plateau and then more slowly falls to another (Fig. 2B).

Distribution Range. See Fig. 6. Several collecting trips at the appropriate time of the year have been conducted in the state of San Luis Potosi, and only one population of *multipulsator* has been found on the east side of the Continental Divide. No *G. assimilis* are known from that state.

Variation. Individuals vary from almost entire body solid black to those with tan or reddish body parts. In the latter, the head may have distinctive longitudinal stripes. Tegmina also vary from tan to black, the latter especially common in cooler, moister habitats. Adult females with dark tegmina frequently have a light stripe along the forewing angle. It is unknown if colors change with generation and/or time of year maturing.

Habitat. North of San Diego Co., including the Channel Islands of Santa Cruz and Santa Catalina (Rentz and Weissman 1981), usually associated with water (salt and fresh water marshes, coastal beaches, cultivated and irrigated fields, reservoirs) and usually found singing from under dense vegetation. From Camp Pendleton, San Diego Co., and continuing south, including Mexico, individuals still associated with water but also found in cracks in dry grass fields. Found from sea level to 1,700 m.

Seasonal Occurrence. Collected year around. No diapause known at any life stage. Apparently two or more generations per year. This is the only *Gryllus* species heard singing in lowland, cool coastal southern California areas in January, although *Gryllus lineaticeps* Stål can be heard singing from higher, dry, warmer inland areas (such as the Santa Monica Mountains) during this same period.

Discussion. The authors had extensive discussions whether *G. multipulsator* should be treated as distinct from *G. assimilis*, even with their significant genetic divergences (see below), given the often arbitrary nature of such decisions. The deciding factors were a combination of geographical separation (Fig. 6) and almost no overlap in the number of pulses per chirp (Fig. 3). Specifically, the songs of 125 males of *multipulsator* from throughout its range were analyzed. All males had 11 or more P/C except for one male from Baja California Sur (Santa Monica) and this male had chirps with both 10 and 11 pulses. Two other recorded males from this locality had 12 and 14 P/C. Of 101 field-collected *assimilis* males recorded from Texas, Mexico, Honduras, and Costa Rica, only three (one each from Yucatan, Oaxaca, and Costa Rica) had 10 P/C, whereas the remainder had nine or less P/C. Of 17 recorded Florida *assimilis* males (two were F₁ and 15 were F₃₉), three had 10 P/C. Ultimately all Mexican populations of *multipulsator* are found west of the Continental Divide in Mexico's Sierra Madre Occidental (except for one at San Luis Potosi at 1,773 m in those same mountains).

Singing adult males can be very difficult to catch because of dense, thick vegetation. Females were rarely encountered and best found in association with males or attracted to oatmeal trails laid in the vicinity of singing males. Adult females, and nymphs of both sexes, will sometimes take refuge under objects (such as rocks, boards) and can be captured in modest numbers.

Gryllus contingens F. Walker

1869 *Gryllus contingens* F. Walker, Cat. Dermapt. Salt. Br. Mus. 1:21. Type localities: St. Vincent and Brazil. Placed in synonymy by Weissman et al. (1980). Here removed from synonymy. Given the situation that this species was not described from Jamaica, that other species of *Gryllus* occur on islands in the West Indies (e.g., Kevan 1980) and that several other narrow headed *Gryllus* species from Mexico and Central America (D.B.W., unpublished data) are long winged with hirsute pronota (the three major morphological criteria for identifying museum specimens of *G. assimilis*), it seems prudent to remove this synonymy at this time and reinstate the legitimate status of *contingens* pending further field work.

Gryllus mundus F. Walker

1869 *Gryllus mundus* F. Walker, *ibid.*: 23. Type locality: Brazil. Placed in synonymy by Weissman et al.

(1980). Here removed from synonymy with similar justification as under *G. contingens* above.

Discussion

Although all three species discussed in this article have pubescent pronota, this trait varies between individuals within a population. Some individuals of each species have such reduced amounts that their pronota are light reflective and shiny. But compared side by side with an always nonpubescent specimen of another species, such as *G. lineaticeps*, the reflective diminution seen in all individuals of these three species is obvious.

