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Crickets of the genus *Gryllus* in the United States (Orthoptera: Gryllidae: Gryllinae)

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There are unknown unknowns: Donald Rumsfeld

Abstract

Gryllus field and wood crickets of the United States, mostly west of the Mississippi River, are reviewed and revised. We validate the following 18 *Gryllus* cricket names: *G. armatus, G. assimilis, G. brevicaudus, G. cayensis, G. cohni, G. firmus, G. fultoni, G. integer, G. lineaticeps, G. multipulsator, G. ovisopis, G. pennsylvanicus, G. personatus, G. rubens, G. texensis, G. veletis, G. vernalis,* and *G. vocalis.* We synonymize *G. alogus* under *G. vocalis.* We designate a lectotype for *G. armatus.* We describe the following 17 new *Gryllus* species: *G. chisosensis, G. leei, G. lightfooti, G. longicercus, G. makhosica, G. montis, G. navajo, G. planeta, G. regularis, G. saxatilis, G. sotol, G. staccato, G. thinos, G. transpecos, G. veintinueve, G. veletisoides,* and *G. vulcanus.* We present biology, distribution, and genetic analysis of all taxa and discuss their nearest relatives.

Key words: cryptic species, sister species, parasitoids, tachinid flies, barcoding, multilocus DNA analysis, hybrid zones, *Acheta domesticus, Gryllus bryanti, Gryllus bimaculatus, Gryllus locorojo*

Introduction

This paper presents the results of 45+ years of fieldwork on the *Gryllus* field and wood crickets of the United States, mostly west of the Mississippi River, and extends the New World geographic area now thoroughly covered for *Gryllus* to include all of North America north of Mexico. These results build on previous work on eastern US *Gryllus* by Scudder (1902), Blatchley (1920), Fulton (1952), Alexander (1957), Alexander & Bigelow (1960), Alexander & Walker (1962), Walker (1974, 2000, 2001), Cade & Otte (2000) and Weissman *et al.* (2009). We consider ten eastern US *Gryllus* taxa to be valid: *G. assimilis* (Fabricius); *G. pennsylvanicus* Burmeister; *G. firmus* Scudder; *G. rubens* Scudder; *G. vernalis* Blatchley; *G. fultoni* (Alexander); *G. veletis* (Alexander & Bigelow); *G. ovisopis* Walker; *G. texensis* Cade & Otte; and *G. cayensis* Walker. All eastern taxa are discussed in this paper but some not as thoroughly as strictly western US species.

Western US *Gryllus* were addressed by Scudder (1901, 1902), Rehn & Hebard (1915), Weissman *et al*. (1980, 2009), and Cade & Otte (2000) and we recognize the following, previously described, eight taxa: *G. lineaticeps* Stål; *G. personatus* Uhler; *G. integer* Scudder*;* *G. vocalis* Scudder; *G. armatus* Scudder; *G. brevicaudus* Weissman, Rentz, & Alexander; *G. cohni* Weissman, and *G. multipulsator* Weissman. With this study and the addition of 17 new taxa, we increase the total US number to 35 species. We also choose a lectotype for *G. armatus* and synonymize *G. alogus* Scudder under *G. vocalis.*

Supplying new names for unrecognized US *Gryllus* taxa is not a simple exercise in alpha taxonomy because these crickets have been used in many fields of population biology, genetics, and ecology. For example, US *Gryllus* have been excellent subjects for studies on evolution of female calling-song preferences (e.g. Hedrick & Weber 1998, Martin & Wagner 2010, Gray *et al.* 2016a), parasitoid-host interactions (e. g. Adamo *et al.* 1995, Gray & Cade 1999a, Thomson *et al.* 2012), hybrid zone issues (e. g. Ross & Harrison 2002), character displacement (e. g. Walker 1964, Gray & Cade 2000a, Izzo & Gray 2004, Jang & Gerhardt 2006a, b, 2007; Jang *et al.* 2007), physiology (e.g. Zera 2005), life-history evolution (e.g. Roff 1984), among other disciplines. In all cases, these researchers need to be able to attach a name to their organism (e.g. Sakaguchi & Gray 2011, Thomson *et al*. 2012, Blankers *et al.* 2015).

Additionally, ability to recognize all native US *Gryllus* taxa is important because of the potential agricultural and native faunal threats posed by escaped, non-native cricket species presently being cultured by the pet food industry (Weissman *et al.* 2012).

Most discussions in this paper refer to specimens obtained since Weissman *et al*. (1980) because these later collected individuals have more extensive numbers of recordings, DNA data, and accurate cercus lengths measured immediately upon death, before they curl with drying.

Materials, methods, and terminology

How to use this paper. We hope to enable both amateurs, without access to tape recorders, light microscopes, and DNA sequencing techniques; and biologists with access to some or all of these techniques, to ID their US *Gryllus* field and wood crickets, although amateurs will be limited with certain species. As calling song is the primary character in classifying US *Gryllus,* we recommend that everyone's first step should be to visit the SINA web site, Singing Insects of North America (https://sina.orthsoc.org/), originally set up by Thomas J. Walker of the University of Florida, and that will be maintained into the future by the Orthopterists' Society. Once at that site, click on "Crickets" then click on "List of species" and go to the various *Gryllus* names. We have divided US calling songs into 9 subjective categories, as might be heard by the average adult's ear. These groupings, and a listing of all the US *Gryllus* species whose calling songs fit into each category, at around 25°C, and can be heard on SINA, are these:

1. Slow (<4 chirps/sec), short chirps (4–6 pulses/chirp) with individual pulses not identifiable, as exemplified by *G. brevicaudus*, *G. leei, G. lightfooti, G. makhosica, G. montis, G. navajo,* most populations of *G. pennsylvanicus, G. planeta, G. saxatilis, G. sotol, G. thinos, G. transpecos, G. veletis, and G. veletisoides.*
2. Slow (<4 chirps/sec), short chirps (4–6 pulses/chirp) with individual pulses identifiable, as exemplified by *G. chisosensis, G. firmus, G. longicercus,* some central US populations of *G. pennsylvanicus,* and *G. vulcanus.*
3. Slow (<3 chirps/sec), long chirps (>6 pulses/chirp), as exemplified by *G. assimilis* and *G. multipulsator.*
4. Fast (>4 chirps/sec), short chirps (2–3 pulses/chirp), as exemplified by *G. fultoni, G. veintinueve, G vernalis,* and *G. vocalis.*

5. Fast (>4 chirps/sec), long chirps (>6 pulses/chirp), as exemplified by *G. lineaticeps, G. personatus,* and some *G. staccato.*
6. Slow trill, as exemplified by *G. regularis.*
7. Fast trill or unable to tell if 1, 2 or 3 pulses/chirp, as exemplified by *G. armatus*, some *G. cohni, G. integer, G. rubens,* and *G. texensis.*
8. Irregular song with variable grouping of pulses, as exemplified by some *G. staccato* and some *G. cohni.*
9. Absence of calling song, as exemplified by southeastern US *G. cayensis* and *G. ovisopis.*

Once the song pattern is established, then referring to the 'Distribution map' and 'Discussion' under each species in that song pattern group, will narrow options considerably. For those individuals with the interest and equipment needed for using a dichotomous key, see 'Key to adult males of *Gryllus*' starting on page p. 27.

Nevertheless, in some cases, the reader will need to examine the right tegmen file, most easily done using a high powered light microscope, or look at a sonogram representation of a recorded calling song. We provide a summary Measurement Spreadsheet, Table 1, on page p. 18, which delimits the range of the important physical and song characters of each species. As a last resort, DNA analysis may be needed but we discuss, on page p. 14, the potential problems associated with barcoding using only one mitochondrial gene. In other words, confident identification of certain taxa may take some work. We also caution that *Gryllus* songs and morphology within populations are variable and that multiple, adult male specimens should be collected and analyzed, especially in those states like Arizona, California, New Mexico, Utah, and Texas (see Fig. 5, p. 23) that contain more than 10 species of *Gryllus.* In fact, there are two Arizona (Sedona and Ajo/Why) and one Texas (Rio Grande Village) locality where 6 species of *Gryllus* can be synchronic. The good news is that all 6 species can be distinguished, in the field, by human ears.

Song parameters and terminology. As used in this paper, are as follows (Fig. 1). We note, however, that this terminology is variable across published studies, with many, primarily European, research groups using 'syllable' for what we call a 'pulse.'

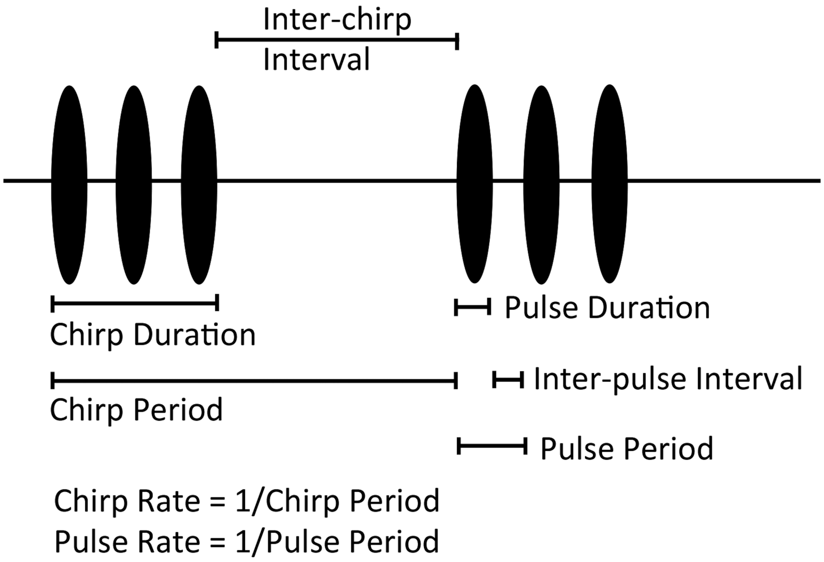

FIGURE 1. Labeled parts of a *Gryllus* calling song, here in a male with 3 pulses/chirp. In this paper, all reported pulse rates are calculated between the last 2 pulses in a chirp.

Assignment of scientific names. Past taxonomic practices, especially those of Scudder in 1901 and 1902, resulted in scientific names being attributed to a series of specimens from different localities. This practice was true for *G. integer, G. vocalis,* and *G. armatus* within the study area. We used the following procedure to help choose a lectotype: find a male, in the type series, in good condition with a more or less precise locality. Collect that locality and find a male that agrees morphologically, including the wing file teeth number, with the male from the type series. We now have the song and can accurately assign the name. A more problematic situation is where Scudder's holotype is a single female, such as occurs with *G. alogus* and *G. personatus*, because there is no wing file to examine. The latter species was easy to handle because this female is morphologically distinct, even though we have not found *G. personatus* in the type locality of "Kansas," but did find it in neighboring Colorado. The holotype of *G. alogus* (from "Albuquerque, New Mexico") was more problematic since she has no distinctive features—see discussion under *G. vocalis* below.

Museum specimens. Very few museum specimens, either pinned or in alcohol, were included in this study for several reasons: (1) None have calling song information, which is essential for any taxonomic study in this group. (2) Color, unless specimens were dried quickly, is not reliable. (3) Accurate cercus lengths cannot be measured since such appendages curl upon death, even in specimens dried quickly or when cerci are coated with nail polish. Because we did not use museum specimens, our distribution maps only show populations/specimens that we personally collected, or where live specimens were sent to us. Distribution maps for more eastern US species are found in references cited under that species.

Specimens examined and locality information. For newly described species, most collected specimens are considered paratypes with collection information given. Species already described will be treated in two ways: 1. If very widespread and readily located, such as *G. lineaticeps,* then only locations of significance, such as highest elevation or most northern collection locality, will be listed. We want to facilitate future research looking to track species' distributions movements, based on climate change, should they move up mountains or farther north. 2. For more localized or difficult to find species, complete collection data are presented.

Since almost 100% of specimens discussed were collected by the authors, such information is not included in the paper for reasons of economy. Where specimens were collected by others, we list those collectors. Collector information and GPS data, where obtained, are on the labels associated with each specimen, or in DBW's notebooks, which will be deposited at California Academy of Sciences (CAS).

Specimen label data. Most pinned specimens have one or two hand-written labels on the pin below the traditional printed locality label(s). These labels have abbreviations which we detail here since they either pertain to measurements of that specimen or refer to biological information which can be cross-referenced in DBW's notebooks. **"S"** stands for stop number, thus S02–12 would be stop #12 in the year 2002. **"R"** stands for recording, many of which, for the years 1993 to 2014, have been digitized and deposited at the Macaulay Library (ML) of Natural Sounds, Cornell Lab of Ornithology. Those recorded specimens have a corresponding, unique ML number below the pinned specimen. Representative recordings are posted on Singing Insects of North America website (https://sina.orthsoc.org/) and will be used in the key below. **"G"** references the leg taken from that specimen for DNA analysis. **"A"** stands for date on which a field captured nymph molted to adult in the laboratory. **"C"** stands for the length, in mm, of the longest intact (i.e. tapered to a point) cercus, indicated as **RC** for right cercus and **LC** for left cercus. If preceded by a * on a female specimen, that indicates that at least one cercus, in situ, extended past tip of ovipositor immediately after killing. Some cercus measurements are followed by a "+" indicating that the structure was not intact but almost so. **"HF"** stands for length, in mm, of (usually) the left hind femur. **"O"** stands for length of the ovipositor, "**PW"** stands for pronotal width, and **"PL"** stands for pronotal length. **Body length**, where measured, is from the front of the head to the tip of the abdomen, excluding the cerci and ovipositor. A second label, on pinned males whose right tegmen was removed and stored in a gelatin capsule under the pinned male, has four handwritten numbers all pertaining to measurements of the male's tegmen: top line—number of teeth in the file ("X2" if counted in both directions); second line—length of file (mm); third line—width of wing as measured from inner edge of tegmen to CU_1 vein; fourth line is length of tegmina.

Adult females that have an ~two-week period written on their label, were given the opportunity to oviposit for those two weeks. Results of such trials, usually examining the presence or absence of an egg diapause, are reported under that species and in the appropriate laboratory notebook by the collection stop of that female.

Field collecting techniques. We attempted to minimize damage to both cerci, when catching crickets, because maximum length of cerci is a valuable character. In the hands-free capture technique employed by DBW, an individual was herded into a transparent plastic tube before transferring it, singly, into a 60-ml plastic centrifuge tube. DAG collected crickets by hand without damaging them by catching them such that the cricket becomes enclosed in a space between the palm and cupped fingers.

Flight capable species of crickets are often concentrated in small towns and around human habitation and buildings, especially those with bright lights at night; such areas may provide more hiding places and access to moisture and food. Some Groups, such as the Lightfooti, and the Longicercus and Saxatilis rock chirpers, are almost only found in natural habitats, and rocky road cuts, away from people. DBW and DAG tend to employ different collecting strategies. DBW drives around at night with windows down listening for singing males. Once a male is heard, leaving the car frequently reveals several species singing at one locality. We also recommend driving slowly through desert towns frequently stopping at gas stations, especially during summer monsoon season, that have bright florescent lights on all night (such gas stations can also be fruitful places to collect in the early morning hours before the birds arrive to glean the area clean). Using this technique, one can cover 100 to 200 road kilometers at night and collect all night if temperatures remain warm enough. DBW does drive faster between towns but makes periodic stops, in natural habitat, to listen for singing males. DAG prefers to camp in natural habitat areas and wander around at night with a headlamp, listening and looking.

Singing males are best triangulated by two persons approaching the cricket at 90 degrees to each other. When we are close, the cricket usually stops singing but remains in place. If associated with cracks either in towns or in fields (such as *G. lineaticeps*), seeing exactly where the male retreats to can indicate where to slowly pour water to flush the cricket. We stop at one gallon if unsuccessful in flushing the cricket from a soil crack or crevice. It is oftentimes possible to use a thin stick or piece of grass to coax a cricket from smaller cracks.

Crickets singing from grass (such as *G. vocalis*, *G. veletis* and *G. pennsylvanicus*) are more difficult to apprehend. If near an edge, such as an area of un-mowed tall grass bordering a road or open area, then many can be flushed from the grass by rapid stomps behind where the cricket was last singing (while adult males singing in such locations usually stop singing on approach, they seem to hold their positions until the stomping begins). Those singing from a large area of deep grass can be triangulated and the area pounced on, using two hands, hoping to pin the male. A second person then slowly peels back the grass while the “pouncer” applies continuous pressure. In such habitats, objects such as rocks or boards frequently shelter crickets, usually adult females. We have also effectively used oatmeal trails along the edges of grassy fields with singing males.

Most taxa in the Longicercus and Saxatilis Groups inhabit rock piles or rocky road-cuts. These male crickets frequently continue to sing while their rocks are being removed, making location easy. Oatmeal trails can also be laid between the paved road surface and the actual face of the road-cut, frequently attracting both sexes and nymphs.

Best time of year to collect. If interested in collecting a series of a particular target species, we recommend consulting localities and dates given in the ‘Specimens examined’ section of the species descriptions that follow. If one desires to survey a specific area for *Gryllus* species, and since most US *Gryllus* taxa overwinter as late nymphs, collecting in May/June will usually yield the best results. This is even true for those single generation taxa that inhabit high elevations, such as *G. veletis* at Cloudcroft, NM, at 2500m; *G. montis* along the Arizona/New Mexico border at 2440m; and *G. vulcanus* at El Malpais, NM, also at 2440m. Problems may arise in the following three situations: 1. Species from southern US localities that have two generations/year, could be between generations one and two during this survey period. There would be nymphs present but few or no adult males singing. 2. Species that overwinter as eggs would not become adult until late summer and would be missed by a May/June survey since no males would be singing. A second survey in September should uncover those taxa with either an egg diapause or 2 generations/year. 3. Those species without an egg diapause that are somehow rain sensitive, and inhabit Southwestern desert areas. These taxa appear to become adult in June/July in anticipation of summer monsoon rains that usually start in July.

Tentative *Gryllus* species’ numbers. To help keep track of field collected specimens, song and morphological-types were assigned a *Gryllus* species’ number. To facilitate cross-referencing with DBW’s notebooks, these numbers are listed as each species is discussed. These species numbers are shown in the text in ‘single quote marks’ and not italicized indicating that such numbers are not formal names and are not available for future reference. Some of these numbers have already been used in publications (e.g. Sakaguchi & Gray 2011, Thomson *et al.* 2012, Blankers *et al.* 2015) while we prepared this manuscript. Under each species description, we attempt to identify publications based on work with that species when otherwise unclear or confusing.

How to identify females to species. Adult females generally lack the distinctive identification characters (especially wing file and song) present in males. In more northern US localities with few *Gryllus* taxa, it is generally not difficult to associate males and females. Southern US localities, especially places in Arizona like Sedona and Ajo/Why where six species of *Gryllus* may occur sympatrically, several techniques may be employed to ID females: 1. Females may be physically near a singing male, sometimes in the same refuge. She may even have an attached spermatophore. 2. Females may have diagnostic physical characters such as long cerci for *G. longicercus*, long ovipositors for *G. pennsylvanicus* and distinctive facial markings such as seen in *G. personatus* and *G. staccato*. 3. DNA can be analyzed and associated with the respective males. 4. Eggs can be easily obtained and nymphs raised to adult to determine the calling song of sons.

Long vs. short hind-winged individuals. Many *Gryllus* species have populations that contain both short and long hind-winged individuals. Factors that may be important include nutritional status, permanence of habitat, and first vs. second generation individuals. Short hind winged individuals must be distinguished from dealate individuals, the latter having shed their hind wings (Weissman & Rentz 1977b, Walker 1977). This condition is easy to determine in males whose right tegmen has been removed for file analysis because the hind wing, if present, is readily visible.

Common names. There are four previously named US *Gryllus* that almost exclusively inhabit woodlands: *G. cayensis, G. fultoni, G. ovisopis,* and *G. vernalis.* We add two more with the *G. montis* complex and *G. planeta*, and we continue the tradition of calling them all "wood crickets." The remaining taxa have been called "field crickets" even though some of them are only associated with rocky habitats and others with open, sandy desert habitats where they can be semi-arboreal. We propose common names for all species but as these names are not Entomological Society of America (ESA) approved "formal" common names, they can't be used in any ESA publications, as we discovered in Weissman *et al.* (2009), when we attempted to call *G. assimilis*, which, for years, has been called the Jamaican field cricket in the literature, in that article's title.

***Gryllus* cricket rearing techniques.** Nymphs and adults were housed in cardboard or plastic pint containers with screen tops. Organic romaine lettuce, dried oatmeal and cat food, and fish food flakes were provided for food and water (Wineriter & Walker 1988). Adult females of most species readily oviposit into moist vermiculite or fine sand, which must be kept moist but not flooded for egg development. Most species do not require special diapause conditions, with the exception of the egg diapausing *G. pennsylvanicus* and *G. ovisopis* which fare better with a 60-day diapause period at ~4^{o}C.

Parasitoids. Tachinid fly larvae sometimes emerge from adult male, field-collected individuals. The larvae quickly pupate after emergence, and can often be reared to adult flies by maintaining the pupae on moist papertowel at ~25^{o}C. It is best to clean the pupa of any bits of cricket food or frass adhered to it first. Alternatively, burying the pupae 1 cm deep, in dry sand, is also effective. In our experience, most are *Ormia ochracea* (Bigot) or, less commonly, *Exoristoides johnsoni* Coquillett (see O'Hara & Gray 2004; Paur & Gray 2011b).

Determination of egg diapause. Presence or absence of egg diapause is easily determined in *Gryllus* and is important for phylogenetic considerations. Adult field-collected females, assumed to be mated when singing males are present in the population, were kept in pint cardboard containers with plastic petri dishes measuring 60 mm diameter and 20 mm deep and filled with fine, sterilized sand slightly moistened throughout with filtered water. After two weeks, the dishes were removed from the female's container, the top layer of contaminants cleaned off the sand, a lid was placed, and the eggs were incubated at room temperature. Sand moisture was replenished as needed. One of four events occurred:

1. The eggs never hatch or become black with fungus. Assuming there are eggs present, and they are usually visible through the sides of the petri dish, perhaps the female was a virgin or the eggs became infected before development was completed.
2. There is a good hatch starting around 20 days after the female is removed and continuing for about 7 days. These events indicate the absence of an obligate egg diapause.
3. There is a very slow hatch, sometimes only one or two per day, starting some 70 days after the female is removed and continuing for several weeks thereafter. Such events correspond with an obligate egg diapause. Placing eggs that must diapause in a refrigerator at 2–4°C for 2 months, after being kept at room temperature for 30 days post oviposition, is also effective for breaking an egg diapause and results in a more synchronous egg hatch.
4. There is a combination of hatching, starting around 20 days after the female is removed, as is seen in taxa without an egg diapause, and hatching continues, at low rates, for several months after, a condition seen in taxa with an obligate egg diapause. This actual situation is discussed under *G. firmus* (p. 54).

Killing, measuring, and preserving. Crickets were killed in the field in cyanide and in the laboratory, usually by freezing after being recorded or given the opportunity to oviposit. In either case, specimens were then immediately measured for hind femur, cercus, and ovipositor lengths. Body length was not measured because this metric can change by as much as 6–8 mm upon drying, especially in gravid females, but also in males (see further discussion under *G. veletis,* p. 132). For subsequent measurement comparisons between species, we used "fixed" metrics such as hind femur length, teeth in file, etc. Interestingly, Alexander & Bigelow (1960, p. 339) found body length to be more valuable than other fixed lengths such as femur length, width of pronotum, etc. We found hind femur length a best predictor—see discussion in the *G. firmus*—*G. pennsylvanicus* Hybrid Zones section, p. 61.