Our results indicate fairly distinct mitochondrial genetic lineages, but with some overlap between *G. multipulsator* and *G. assimilis*. DNA analysis as a supplement to taxonomic investigation can be a valuable tool in taxa recognition (Hebert et al. 2003, 2004; Pons et al. 2006). However, especially in the case of very closely related taxa, the discrepancy between gene trees and true species trees is expected to be greater, with gene trees progressing from polyphyly to paraphyly to reciprocal monophyly via lineage sorting (Avice 2000). Our results indicate modest genetic divergence between *G. multipulsator* and *G. assimilis* mtDNA sequences, consistent with what one might expect for recently derived and geographically isolated species. The likelihood of introgressive hybridization, were these taxa to become sympatric, cannot be determined by these data, but could instead depend upon levels of prezygotic isolation. Previous work with the closely related cricket species *Gryllus rubens* Scudder and *Gryllus texensis* Cade & Otte produced similar results: clear species differentiation, but without reciprocal monophyly (Gray et al. 2006). Further analysis of *G. rubens* and *G. texensis* mtDNA sequence data suggests that those taxa do not hybridize extensively in sympatry (Gray et al. 2008), which leaves open the possibility that *G. multipulsator* and *G. assimilis* would similarly show sufficient levels of isolation to remain distinct, despite mtDNA sequence polyphyly. In any case song-wise, morphology-wise, and gene-wise our results demonstrate a widespread and coherent (=monophyletic) complex of three New World species.

Areas for future research include examining other mtDNA and nuclear genes to see if this additional information would clarify the relationship between these three species, and the origin of recently introduced *G. assimilis* in Florida. Additional hybridization trials, involving *jamaicensis*, and comparative DNA analysis, could clarify the relationship between the two Jamaica species. Hybridization trials should be easy to conduct because no species has a dormancy period at any stage of development and they probably readily mate in the laboratory. Of interest is the apparent decreased fecundity in our *G. assimilis* control crosses, perhaps reflecting their inbred status as an F₃₉ laboratory generation. Female choice experiments could examine whether the increased pulses per chirp or the slower rate of decrease in PR within chirps in

G. multipulsator versus *G. assimilis*, affect male attractiveness. Ecological separation on Jamaica could also be further investigated.

Note. A single male *G. multipulsator* was collected in Mexico in 2008 from Michoacan, 26 km E Morelia, 2,103 m (14 P/C), and from Hidalgo, Zimapan, 1,737 m (12 P/C). This confirms additional penetration into the mountain ranges north of Mexico City. While the latter locality is east of the Continental Divide, the nearest located *G. assimilis* population is 72 air km NE of Zimapan at 730 m. Although not an official ESA approved common name, *G. assimilis* is commonly referred to in the literature as the Jamaican field cricket.

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Appendix 1. Sample identity and collection locality information