The right tegmen was removed from males by cutting at its base, placed in a gelatin capsule, and subsequently placed on the same pin as the male, after he has dried. A middle or hind leg is removed from freshly killed individuals and placed in 95 or 100% ethanol for later DNA analysis (the front legs have tympana which may be taxonomically useful and best kept with the specimen). After much trial, good color preservation was obtained by pinning specimens in a Schmitt box and drying them as quickly as possible in the car by placing the closed Schmitt box in the sun. We find that preserving specimens in 70% ethanol requires more museum space, does not preserve the DNA for more than a short time, and makes comparison between specimens more difficult. Plus, colors are not well maintained. Freeze drying specimens, in a home kitchen freezer, can preserve colors in most taxa (although not in reddish colored *G. personatus*) but then attempting to measure cercus length in these dry specimens can easily result in breakage. Placing specimens in alcohol usually results in damage to cerci unless done extremely carefully with few specimens per container.

Many sites had to be collected more than once to obtain additional specimens for analysis, once the importance of cercus length was realized, and when the usefulness of DNA analysis became apparent.

Cerci length. Cerci length can be a valuable character, especially for species with very short cerci (e.g. *G. veletis*, *G. veletisoides,* and *G. pennsylvanicus*) or very long cerci (e.g. *G. longicercus*). But, and the reason multiple specimens should be collected for measurement, is that if a cercus is broken during molting, attempted predation, trauma, etc., such a cercus can partially regenerate during two or more subsequent molts. These cerci, in adults, can look tapered and whole, but measuring such cerci would yield a low value. Because cercus length varies so much in field collected adults, absolute length is a character of different usefulness in different species. Interestingly, it was this character that first drew our attention to *G. planeta* because the cerci were 1–3 mm too long for *G. veletis* and 1–3 mm too short for *G. montis.*

In those species with short (i.e. <10 mm) cerci, most should be intact, even in older adults, and provide more reliable measurements. Medium length cerci would be from 10 to 14 mm; while long cerci would exceed 14 mm in length.

Field versus laboratory recordings. A large series of recordings can be obtained by coupling a parabola to a portable tape recorder. Recording temperature is usually taken at the parabola. In contrast, we did the following: All males were returned alive to the laboratory where recordings were done at a known temperature (as close to 25°C as possible) and where the individual singing was isolated in its own container. Both procedures are important because temperature of the cricket, if sitting on a warm rock or just having emerged from its burrow, may be very different than air temperature at the parabola, and such differences probably increase during the night (Walker 1998, p. 180). Temperature is important since several singing parameters change linearly with temp (Walker 1975, Martin *et al.* 2000). Also, several western US *Gryllus* species are frequently microsympatric at any one site, which can make association of the singing male with his song difficult. And we have water-flushed up to 14 adult *Gryllus*, of 3 species, from a single crack at a gas station in Buckeye, Arizona.

There are other advantages of not doing field recordings. 1. The researcher is freed from hauling around a bulky parabola and tape recorder. 2. More specimens, including females and nymphs, will be collected since the emphasis is not on recording males. 3. Parasitoid tachinid fly data can be obtained since already parasitized males, which were singing in the field, when returned to the laboratory for recording, will probably not sing. Their fly larvae emerge within 7–9 days of being infected and these pupated larvae can be raised to adult to identify the fly species, and get an idea of parasitism rates (see above). 4. Taciturn species, such as *G. ovisopis* and *G. cayensis,* are more likely to be collected since the researcher is walking around and looking for crickets. 5. Late instar nymphs of species that are not yet adult and, therefore, not singing, are more likely to be collected, especially if one uses an oatmeal trail. 6. Little is learned about the microhabitat preferences of singing males. 7. Eggs can be collected from females to determine egg diapause status and if raised to adult, her sons will help determine which species this female belongs to by recording their songs. This latter process is more important in Mexico than in the US because females of many sympatric Mexico taxa are morphologically similar. Additionally, eggs of unique females can be raised to yield series of males and females.

There are, of course, negative tradeoffs: 1. Not all collected males will survive a week of fieldwork and be alive when returned to the laboratory. Species that live in coastal, humid areas, even if hot, seem most sensitive to being transported to areas of lower humidity, especially those individuals going from coastal Mexico to California. 2. Some species, such as Longicercus Group males, can take weeks to start singing in the laboratory (maybe they miss their rocks?). 3. More work is involved in keeping such specimens alive in the field: we bring along organic romaine lettuce for water (and an ice chest to keep this lettuce cool), 240 ml margarine tubs with lids for housing, paper towels to decreased moisture level within the tub and to provide separation for the 2 or 3 individuals in each tub, and dry oatmeal for food. Plus, the specimens must be kept out of the desert sun when day collecting (in the hot southwest, a spare ice-chest is useful). 4. The extra hassle of carrying live crickets aboard an airplane and having to go through secondary customs when entering the US, in addition to obtaining USDA/APHIS permits to import live material (dead insects must be declared to customs officials but can generally be imported into the US without permits). 5. Some males can be heard but not collected because they are singing on the wrong side of a locked fence. With a parabola, they could still be recorded. 6. A noisy motel room full of singing crickets almost always necessitates the use of ear plugs to sleep well.

Finally, there is also an advantage of doing both field and laboratory recordings on the same male because some males sing differently with time (and see Fitzsimmons & Bertram [2011] for extensive analysis in *G. veletis*). We present two examples: A *G. armatus* male recorded in the field from Tuba City, Arizona (S91-82), had a short introductory trill at 22°C and then 2p/c. Five days later, in the laboratory at 25°C, this male sang without an introductory trill and with 2–3p/c. A *G. texensis* male recorded in the field from Yell Co., Arkansas (S93-47), had pulses grouped in 3's with a PR of 49 when recorded at 24.5°C. Nine days later, in the laboratory at 25°C, this male sang a trill with a PR of 65. Neither of these males appeared teneral upon capture. Other documented instances of significant song changes, with time, in the same male, include Alexander (1957, p. 596) in *G. pennsylvanicus* and Weissman *et al.* (2009, p. 373) in *G. assimilis.*

File analysis and measurements. Stridulatory files were examined by placing the removed right tegmen, dry mounted, under a cover slip. File teeth were counted at 500X magnification with a compound microscope. At the edge of the file closest to the midline of the cricket, the teeth can be small and indistinct (Fig. 2). We counted as teeth in this area, those "lines' that appeared with darkened edges (see Fig. 3) because scanning electron micrographs showed these teeth to have relief. Since 1982, teeth were counted in only one direction. An ocular micrometer was used to measure file length across its curve (Fig. 3c).

While we attempted to measure length of file only where countable teeth occur, a small error will likely occur unless this precise location is determined at higher power than used for general measuring. Tegminal width was measured as maximal distance from medial edge to forewing angle (start of lateral field) by using the Cu_1 vein as a landmark. While removing the tegmen damages the specimen, it permits rapid and accurate counting of teeth which results in more files being analyzed. Such removal also makes assessment of hind wing presence or absence easier since one can directly see if specimens are dealate.

We find that within a species, even when considering many localities and individuals of divergent sizes, file tooth range is generally no more than 30 teeth. A much larger range should stimulate the consideration of a cryptic species complex (but see discussion under *G. pennsylvanicus*, p. 48*)*.

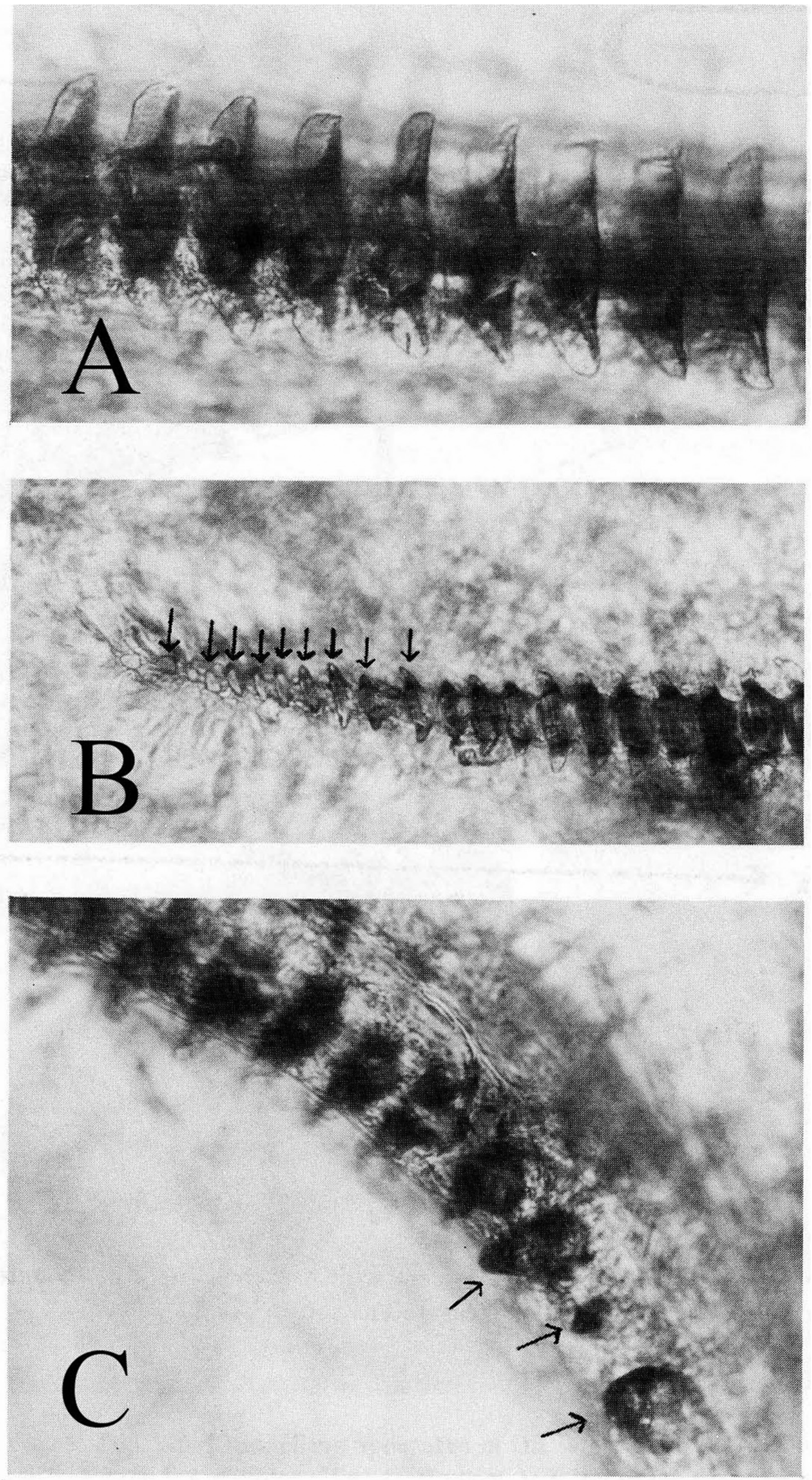

FIGURE 2. Microstructure of *Gryllus* stridulatory file. A. teeth near middle of file; B. teeth from apex of file closest to midline of cricket; only those teeth in this section with darkened edges (arrows) were counted; C. teeth from apex of file nearest lateral margin of cricket; teeth in this area may be reduced but always have relief when visualized with the scanning electron microscope.

Recording calling songs and analysis. Singing males were recorded in the laboratory in individual containers as close to 25°C as possible using a Uher 4000 Report IC reel-to-reel tape recorder with a Sennheiser K34 power module and ME40 microphone (DBW) or directly to computer (DAG) with various microphones over many years.