Sample	Species	Collector	Country	State	County	Locality ^a	Recording
G436	<i>G. assimilis</i> ^b	D. Lewis	Jamaica			Mandeville	DL1
G437	<i>G. assimilis</i> ^b	D. Lewis	Jamaica			Mandeville	DL2
WG1	<i>G. assimilis</i>	D. A. Gray	USA	Florida	Miami-Dade	Florida City	
WG2	<i>G. assimilis</i>	D. A. Gray	USA	Florida	Miami-Dade	Florida City	
G24	<i>G. assimilis</i>	DBW	USA	Florida	Miami-Dade	Homestead, S03-48	R03-77
G25	<i>G. assimilis</i>	DBW	USA	Florida	Miami-Dade	Homestead, S03-48	R03-73
G128	<i>G. assimilis</i>	DBW	USA	Texas	Hidalgo	Bentsen, Rio Grande Valley State Park, S02-34	R02-56
G194	<i>G. assimilis</i>	DBW	Mexico	Coahuila		Cuatrociénegas, S01-89	R01-152
G193	<i>G. assimilis</i>	DBW	Mexico	Coahuila		Cuatrociénegas, S01-89	R01-179
G65	<i>G. assimilis</i>	DBW	Mexico	Coahuila		Near Cuatrociénegas, S03-127	R03-261
G112	<i>G. assimilis</i>	DBW	Mexico	Quintana Roo		Road to Punta Allen, S02-10	R02-9
G88	<i>G. assimilis</i>	DBW	Mexico	Coahuila		Near Cuatrociénegas, S03-127	R03-293
G113	<i>G. assimilis</i>	DBW	Mexico	Quintana Roo		Road to Punta Allen, S02-10	R02-10
G64	<i>G. assimilis</i>	DBW	Mexico	Coahuila		Near Cuatrociénegas, S03-127	R03-260
G82	<i>G. assimilis</i>	DBW	Mexico	Coahuila		Near Sacramento, S03-124	R03-278
G129	<i>G. assimilis</i>	DBW	USA	Texas	Hidalgo	Bentsen, Rio Grande Valley State Park, S02-34	R02-78
G338	<i>G. assimilis</i>	DBW	Mexico	Morelos		Near Cuernavaca, S99-55	R99-124
G316	<i>G. assimilis</i>	DBW	Mexico	Tamaulipas		Ocampo, S99-42	R99-70
G286	<i>G. assimilis</i>	DBW	Costa Rica	Guanacaste Prov.		La Pacifica, 4 km NW Canas, S00-20	R00-31
G279	<i>G. assimilis</i>	DBW	Costa Rica	Guanacaste Prov.		La Pacifica, 4 km NW Canas, S00-20	R00-20
G438	<i>G. assimilis</i> ^b	D. Lewis	Jamaica			Portland Ridge	DL3
G439	<i>G. assimilis</i> ^b	D. Lewis	Jamaica			Milk River	DL4
G115	<i>G. assimilis</i>	DBW	Mexico	Quintana Roo		Road to Punta Allen, S02-10	R02-34, 37
04-100	<i>G. assimilis</i>	A. Izzo	Mexico	Oaxaca		Oaxaca City	See notes ^c
G46	<i>G. multipulsator</i>	DBW	Mexico	Baja Sur		Cape Region, Miraflores, S03-5	
G575	<i>G. multipulsator</i>	DBW	Mexico	Baja Sur		Cape Region, Miraflores, S03-5	
G574	<i>G. multipulsator</i>	DBW	Mexico	Baja Sur		Cape Region, Miraflores, S03-5	
G47	<i>G. multipulsator</i>	DBW	Mexico	Baja Sur		Cape Region, Miraflores, S03-5	
G21	<i>G. multipulsator</i>	DBW	USA	California	Riverside	Near University of California Riverside, S03-41	R03-42
G578	<i>G. multipulsator</i>	DBW	USA	California	Riverside	Near University of California Riverside, S03-41	R03-20
G577	<i>G. multipulsator</i>	DBW	USA	California	Riverside	Near University of California Riverside, S03-41	R03-42
G576	<i>G. multipulsator</i>	DBW	USA	California	Riverside	Near University of California Riverside, S03-41	
G251	<i>G. multipulsator</i>	DBW	USA	California	Santa Barbara	Santa Cruz Island, S04-65	R04-82
G248	<i>G. multipulsator</i>	DBW	USA	California	Santa Barbara	Santa Cruz Island, S04-65	
G3	<i>G. multipulsator</i>	DBW	Mexico	Baja Sur		Cape Region, Miraflores, S03-5	R03-4, 12
G572	<i>G. multipulsator</i>	DBW	Mexico	Baja Sur		Cape Region, Miraflores, S03-5	R03-2
G395	<i>G. multipulsator</i>	DBW	Mexico	Sinaloa		Concordia, S99-85	R99-193
G394	<i>G. multipulsator</i>	DBW	Mexico	Sinaloa		Concordia, S99-85	R99-187
G2	<i>G. multipulsator</i>	DBW	Mexico	Baja Sur		Cape Region, Miraflores, S03-5	R03-11
WG7	<i>G. multipulsator</i>	A. Izzo	USA	Arizona	Yuma	Yuma	
WG6	<i>G. multipulsator</i>	A. Izzo	USA	Arizona	Yuma	Yuma	

^a S number references DBW field notes.^b Jamaican specimens identified as *G. assimilis* based on morphology and song.^c Female specimen, two laboratory-reared sons recorded DAGSL nos. 2004-123, 2004-124.