Early on, signals were analyzed on a Tektronix 2214 Digital Storage Oscilloscope and illustrated in RavenLite 1.0 (Cornell Lab of Ornithology). Currently, songs are analyzed using either RavenLite 2.0 or Audacity. In previous publications (e.g. Weissman *et al.* 1980), we determined pulse rate by measuring the pulse period between the last three pulses in a chirp and recording this range. Starting in 1985, DBW only measured the single interval between the last two pulses since in chirping species, this is usually the lowest value. Even in males that have four pulses/chirp, we see a decrease in the pulse rate, through the chirp, because the pulse duration increase. This situation is discussed under *G. multipulsator* (see p. 79), and in Weissman *et al.* (2009), where there can be up to 17 pulses in a chirp. In taxa that trill, we measured the intervals between several pulses because in some species (such as *G. cohni*), this interval is variable. Almost 4000 of DBW's songs have been digitized by Cornell Lab of Ornithology, Macaulay Library of Natural Sounds (ML). The corresponding ML file number is on the label of each corresponding specimen.

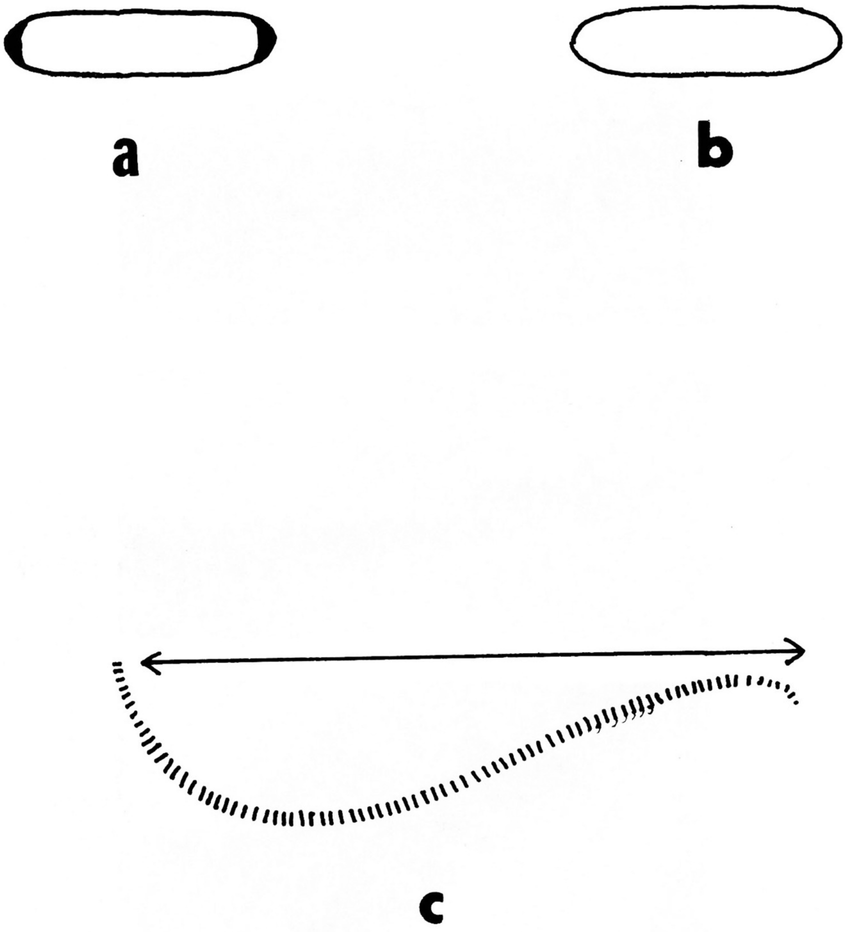

FIGURE 3. File lamella in *Gryllus* species. Only teeth with darkened edges are counted—compare a (counted teeth) versus b (uncounted teeth). Length of file is measured as shown in c.

DNA extraction, PCR amplification, and sequencing. In this publication, we report results of gene trees based on ~500 base-pairs of mtDNA sequence for the *16S Ribosomal RNA* gene (hereafter 16S) and for ~800 base-pairs of the nuclear DNA sequence of the *Ribosomal Internal-Transcribed Spacer 2* gene (hereafter ITS2). These loci were sequenced successfully for >2300 individuals for 16S and >550 individuals for ITS2. PCR primers and details can be found in Weissman *et al*. (2009) and Gray *et al*. (2016b). These gene trees were used to help verify specimen identity throughout a species' geographic range, to associate females and males, and to assist with alpha taxonomy. Appendix A (p. 269) provides GenBank Accession numbers for representative sequences for each species. A companion paper (Gray *et al.* 2019) used the Anchored Hybrid Enrichment approach (Lemmon *et al.* 2012) to resolve the phylogeny of the genus and, in some cases, to confirm that apparently polyphyletic clades in the 16S and ITS2 data are polyphyletic in the multilocus species tree (e.g. *G. montis* and *G. firmus*). In this paper, we refer to that analysis as the 'multilocus data' or 'multilocus tree'. Only rarely do we refer to additional results with the *Cytochrome Oxidase C subunit 1* gene (hereafter COI), because they proved problematic (see discussion under 'Barcoding', p. 16).

DNA analysis. In our earlier work, consensus sequences were obtained by manual alignment of forward and reverse sequences using BioEdit v.7.0.5.3 (Hall 1999) and electropherograms viewed using Chromas Lite v.2.01 (http:// www.technelysium.com.au/chromas_lite.html). Starting about 2010, we used Geneious (Biomatters, currently v. 9.0.5) both for determining consensus sequences for individuals as well as for alignment and analysis. We note that the ITS2 sequence for some species has a highly variable ATT and AC repeat region near the middle of the sequence that necessitated the consensus sequence be derived from one strand only in each direction starting at opposite ends. DNA distance data, where provided, are based on Tamura-Nei distances; the single locus gene trees discussed are Neighbor-Joining trees based on those distances, as implemented in Geneious. Although simplistic, this is appropriate as the 16S and ITS2 data analyses are not intended to be interpreted as a true phylogenetic analysis; for that we rely on the multilocus data.

Chromosomes and cytology. We have successfully used karyotypes for comparative taxonomic purposes elsewhere in the Orthoptera: grasshoppers of the oedipod genus *Trimerotropis* (Weissman 1984), various families within the Stenopelmatoidea (Vandergast *et al*. 2017), and within the Jerusalem cricket genus *Stenopelmatus* (Weissman 2001). While others (e.g. Randell & Kevan 1962, Lim *et al.* 1973) have claimed good results with US *Gryllus*, we have not examined such relationships because testes must be removed from penultimate or last instar males to find meiosis for examination. In the absence of an adult male song, this limitation, to insure accurate species identification, probably requires raising late instars from eggs and then recording the song of brothers of the male whose testes were removed.

***Gryllus* species possibly feral from the pet-food industry.** We include two non-native *Gryllus* species, *G. locorojo* and *G. bimaculatus,* in this paper because they have been sold as pet-feeder crickets by various stores in the US (Weissman *et al.* 2012). Whether or not either species will ever become established as feral populations, such as has happened with *Acheta domesticus* and *Gryllodes sigillatus,* is unknown, but we discuss specifics here so that they can be identified if such occurs.

Data analysis. All regressions were done after specimens were assigned to a particular taxon, based on song, and then parameters were regressed to show differences. Species measurements (Table 1, p. 18) are presented as ranges without means and standard deviations. We did this not just because we didn't want to have to enter massive amounts of data, but because some geographically widespread taxa have an impressive range of measurements. Should someone want to do a more detailed analysis, the actual specimens at the CAS each have an attached label with that individual's measurements on it.

Examination of male genitalia. Male genitalia are critical for separating the various genera of crickets (Randell 1964). Fortunately, there are few native US Gryllinae (*Miogryllus, Anurogryllus*, and *Gryllita* being the exceptions) that are not *Gryllus.* Most authors discuss the need to relax and then dissect out the genitalia, clear the genitalia in KOH, and then examine. A much easier technique, especially in freshly killed material, but that also works in relaxed specimens, is to simply expose the area above the subgenital plate, using a fine forceps, and the distinctive, 3 lobed epiphallus, with two lateral (L) lobes and a pointed, median (M) lobe, is clearly visible (see Fig. 4).

Value of male genitalia. Differences in male genitalia between species of *Gryllus* are so minor, if present, that we do not illustrate them. Nevertheless, they remain important for generic delineation, especially in Mexico, where many short tegmen, new species of *Gryllus* are found (Weissman & Gray, in prep). Our DNA data confirm that genitalia are not infallible in separating genera, as *Nigrogryllus sibiricus* (Chopard), from Korea, was redescribed as *Gryllus nigrohirsutus* (Alexander, 1991), but maps distinctly from *Gryllus* (Fig. 6, p. 28; and Gray *et al.* 2019).

FIGURE 4. Male genitalia, in situ, top showing the medial (M) and two lateral (L) lobes of the epiphallus. Top is overview while bottom is more magnified. C are the cerci.

Results

Summary species' measurements for morphological and song characters—see Table 1, p. 18

Barcoding DNA 'barcoding' (typically using COI) has become an important means of characterizing biodiversity in some taxa (Hebert *et al*. 2003, but see Cong *et al.* 2017). For about six years, in the early 2000's, we also PCR amplified COI, but became increasingly concerned by discordant results and, in certain taxa, e.g. the G. Lineaticeps Group and in *G. thinos*, what seemed to be clear indications of pseudogenes (electropherograms with multiple ambiguous peaks; amino acid translation resulting in stop codons). We abandoned COI and focused instead on 16S and ITS2. Because these are not translated to amino acids, we obviously could not attempt translation as a check against pseudogenes, however electropherograms were notably cleaner and ambiguous bases much fewer. Nonetheless, with these data we note that for some taxa these genes identified multiple clades as follows: For the mitochondrial 16S gene, we found 2 clades, in fresh material (see next section), in *G. fultoni, G. lightfooti, G. saxatilis, G. veletis, G. vernalis,* and *G. vocalis* and 3 clades in *G. transpecos.* For the nuclear ITS2 gene, we found 2 clades, in fresh material, in *G. firmus* (Florida and Texas)*, G. longicercus, G. navajo, G. regularis, G. saxatilis, G. sotol*, *G. transpecos, G. veletis,* and *G. vulcanus.* Needless to say, these unexpected groupings caused us to double check many specimens and/or sequence additional samples. Sometimes this was fruitful, e.g. *G. veletisoides* was first recognized as distinct based on DNA differences from *G. veletis*. Similarly, we now expect that the separate clades of *G. montis* do in fact represent genuinely separate lineages, given essentially concordant results of 16S, ITS2, and the multilocus data (concordant with respect to the existence and identity of four lineages, not necessarily with respect to the placement of those four lineages).

Old vs. fresh specimen DNA. Soon after our collaboration started in 2003, we uncovered a disturbing situation where legs removed from some dried individuals that were ~20 years old, and that had been dried quickly and never relaxed in a water saturated atmosphere, gave anomalous mapping results for the 16S gene. The gene seemed to sequence OK, but its position in the tree was unexpected given our species' identification. Because we questioned these results, more specimens were collected from the same localities and using this fresh material, individuals ran as expected and significantly different from the earlier, dry material. But what is surprising is that multiple legs from these dry specimens all mapped together in the 16S tree, apparently eliminating the possibility of contamination or mislabeling, and seemingly indicating parallel degradation changes in the DNA in these older individuals. For instance:

1. *G. saxatilis,* S98-99, G1494, G1495 from Westgard Pass, California, collected 1998 and into alcohol 2009. Compared with fresh material, S16-17, G3409, G3411, G3415, mapped differently. Sequences for old versus new samples were 98.42% identical, versus 100% identical within old and within new.
2. *G. armatus,* S91-72, G1723, 1724, 1725, 1727 from Baker, California, collected 1991 and into alcohol 2010. Compared with fresh material, S05-110, G511, G512, G513, G515, G516, G517, G518, mapped differently

Similar concerns have been raised by Chintauan-Marquier *et al.* (2015, p. 11) and Hawlitschek *et al.* (2016, p. 3 & 12).

In contrast, we had several instances where legs were taken after shorter time periods, from pinned specimens, and these sequenced well.

1. 'G. saxatilis tulare', G452, G453 from Tulare Co. (S03-28), collected 2003 and into alcohol some 2 years later, mapped the same, for 16S, as fresh G1299 (S09-34).
2. *G. leei*, G147 from type locality in Utah, collected in 2001 and into alcohol some 2.5 years later, mapped the same for multilocus DNA as did fresh material G3475.
3. *G. cohni* G101 from the type locality in Baja California Sur, Mexico, collected in 1995 and into alcohol in 2015, gave poor results for 16S but multilocus DNA mapped similar to fresh 2016-041 from Arizona. It was because of this similar multilocus mapping, and similar songs combined with the lack of distinguishing morphological characters, that helped us decide to combine both of these populations together as *G. cohni.* Because of their geographical separation, fresh specimens from the type locality in Baja California Sur should be checked, in the future, to confirm.

4. *G. cayensis*: TJ Walker sent DAG legs taken from specimens pinned dry for several decades. For ten samples, COI and ITS2 failed, but 16S appeared to sequence well for 4 collected 23-viii-1958, 4 collected 22–23-ix-1980, and two collected 13-vi-1988; 8 others failed to sequence for any loci. The ten 16S sequences were very similar and clustered together nicely, but not especially close to the multilocus sister species *G. fultoni* and *G. vernalis*.

It is because of these unpredictable results, that we tried to only use material placed into alcohol immediately upon death, including re-collecting a number of localities. Both DNA stability and the possibility of pseudogenes can detract from a 'barcoding' approach to specimen identification. It is interesting to note that the more modern 'next-generation' sequencing approaches that shear DNA into smaller pieces may actually be more robust to degraded DNA than are single locus PCR based approaches that rely on intact DNA many hundreds of base-pairs long.

What is the best metric for size comparisons? Alexander (1957) used various combinations of pronotal width, body, ovipositor and hind femur length. Alexander & Bigelow (1960, p. 339) found body length to be more valuable than other fixed lengths such as femur length, width of pronotum, etc. The Harrison group mostly used ovipositor and body length although they also provided (Larson *et al.* 2013) measurements for pronotal width and hind femur length. Gray *et al.* (2016b) used ovipositor length and pronotal width. As discussed in the *G. firmus—G. pennsylvanicus* Hybrid Zones section, p. 61, we found the highest regression coefficients of determination (R^2 values) with the use of hind femur length, suggesting that it is most highly predictive of size.

Adult body length is a poor gauge of body size in *Gryllus*, especially for females at different stages of oviposition and with different numbers of mature eggs within their abdomens. This problem would be exacerbated in those females that are pinned because of differential shrinkage associated with drying. While body length of adult males preserved in alcohol should be unaffected by preservation, we prefer pinning of both sexes to facilitate color comparison and ease of storage. Crickets that are pinned and then freeze dried should keep their body lengths intact. As an example of shrinkage associated with pinning, individuals of *G. veletis* measured immediately upon killing varied from 13.42/13.70 mm (male/female) from Mirror Pool, North Dakota (S03-52) to 29.5 mm (male from Alpine, Texas, S91-44)/26.78 mm (female from Columbus, Ohio, S03-65). Upon complete drying at room temperature, these four individuals, respectively, measured 13.50/11.69 and 23.23/21.42 mm. Weissman *et al.* (2009, p. 375) discuss a female *G. multipulsator* shrinking from 29.4 mm, when alive, to 22.05 mm once pinned and dry.

Highest numbers of sympatric and synchronic *Gryllus* species. The Arizona towns of Sedona (S94-35 & S94-36): *G. lightfooti, G. longicercus, G. montis, G. regularis, G. staccato,* and *G. vocalis*; and Ajo (S98-74): *G. cohni, G. lightfooti, G. longicercus, G. multipulsator, G. staccato,* and *G. vocalis*; along with Rio Grande Village in Texas (S16-12): *G. armatus, G. assimilis, G. personatus, G. texensis, G. transpecos,* and *G. vocalis*, all have 6 species of *Gryllus*.

Number of *Gryllus* species by state. See Fig. 5. The southwestern US states of California (12 *Gryllus* taxa), Utah (11), Arizona (14), New Mexico (12), and Texas (16) have the most species.

***Gryllus* species that periodically achieve outbreak status.** Outbreaks in *G. veletis* in Colorado, Oklahoma, and Kansas; *G. texensis* in Texas and Oklahoma; *G. assimilis* in Texas; and *G. lineaticeps* in California are documented and discussed under each species.

Life cycles and rainfall interaction. We recognize the following five general life cycles for US *Gryllus*:

1. **One generation/year**, no egg diapause. Species that overwinter as late instars with adults appearing in spring/early summer. Most taxa in this study.
2. **One generation/year**, species with an obligate egg diapause that overwinter as eggs with first adults appearing in mid to late summer. Examples are *G. pennsylvanicus*, *G. ovisopis*, and some populations of *G. firmus*.
3. **Two generations/year**. No egg diapause in either generation. Species that overwinter as late instars with first generation adults appearing in late winter/early spring with second generation adults appearing in summer. Examples are the three taxa in the Lineaticeps Group with other possibilities discussed under various species below. Also known in *G. rubens* (Capinera *et al.* 2004). Presence of a second generation is undoubtedly best determined by someone living in the area and able to continuously assess adult status throughout the spring, summer, and fall. This is especially pertinent in areas of the Southwestern US where rainfall is bimodal with winter rains and summer monsoons (July–August). Should either period be unusually dry, then field crickets will undoubtedly be affected (see below under #5, variable number of generations).

TABLE 1. Summary measurements for morphological and song characters for *Gryllus* species discussed in this paper.

		MALE						
Gryllus species	clades, subpopulations – notebook names	teeth in file	file length	teeth/mm	tegmina length	tegmina width	hind femur length	cercus length
armatus		111–145	2.55–3.9	35.1–54.2	10.9–17.9	3.35–4.9	8.59–13.8	8.6–13.96
assimilis		98–115	2.9–3.9	28.5–34.4	13.6–16	4.4–5.25	11.54–13.91	10.09–13.4
brevicaudus		107–135	2.2–3.3	38.5–47.5	8.7–12.1	3.4–4.25	9.2–11.73	8.2–10.97
bryanti	data from Weissman *et al.* 2019	165–192	3.9–4.3	40.7–45.7	14–16.1	4.7–5.3	11.89–13.9	10.91–13–84
chisosensis		168–192	3.6–4.05	45.2–48.6	10.9–11.6	4.75–5.3	11.4–13.9	14.3–17.71
cohni		126–136	2.8–3.3	40–43.9	10.4–13.4	3.8–4.5	9.95–12.4	10.2–12.2
firmus		156–233	2.8–4.9	41–67.7	9.4–17	3.75–6.1	9.87–15.62	7.4–14.82
	Gainesville, Alachua, FL	172–205	3.9–4.7	41–48.7	15.1–17	5.1–5.85	13.4–15.62	11.4–14.71
	G. #19 – only Brackettville, TX	179–212	3.2–3.9	49.7–63	9.6–12.1	4 to 5	10.1–13.1	7.4–11.15
	G. near #19 –coastal Gulf of Mexico, TX	156–203	2.8–4.9	45.4–67.7	9.5–12.3	3.85–5.1	9.87–14.03	7.8–14.13
	G. #35 – only coastal Cameron Co., TX	183–233	3.3–4.55	48.1–57.5	9.7–14.3	4.05–5.65	10.7–15.18	9.2–13.84
	G. #45 – ‘G. baggetti’ inland, coastal TX	189–232	3.4–4.9	43.6–57.9	11.2–15.4	4.35–6.1	11.76–15.59	10.26–14.82
fultoni		106–137	2.4–3.4	35.9–48.3	9.4–12.3	3.55–4.7	8.8–13.1	6.7–11.1
integer		112–161	2.4–3.5	38.2–53.2	10.5–15.6	3.5–4.65	8.47–11.92	7.01–11.8
leei		131–160	2.6–3.4	44.4–53.5	8.9–11.2	3.6–4.6	8.73–11.34	9.61–13.7
lightfooti		116–163	2.3–4.1	37.5–55.9	7.3–13.7	3.1–5.1	8.88–13.4	6.7–15.1
lineaticeps		113–153	3–4.2	30.1–46	12.3–18.8	4–6.1	9.8–14–49	8.5–14.22
locorojo	from pet food store	150–189	3.0–4.0	44.7–52.9	13.4–16.4	3.9–5.0	10.77–12.92	9.25–10.82
longicercus		155–231	2.9–4.4	44.5–64.5	8.8–14.5	3.8–5.4	9.6–13.86	11.2–19.6
makhosika		(145) 160–181	3.45–4.3	39.5–46.6	11–13.3	4.5–5.5	11–13.1	12.4–15.53
montis		111–171	2.5–4.15	31.3–52.5	8.2–13.5	3.7–5.5	9.61–13.09	8.49–13.32
	Clade 1 – multilocus species’ tree	114–131	2.5–3.2	39.7–45.6	8.5–9.7	3.9–4.3	9.77–11.26	8.69–10.43
	Clade 2 – multilocus species’ tree	120–159	2.85–3.5	37.1–52.5	9.2–10.8	3.9–4.6	9.78–12.32	9.32–13.32
	Clade 3 – multilocus species’ tree	111–171	2.95–4.15	31.3–51.3	9.4–13.5	4–5.5	9.61–13.09	8.49–13.31
	Clade 4 – multilocus species’ tree	117–150	2.7–3.6	38.8–46.7	8.2–11.6	3.7–4.8	10–12.43	9.43–12.1
multipulsator		98–143	2.8–4.6	26.7–44	12.2–16.8	3.9–5.7	10.5–15.6	8.7–15.2
navajo		133–172	3.05–4.1	36.4–53.4	9.9–13.2	4.2–5.2	9.5–13.6	10.2–15.35
pennsylvanicus		124–223	2.6–4.3	37.7–56.5	8.4–15.2	3.4–5.7	8.42–14.32	6.21–12.57
personatus		105–149	2.9–4.4	31.3–40	11.9–18.4	4.15–5.75	9.7–15	8.7–15.75
planeta		117–136	2.75–3	41–45.7	8.7–9.8	3.6–4.1	9.55–10.73	8.23–10.38

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TABLE 1. (Continued)