Appendix 2. Results of analyses of recordings of *assimilis*-type calling songs in Walker Tape Library, including those graphed in Figs. 4, 5, and 7

Record no. (WTL)	Species	Country	Temp (°C)	Avg p/s	Avg p/s @25C	Dom. freq.	Modal pulse no.
1966-203	<i>jamaicensis</i>	Jamaica	23.0	45.0	50.0	4.7	11
1968-694	<i>jamaicensis</i>	Jamaica	26.0	47.1	45.8	4.9	12
1970-198	<i>jamaicensis</i>	Jamaica	26.4	47.3	44.4	4.6	10
1970-199	<i>jamaicensis</i>	Jamaica	26.3	47.2	44.4	4.5	10
1970-277	<i>jamaicensis</i>	Jamaica	24.8	51.2	51.7	4.8	10
1970-289	<i>jamaicensis</i>	Jamaica	26.0	44.0	41.9	4.7	9
1968-519	<i>assimilis</i>	Jamaica	24.6	73.6	75.1	3.6	8
1968-545	<i>assimilis</i>	Jamaica	24.3	77.0	79.8	3.5	8
1968-651	<i>assimilis</i>	Jamaica	22.2	65.4	76.1	3.5	9
1968-654	<i>assimilis</i>	Jamaica	22.3	65.0	75.2	3.5	10
1968-656	<i>assimilis</i>	Jamaica	21.0	68.6	85.8	3.9	8
1970-097	<i>assimilis</i>	Jamaica	22.8	86.0	96.7	3.6	8
1970-131	<i>assimilis</i>	Jamaica	26.8	83.0	76.2	3.5	8
1970-249	<i>assimilis</i>	Jamaica	25.4	86.9	85.2	3.2	9
1970-323	<i>assimilis</i>	Jamaica	20.0	67.8	90.4	3.6	9
1973-271	<i>assimilis</i>	Haiti	27.8	93.1	81.7	3.4	10
1973-273	<i>assimilis</i>	Haiti	26.4	87.7	82.0	3.3	9
1973-371	<i>assimilis</i>	Dom. Republic	21.0	70.4	88.0	3.2	9
1973-403	<i>assimilis</i>	Dom. Republic	26.0	88.0	83.8	3.4	9
1973-420	<i>assimilis</i>	Dom. Republic	21.0	64.5	80.6	3.4	10
1973-456	<i>assimilis</i>	Dom. Republic	22.0	87.5	103.0	3.4	8
1970-367	<i>assimilis</i>	G. Cayman	27.4	94.6	69.9	3.7	9
1965-851	<i>assimilis</i>	Florida	14.5	45.8	96.5	3.3	8
1968-508	<i>assimilis</i>	Florida	24.5	81.5	83.6	3.5	7
1978-262	<i>assimilis</i>	Florida	26.4	89.9	84.0	3.6	9
1978-263	<i>assimilis</i>	Florida	26.4	87.0	81.3	3.5	10
1966-229	<i>assimilis</i> [?]	Puerto Rico	26.0	64.6	61.6	4.3	8
1969-053	<i>assimilis</i> [?]	Puerto Rico	24.8	57.1	57.7	3.9	9
1969-067	<i>assimilis</i> [?]	Puerto Rico	21.8	53.1	63.2	3.9	9
1969-240	<i>assimilis</i> [?]	St. Croix	23.3	64.5	70.5	4.1	8
1969-241	<i>assimilis</i> [?]	St. Croix	23.3	62.0	67.8	4.1	8
1992-M1	<i>assimilis</i> [?]	Montserrat	27.4	80.8	72.1	3.9	7.5
1992-M2	<i>assimilis</i> [?]	Montserrat	23.4	62.4	67.8	4.1	9
1992-M3	<i>assimilis</i> [?]	Montserrat	27.0	73.4	66.7	4.7	8
1966-12	<i>assimilis</i> [?]	Trinidad	23.5	87.3	94.4	4.3	9
1966-65	<i>assimilis</i> [?]	Trinidad	23.3	80.3	87.8	4.3	9
2003-22	<i>multipulsat</i>	Baja Calif.	26.8	69.9	64.2	4.1	
2003-23	<i>multipulsat</i>	Baja Calif.	25.4	72.7	71.3	4.1	12
2003-24	<i>multipulsat</i>	Baja Calif.	25.4	73.4	71.9	4.1	15.5
2003-25	<i>multipulsat</i>	Baja Calif.	25.4	64.4	63.1	4.1	13.5
2003-27	<i>multipulsat</i>	Baja Calif.	25.6	72.9	70.8	4.2	13