		MALE						
Gryllus species	clades, subpopulations – notebook names	teeth in file	file length	teeth/mm	tegmina length	tegmina width	hind femur length	cercus length
regularis		110–137	2.9–3.9	30.5–43.1	12.1–15.1	4.1–5.15	11.02–13.9	9.1–12.32
rubens		85–109	2.6–3.4	29.9–38.3	10.3–15.3	3.25–4.6	9.9–12.6	7.56–11.15
saxatilis		122–190	2.8–4.9	33.1–52.9	8.6–16	3.6–6.3	8.3–14.41	8.6–17.03
	stop 17–7 only, nearest to type locality *G. leei*	149–178	3.55–4.3	34.7–47.4	11.2–13.8	4.65–5.4	10.5–12.41	10.01–13.7
	G. #11 – Great Basin, eastern OR & WA, ID	135–181	2.8–4.4	38.1–52.9	8.6–15.2	3.6–5.5	8.9–12.99	8.8–14.9
	G. #22 – UT, northern AZ, WY	142–182	2.9–4.25	36.5–51.7	9.7–14.7	3.9–5.45	8.3–13	8.6–15.3
	G. #38 – ‘G. mojave’ – Mojave Desert	149–179	3.3–4.3	38.6–49.3	12.1–15.6	4.35–5.7	9.9–12.7	10.3–15.69
	‘G. tulare’ – Tulare Co., CA	122–174	3.4–4.8	33.1–40.5	12–15.4	4.65–6.1	11.07–14.41	11.24–14.84
	‘G. mormoni’ – around Folsom Lake, CA	131–170	3.1–3.9	38.5–48.8	9.9–13.1	3.9–5.3	9.79–13.23	10.44–14.24
sotol		146–173	3–3.8	42.3–52	9.6–11.9	3.9–5	10.43–12.79	10.5–13.86
staccato		128–174	2.6–4	37.3–54.6	10.9–17.9	3.8–4.9	9.8–15.4	9.08–14.92
texensis		95–137	2.4–3.9	29.2–42.6	11.6–16.8	3.7–5.2	9.5–14.9	7.7–13.5
thinos		91–126	2.7–3.55	29.7–41.1	8.9–11.2	4–4.85	10.69–13.23	9.7–13.83
transpecos		125–161	2.9–4.55	32–48.3	9.4–13.3	3.9–5.8	9.8–14.4	10.4–16.52
	G. #16 – Van Horn Pass only	134–160	2.9–3.8	38.9–48.3	9.9–12.3	3.9–5.1	9.8–12.12	10.6–15.49
	G. #24 – Big Bend National Park only	125–151	3.3–4.55	32.1–41.4	10.7–13.3	4.6–5.8	11.3–14.4	11.2–16.52
veintinueve		127–161	2.8–3.8	37.2–50.3	9.7–12.6	3.4–5.05	9.56–13.91	6.79–11.05
veletis		116–175	2.45–4.8	30.7–52.5	9.3–16.6	3.5–6.2	7.12–14.8	5.03–11.13
	G. #27 – CO, KN, OK, TX	122–175	3.1–4.4	31.3–50.6	11.9–16.1	4.45–6.1	9.4–13.4	6.6–10.62
	G. #30 – only Tulsa, OK	136–168	3.3–4.1	34.9–48	12–15.3	4.35–5.4	10.8–14.3	7.4–9.7
	G. #36 – western TX	122–161	3.4–4.8	31.3–39	10–16.6	5–6.2	11.15–14.8	8.5–11.13
	G. #43 – ‘G. roadside’ – NM	116–165	2.8–4.4	30.7–45.8	9.3–15.2	3.8–6	9.01–13.56	6.18–10.75
veletisoides		112–148	2.5–3.7	34.5–50	8.6–14.5	3.3–5	8.81–12.64	6.8–10.15
vernalis		142–168	2.1–2.95	58.8–71.1	7.2–8.8	3.1–3.9	9.17–10.55	7.35–8.4
vocalis		105–157	2.4–3.9	33.6–54.6	9.1–16.6	3.35–5.3	8.9–13.6	7.3–12
	G. alogus (aka G. #18)	105–135	2.4–3.3	36.6–54.6	9.7–12.4	3.55–4.55	9.8–12.9	8.1–10.55
vulcanus		159–200	2.9–3.7	48.9–59.4	9.7–11.6	3.8–4.85	10–11.8	11.53–15.2

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TABLE 1. (Continued)

		SONG PARAMETERS				FEMALE		
Gryllus species	clades, subpopulations – notebook names	pulses/chirp	chirp rate/minute	pulse rate**	dominant frequency (Hz)	cercus length	hind femur length	ovipositor length
armatus		(1) 2 (3)	975–2140	(38.5) 58.9–100	4588–5377	8.8–13.53	9.5–13	10–16.96
assimilis		(6) 7–9 (10)	30–180	40–62.5	3200–3900	10.06–13.72	12.2–14.31	15.13–18.59
brevicaudus		(3) 4–6	60–216	20.8–33	4791–5587	8.97–10.31	8.2–12.06	8–11.06
bryanti	data from Weissman *et al.* 2019	1 (2)	42–90	0.8–2.1	4863–5156	11.88	13.46	15.84
chisosensis		4, 5	90–150	13.9–16.7	4225–4859	no datum	13.16	14.53
cohni		1 (but can group)	1500–1920	21.7–41.7	4300–5283	11–12.5	11.1–12	12.7–14.5
firmus		2–5 (6)	48–225	8.6–20	3847–5300	7.8–15	10.9–17.59	11.8–23.19
	Gainesville, Alachua, FL	(3) 4	90–210	12.5–17.9	3913–4192 (4.2–4.4a)	11.8–14.2	14.04–17.59	18.42–23.19
	G. #19 – only Brackettville, TX	(3) 4–5 (6)	48–150	11.9–17.9	4531–5300	8.4–9.2	11.6–13.2	14.4–16.8
	G. near #19 –coastal Gulf of Mexico, TX	(2) 3–5 (6)	75–210	10.4–17.9	4545–5181	7.8–14.3	10.9–14.18	11.8–17.71
	G. #35 – only coastal Cameron Co., TX	3 to 4	90–210	8.6–20	4286–4879	11–13.67	14–14.8	17.4–18.9
	G. #45 – 'G. baggetti' inland, coastal TX	3 to 5	105–180	9.4–17.9	3847–4869	11.98–15	12.81–16.84	17.9–20.54
fultoni		3 (4)	240–390	33.3–58.8	4234–4489	8–10.63	11.4–13.84	11.51–15.58
integer		(1–2) 3 (4)	420–1020	44–91	4413–5139	6.9–10.49	8.4–10.92	12.1–17.75
leei		(3) 4 (5)	105–202	17.5–21.7	4017–5211	10.99–13.19	9.48–11.54	10.22–12.34
lightfooti		(2) 3–5	90–270	16.7–29.4	4419–5288	9.52–15.67	9.52–13.7	10.35–15.18
lineaticeps		5–9 (10)	78–300	31.3–83.3	3916–5071 (5500c; 4.49–5.77*)	9.3–13.93	10–16.1	10.4–16.5
locorojo	from pet food store	1 to 3	30–90	25–41.7	4646–4835	9.32–13.74	8.98–11.37	10.34–13.84
longicercus		(2) 3–5 (6–7)	60–150	7.7–14.7	4055–4864	12.18–19.96	10.5–15.49	10.47–17.00
makhosika		3–4 (5)	105–187	16.1–20.8	3929–4517	13.56–14.3	12.21–13.1	12.4–14.4
montis		3–5 (6)	60–210	16.7–26.3	3195–4541	8.9–13.9	9.83–13.8	11.35–19.80
	Clade 1 – multilocus species' tree	3–4 (5)	75–180	20.4–26.3	3562–4293	9.46–11.44	10.51–12.17	12.61–19.80
	Clade 2 – multilocus species' tree	(3) 4–5 (6)	90–180	19.2–26.3	3345–3873	10.18–12.96	10.9–12.58	12.97–17.22
	Clade 3 – multilocus species' tree	3–5 (6)	60–180	16.7–25	3195–4307	8.9–13.9	10.1–13.8	11.35–18.59

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TABLE 1. (Continued)

		SONG PARAMETERS				FEMALE		
Gryllus species	clades, subpopulations – notebook names	pulses/chirp	chirp rate/minute	pulse rate**	dominant frequency (Hz)	cercus length	hind femur length	ovipositor length
	Clade 4 – multilocus species' tree	(3) 4–5	105–210	19.2–26.3	3709–4541	10.96–12.1	9.83–12.2	12.23–16
multipulsator		(10) 11–15 (16, 17)	48–150	40–85	3976–4633	9.7–12.2	11.6–14.8	12–17.1
navajo		(3) 4–5 (6)	75–180	16.1–25	3886–4383	9–15.4	10.5–13.7	11.1–16.06
		(2) 3–5	60–210	10.9–22.7	4307–4992 (4.16–5.11b)	6.4–12.66	8.9–14.03	10.43–22.29
personatus		(4) 5–8 (9)	68–270	47.6–76.9	4200–4502 (3.78–4.47*)	10.4–17.28	10.59–15.2	12.03–19.7
planeta		3 (4)	150–202	25–27.8	3676–4562	8.46–9.83	10.54–10.87	11.36–12.12
regularis		1 (2)	1,920–3,000	29.4–50	3721–4406 (4.14–4.67*)	10.5–11.4	11.4–13.3	13.4–15.1
rubens		1	2,700–3,720	45.5–65	4580–4946 (4.18–5.88*)	8.83–11.2	11.11–12.89	12.1–16.4
saxatilis		(2) 3–5 (6–7)	48–280	13.2–27.8	3593–5288	8.4–16.5	8.46–14.6	10.2–18.2
	stop 17–7 only, nearest to type locality *G. leei*	3 to 4	98–202	17.5–21.7	3593–4097	9.74–12.98	10.7–13.35	13.77–16.55
	G. #11 – Great Basin, eastern OR & WA, ID	3–5 (6)	75–240	13.2–27.8	4184–4610	9.9–14.4	8.46–13.6	10.2–15.52
	G. #22 – UT, northern AZ, WY	(2) 3–5 (6)	84–262	16.7–27.8	3719–4094	8.4–15.73	9.8–14.2	10.7–16.3
	G. #38 – 'G. mojave' – Mojave Desert	(3) 4–5 (6)	(60) 150–180 (240)	16.1–25	4163–5137	11.2–16	10–13.6	10.8–14.92
	'G. tulare' – Tulare Co., CA	(3) 4 (5)	90–225	15.2–23.8	3747–4479	11.24–15.9	11.7–14.4	12.94–15.68
	'G. mormoni' – around Folsom Lake, CA	4 to 6	90–190	16.7–21.3	4310–4977	9.97–12.64	9.6–13.13	11.36–14.42
sotol		3–5 (6)	120–160	16.4–22.7	3463–4746	10.3–13.53	10.55–13.06	11.5–15.52
staccato		1 to 12	120–720	76.9–100	5366–6351, 5500c (4.79–5.84*)	10.32–16.65	10.72–14.59	11.85–16.9
texensis		1	3,300–5,700	62.5–90.9	4713–5825 (4.66–5.56*)	8.69–13.63	10.24–14.13	10.58–16.76

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TABLE 1. (Continued)

		SONG PARAMETERS				FEMALE		
Gryllus species	clades, subpopulations – notebook names	pulses/chirp	chirp rate/minute	pulse rate**	dominant frequency (Hz)	cercus length	hind femur length	ovipositor length
thinos		(4) 5–7	30–135	17.9–33.3	4352–4697	10.2–12.38	10.46–14.1	12.31–15.3
transpecos		(3) 4–6 (7)	75–180	18–31.3	3699–4524	11.6–17.39	10.95–14.6	10.5–14.78
	G. #16 – Van Horn Pass only	(3) 4–5 (6,7)	75–172	20–25.6	4261–4752	12.1–13.8	11.2–13.1	10.9–14.78
	G. #24 – Big Bend National Park only	(3) 4–5 (6)	82–172	20.8–30.3	3939–4944	11.6–16.2	12.19–14.6	11.9–14.4
veintinueve		2 to 4	133–255	19.2–27.8	3582–4329	6.87–9.62	10.12–12.96	10.28–14.59
veletis		(2) 3–5 (6,7)	60–345	16.1–35.7	4100–5582	5.45–11.25	7.45–15.3	7.48–17.58
	G. #27 – CO, KN, OK, TX	(3) 4–5 (6, 7, 10)	75–270	22.7–31.3	4554–5074	6.8–10.68	9.2–13.5	11.4–16.04
	G. #30 – only Tulsa, OK	(2) 3–4 (5)	180–345	22.7–29.4	4632–5558	7.8–9.6	11.7–14.3	11.3–13.9
	G. #36 – western TX	(3) 4–5	90–240	18.5–31.3	4386–5582	7.37–11.25	10.22–15.3	12.42–15.74
	G. #43 – ‘G. roadside’ – NM	(3) 4–5	60–180	20.8–33.3	4359–4952	6.61–10.78	9.54–13.7	10–17.58
veletisoides		(3) 4–5 (6)	75–270	19.2–38.5	3937–4773	7.4–10.24	9.5–12	10.5–14.77
vernalis		3 (4)	135–255	23.8–31.3	4178–5251	7.68–8.98	9.81–11.63	10.97–12.58
vocalis		(2) 3 (4–5;6–9)	270–600	23.8–45.5	4209–4908	7.7–13.18	9.8–14.1	10.2–17.9
	G. alogus (aka G. #18)	(2) 3 (4–5)	270–540	27.8–45.5	4209–4556	7.7–12.6	9.8–13.1	10.2–17.9
vulcanus		(3) 4–5 (6,7)	75–135	10.9–13.9	3952–4777	11.89–15.8	10.7–13	11.05–13.4

a from Mitra *et al*. 2011

b from Bertrand *et al.* 2013

c from Blankers *et al.*2016

* from T. Blankers, pers. comm., 2nd generation offspring

**uncorrected for temperatures between 23-27°C

FIGURE 5. Number of *Gryllus* species, by state. Kansas shows 6 + 1, because we never found *G. personatus* there, even though its type locality is "Kansas."

To have two generations/year, it appears that eggs laid by first generation females need to start hatching in April–May to have sufficient time to become adults, mate, lay eggs, and have these eggs hatch and grow to late instars to overwinter. Time from egg hatch, from first generation adults, to the appearance of second generation adults is between 2.5–3.5 months at around 25°C. Number of singing males is usually greater in the second than first generation, although tachinid parasitoids can affect such assessments (e.g. *G. longicercus* [p. 221] at its type locality of Kofa, Arizona). Second generation males may be more widespread (especially if winged) and are found in most areas where first generation males are heard. They occur in warmer weather and are also more noticeable since they can sing longer into the night due to higher ambient temperatures. If one plots number of singing males vs. time, in a taxon with two generations, a bimodal, but not necessarily totally discrete, picture probably emerges.

Yet having the time to have two generations/year doesn't mean that all species will. For instance, non-egg diapausing *G. brevicaudus* is one of the earliest singers (February/March) in the San Francisco Bay Area but never has a second generation there while two other synchronic and sometimes microsympatric Bay Area taxa (*G. lineaticeps* and *G. integer*) do have a second generation. And to show how complicated the situation can be, several *Gryllus* species appear to have an "inconsequential" second generation. For instance, we find that in some, but not most, years adult males of Bay Area *G. veletisoides* (Los Gatos, California), *G. veletis* from Utah (S04-107), and *G. fultoni* in Florida (T. J. Walker, pers. comm.), can be heard in late summer in areas that have spring singing males every year. If the females associated with these second-generation males lay eggs that promptly hatch, the resulting nymphs will not have enough time to reach the obligatory, late instar stage that permits a successful overwintering. Further discussions appear below under the relevant taxa and in Wiklund *et al.* (1991).

In practical terms, determining one vs. two generations/year is impossible without several visits during different months to the same locality during the same year to see what species are singing. In general, we assume that if we visit a locality in June and find singing males with intact cerci (indicating recent molts to adult), and perhaps some last instar nymphs, then these are first generation adults and there will not be time for a second generation that year. On the other hand, in some warm/hot southern US areas, such as Arizona and Texas, individuals becoming adults in July and August could represent the second generation.

4. **Continuous generations** with no diapause at any stage. Adults present year around with two to three generations/year. Examples are *G. assimilis*, *G. multipulsator*, and Florida *G. firmus* (Capinera *et al.* 2004).
5. **Variable number of yearly generations.** In years in the Southwest with extensive drought, there may be no summer adults heard. Maximum egg longevity in the ground is unknown for any *Gryllus* species but, in the laboratory, eggs of all Sonoran Desert taxa, incubated in moist sand and kept warm, hatch without a diapause. All *Gryllus* eggs need to absorb liquid water to develop (Hinton 1981), and this amount varies from 60–120% of the weight of newly laid eggs (Walker & Masaki 1989). Sonoran Desert areas of the Southwest receive up to 50% of their yearly rainfall during the summer monsoon period of July and August. As discussed under *G. sotol* (p. 213), *G. lightfooti* (p. 204), and *G. leei* (p. 246), populations of each of these taxa could have two generations/year, given properly timed rainfall, because nymphs grow quickly in the laboratory.

The following example shows how complicated the field situation can be: We collected the Ajo/Why area of Pima Co., Arizona, on 20-viii-1998 (S98-71, 72, & 74), and found 6 species of *Gryllus,* many in good numbers, and postulated that these were second generation adults, because of the extreme summer temperatures there, with the first generation being present in spring. We returned to this area on the following dates with these results:

A. 15-v-1999 (S99-26). Only cricket heard in the entire area was one *G. staccato*. No juveniles seen in areas that had numerous adults just 9 months earlier.
B. 1-viii-2009 (S09-102). *G. staccato* sparse, one *G. multipulsator*, two *G. vocalis* heard.
C. 8-iv-2010. Only two *G. staccato* and one *G. multipulsator* heard.
D. 17-ix-2011 (S11-99). *G. staccato* common, *G. multipulsator* sparse, and one *G. longicercus* heard.
E. 29 & 30-vii-2015 (S15-109). *G. lightfooti* and *G. staccato* scattered but not common, one *G. longicercus* heard.

We would like to see research into how long *Gryllus* eggs can remain viable in dry soil, since one predicted result of climate change is increased droughts in certain areas. This information may be particularly relevant in the Southwest since Hinton (1981, p. 177) notes that among insects "there are no kinds of eggs that will enter a state of cryptobiosis (reversible standstill of metabolism) by dehydration at physiological temperatures." There are other Southwest Orthoptera that are late maturing, in every year, regardless of rainfall: *Gryllita* crickets, *Machaerocera* and *Aztecatus* grasshoppers.

In contrast with the Sonoran Desert, California's Mediterranean type climate zone receives over 85% of total yearly rainfall during the winter months (Aschmann 1973), and any summer rainfall quickly evaporates due to warm temperatures. An adult reproductive diapause is unknown in any western US *Gryllus* but is certainly possible given its prevalence in other California Mediterranean climate Orthoptera (see Weissman & French 1980).

Categories of calling songs. Given the diversity of calling songs in western US *Gryllus*, and even more so in Mexico, and the ease with which calling song oscillograms can be displayed on a computer, we have found it helpful to have some "short hand" descriptors so that song types can be discussed between researchers and notations made in field notebooks for later reference. Such a shorthand is especially valuable when dealing with localities with high species' richness. We also use these descriptors in the "Key to males" on p. 27. We recognize four broad song categories (trillers; fast, short chirpers; fast, long chirpers; and slow chirpers) and several subcategories within North American *Gryllus* and compare them to the hypothetical oscillogram song patterns presented in Alexander (1962), although we agree with Desutter-Grandcolas & Robillard (2003) that such a classification is too imprecise to be phylogenetically useful. Our descriptions here are intended to represent what an ear in the field might hear, not what are homologous units of sound production from a physiological or neurobiological perspective.

1. **TRILLERS.** A ‘true’ trill is a long-repeated series of unpaired single pulses, however a subjective “trilling” song can be from one to three pulses/chirp. In those songs with a high pulse rate (>50 per second) or singing at temperatures exceeding 28°C, even three pulses per chirp (as in *G. integer* and *G. armatus*) can be indistinguishable, in the field, from a true, one pulse trill, especially in cases where researchers are older and their hearing somewhat diminished.

1a: 1 pulse/chirp trill, pulse rate even and varies from 30–50 (*G. regularis*) and from 55–90 (*G. rubens* and *G. texensis*). Comparable to A_1, A_2, and A_3 of Alexander (1962).

1b: 1 pulse/chirp trill, pulse rate uneven and varies from 20–40 (*G. cohni*). No comparable pattern in Alexander (1962).

1c: 2 or 3 pulses/chirp, and sometimes labeled “stutter-trillers” because of irregular chirp delivery. *G. armatus* and *G. integer* have 2–3 pulses/chirp and their songs are difficult to distinguish from an actual one pulse triller, especially if temperatures are high. *G. armatus* typically has a 2p/c and can usually be distinguished from sympatric, slower trilling *G. regularis* by ear, especially if singing at less than 20°C. Maybe comparable to B_3 and C in Alexander (1962).

2. **FAST, SHORT CHIRPERS.** A group of 3 pulses/chirp, pulse rate of 20–55, chirp rate 5–8/sec and includes *G. vocalis, fultoni*, and *vernalis*. These songs are widespread in the US and Mexico as far south as Costa Rica (DBW & DAG, unpubl.). With practice, they can usually be distinguished in the field from the trillers because the latter have faster pulse and chirp rates. However, at 30°C, which occurs frequently in the Southwestern US during summer nights, individuals of *G. vocalis* can sound like *G. armatus*. Most similar to B_3 of Alexander (1962).

3. **FAST, LONG CHIRPERS.** A group of >3 pulses/chirp, pulse rate >45, chirp rate variable and includes members of the Lineaticeps Group.

3a. Both irregular pulses/chirp and chirps/sec; pulse rate usually over 70. Found only in *G. staccato*. No comparable Alexander (1962) pattern.

3b. Regular pulses/chirp and chirps/sec. Includes *G. lineaticeps* and some *G. personatus.* B_1 of Alexander (1962).

4. **SLOW CHIRPERS.** A large, heterogeneous group of chirpers with 4 or more pulses/chirp and less than 4 chirps/second.

4a. Regular chirp rate and uniform pulses/chirp. Variable pulse rate across taxa, but consistent within a species. Many taxa and corresponds to B_1 of Alexander (1962).

4b. Long chirps greater than 8 pulses/chirp. *G. assimilis, G. multipulsator* and Brazilian *G.* n. sp. 2 (Martins 2009). This song pattern is distinguished from short bursts of trills because in long chirps, the pulse period noticeably increases during the last few pulses because pulse duration increases. Moore (1989) offers the following definition of a chirp: “a short, discrete group of simple or complex pulses of sound, usually of less than 0.5 s duration.” By extension, trills would be a discrete group of pulses more than 0.5 s duration. Blankers *et al.* (2015) break chirps v. trills at 20 pulses, i.e. <20 pulses = chirp (e.g. *G. multipulsator* is a ‘chirper’) whereas >20 pulses = trill (e.g. lower end of trill duration in *G. texensis*). But neither of these definitions captures all of the variation in *Gryllus* songs, and so we propose the following operational guidelines:

CHIRP	TRILL
fairly constant number of pulses/chirp	more variable pulses/group
fairly regular interval between chirps	more variable intervals
inter-chirp intervals usually short	inter-group intervals can be short or long
oscillogram pulse amplitude increases through chirp	oscillogram pulse amplitude unchanged through group
pulse duration increases through chirp	pulse duration constant through group
pulse rate decreases through chirp	pulse rate constant through group
pulse period increases through chirp	pulse period constant through group

The fairly low variability in pulses/chirp and in intervals between chirps for chirpers applies both to variation within and among individuals, as compared to variation in trillers.

The situation of increasing pulse period and increasing pulse duration through the chirp is well illustrated in *G. multipulsator* (see Fig. 69, p. 81), where the average pulse rate starts at >100 for pulse #1 and decreases to <60 for pulse #13. A similar trend is seen in most chirps of more than 4 pulses in most *Gryllus* species (Bennet-Clark 1989, p. 223; Weissman unpubl.).

Systematics and bionomics

Alphabetical list of cricket species discussed in this paper

Acheta domesticus (Linnaeus)	29
Gryllus armatus Scudder	110
Gryllus assimilis (Fabricius)	74
Gryllus bimaculatus De Geer	32
Gryllus brevicaudus Weissman, Rentz, & Alexander	36
Gryllus bryanti Morse	40
Gryllus cayensis Walker	130
Gryllus chisosensis Weissman & Gray, n. sp	187
Gryllus cohni Weissman	162
Gryllus firmus Scudder	54
Gryllus fultoni (Alexander)	126
Gryllus integer Scudder	101
Gryllus leei Weissman & Gray, n. sp	246
Gryllus lightfooti Weissman & Gray, n. sp	204
Gryllus lineaticeps Stål	168
Gryllus locorojo Weissman & Gray	34
Gryllus longicercus Weissman & Gray, n. sp	221
Gryllus makhosica Weissman & Gray, n. sp	250
Gryllus montis Weissman & Gray, n. sp	197
Gryllus multipulsator Weissman	79
Gryllus navajo Weissman & Gray, n. sp	254
Gryllus ovisopis Walker	41
Gryllus pennsylvanicus Burmeister	48
Gryllus personatus Uhler	176
Gryllus planeta Weissman & Gray, n. sp	149
Gryllus regularis Weissman & Gray, n. sp	97
Gryllus rubens Scudder	83
Gryllus saxatilis Weissman & Gray, n. sp	233
Gryllus sotol Weissman & Gray, n. sp	213
Gryllus staccato Weissman & Gray, n. sp	181
Gryllus texensis Cade & Otte	90
Gryllus thinos Weissman & Gray, n. sp	42
Gryllus transpecos Weissman & Gray, n. sp.	216
Gryllus veintinueve Weissman & Gray, n. sp	70
Gryllus veletis (Alexander & Bigelow)	132
Gryllus veletisoides Weissman & Gray, n. sp	191
Gryllus vernalis Blatchley	119
Gryllus vocalis Scudder	153
Gryllus vulcanus Weissman & Gray, n. sp	229

Key to adult males of native US *Gryllus*. Pulse and chirp rates are for males at about 25°C.

1	Calling song absent	2
-	Calling song present	3
2	Known only from pinelands of Everglades National Park	*G. cayensis*
-	Known from southeastern US exclusive of southern Florida	*G. ovisopis*
3	Song a regular or irregular trill or unable to tell if 1, 2, or 3 pulses/chirp	4
-	Song composed of discrete chirps	9
4	Song a regular trill with pulse rate < 65	5
-	Pulse rate > 65 if a trill or grouped into 2 or 3 pulses, > 400 chirps/minute	7
5	Known from eastern Texas east to Atlantic Coast	*G. rubens*
-	Only known west of 100th Meridian	6
6	Song an even, regular trill, Arizona, New Mexico, western Texas	*G. regularis*
-	At least parts of song an irregular trill, Arizona only	*G. cohni*
7	Song a regular trill, pulse rate > 65, western Texas to western Florida	*G. texensis*
-	Song with pulses grouped into 2 or 3	8
8	Song usually without introductory trill, 2 or 3 pulses per chirp	*G. integer*
-	Song usually with introductory trill, usually 2 pulses per chirp	*G. armatus*
9	Slow chirping (3 or fewer chirps/sec), long chirps (> 6 pulses)	10
-	Song with > 3 chirps/sec.	11
10	Chirps with 10–17 pulses, California, Arizona, southern Nevada	*G. multipulsator*
-	Chirps with 6–10 pulses, Texas and southern Florida	*G. assimilis*
11	Fast chirping (> 3 chirps/sec), long chirps (> 5 pulses/chirp)	12
-	Not as above	14
12	California and Oregon only	*G. lineaticeps*
-	Not California or Oregon	13
13	Chirps in 1 male regular and/or irregular, pulse rate > 75	*G. staccato*
-	Chirps always regular, pulse rate < 75	*G. personatus*
14	Fast chirping (> 3 chirps/sec), short chirps (< 4 pulses/chirp)	15
-	Not as above	18
15	Head narrower than pronotum	16
-	Head wider than pronotum	17
16	Live adults with yellow cerci, < 49 teeth/mm, pulse rate > 33	*G. fultoni*
-	Live adults with black cerci, > 58 teeth/mm, pulse rate < 33	*G. vernalis*
17	Restricted to Oklahoma and Texas, chirp rate < 250/minute	*G. veintinueve*
-	Known from western Texas to Pacific Coast, chirp rate > 250/minute	*G. vocalis*
18	Slow chirping (< 4 chirps/sec), short chirps (3-6 pulses/chirp) with individual pulses almost countable at 25°C	19
-	As above but pulses not countable	23
19	Known only from Chisos Mts., Big Bend National Park, Texas	*G. chisosensis*
-	From elsewhere	20
20	Restricted to old lava flows in New Mexico	*G. vulcanus*
-	From elsewhere	21
21	West of 100th Meridian, with rocks, no egg diapause	*G. longicercus*
-	Almost never with rocks, with egg diapause (except Florida and Texas)	22
22	Generally coastal US from Texas to Florida and along eastern seaboard	*G. firmus*
-	Inland across much of US, pulses countable only in Colorado, Nebraska, Oklahoma, Missouri, and Kansas	*G. pennsylvanicus* (in part)
23	Restricted to coastal Texas, < 126 file teeth	*G. thinos*
-	Not as above	24
24	Known only from old lava beds in west-central Utah, cerci longer 9 mm	*G. leei*
-	Not as above	25
25	Known only from Organ Mts., New Mexico, above 1675m	*G. sotol*
-	Not as above	26
26	Known only from Badlands National Park, South Dakota, cerci longer than 10 mm	*G. makhosica*
-	Not as above	27
27	Known only from central California west of Sierra Nevada, tegmen with unique lateral yellow-orange area, ovipositor < 11 mm	*G. brevicaudus*
-	Not as above	28
28	Known only from above 1830m in the Davis Mts. of western Texas, cerci 8.3–10.4 mm in length, under tree cover	*G. planeta*
-	Not as above	29
29	Known only from Oregon and California west of Sierra Nevada, not with rocks, cerci < 10.2 mm long	*G. veletisoides*
-	Not as above	30
30	Known only from western Transpecos Texas, associated with rocks, < 160 file teeth	*G. transpecos*

-	Not as above	31
31	Known only from red sandstone Painted Desert in southeastern Utah and northcentral Arizona	*G. navajo*
-	Not as above	32
32	Known only from sky islands in Arizona and along Arizona-New Mexico border, from 1280m–2560m, under tree cover, cerci always shorter than ovipositor tip in situ	*G. montis*
-	Not as above	33
33	Widespread western species with medium to long cerci, associated with rocks	*G. saxatilis*
-	Not as above	34
34	Widespread Southwestern grassland species, frequently arboreal	*G. lightfooti*
-	Not as above	35
35	Widespread, short cerci, spring and early summer adults, no egg diapause, grassland species.	*G. veletis*
-	Widespread, short cerci, late summer and fall adults, egg diapause, grassland species.	*G. pennsylvanicus* (in part)

Taxonomic Groups of US *Gryllus*

What follows is a treatment of each species considered here arranged together as Groups. Mostly these Groups are comprised of sister taxa as determined by the multilocus DNA analysis, but some Groups are closely related without actually being a monophyletic set of sister species (e.g. *G. chisosensis* and *G. veletisoides*); some are considered together despite being polyphyletic (e.g. the Montis Group); and the “Pet Store Group” of commercially reared crickets is simply a collection of species without regard to taxonomy or phylogeny. This arrangement thus generally follows the concatenated analysis of multilocus data from Gray *et al.* (2019), a summary version of which is given here (Fig. 6).

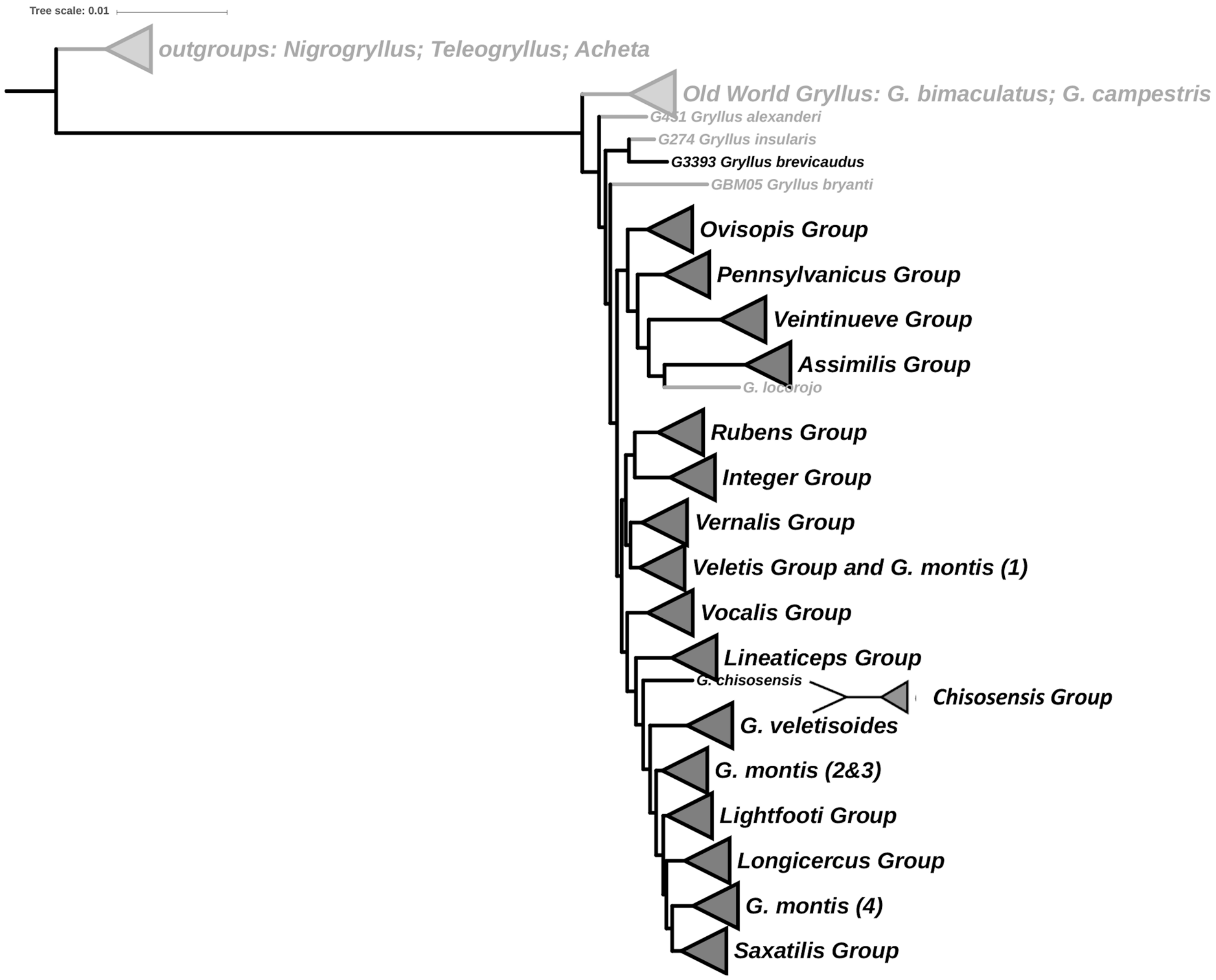

FIGURE 6. Phylogenetic arrangement of taxa redrawn from Gray *et al.* (2019). Taxa in grey text are either not considered here because they are not US *Gryllus*, or are considered only briefly (Pet Store Group; *G. bryanti*).

“The Pet Store Group”

Acheta domesticus (Linnaeus), *Gryllus bimaculatus* De Geer, *Gryllus locorojo* Weissman

A collection of species included here because they are, or were commonly used in the US commercial pet store trade as feeder crickets. We consider them because one of them, *Acheta domesticus*, has already established feral populations in natural habitat in the western US, and both *G. bimaculatus* and *G. locorojo* could potentially become invasive. A currently common pet store cricket, *Gryllodes sigillatus* (F. Walker) is not discussed as it is easily distinguished and, although feral, appears to be confined to urban and suburban areas. Additional details of the pet store crickets can be found in Weissman *et al.* (2012).

Acheta domesticus (Linnaeus)

(European) House Cricket
Figs 7–10

Although not a *Gryllus* and not native to the US, *Acheta domesticus* is widespread in the western US and seems to be expanding its range (Weissman *et al.* 1980, 2012). Additionally, calling songs of feral males, anecdotally, appear to be getting louder (even as we grow older and our hearing gets worse) and the chirps seemingly more regular, thus sounding more like a native *Gryllus* species (Weissman *et al.* 2012). Because we have been spending more time locating these feral males, for identification purposes and to confirm that they are not a *Gryllus*, we include our collection data here (see Fig. 10). Many more eastern US collection sites are given in Walker (2019). Interestingly, this species appears not to have established permanent colonies in Australia, despite being introduced (Rentz & Weissman 2017).
Distribution. Worldwide cosmopolitan cricket.

FIGURE 7. Color variation found in wild *A. domesticus.* Both individuals from Orange Co., CA (S16-12).

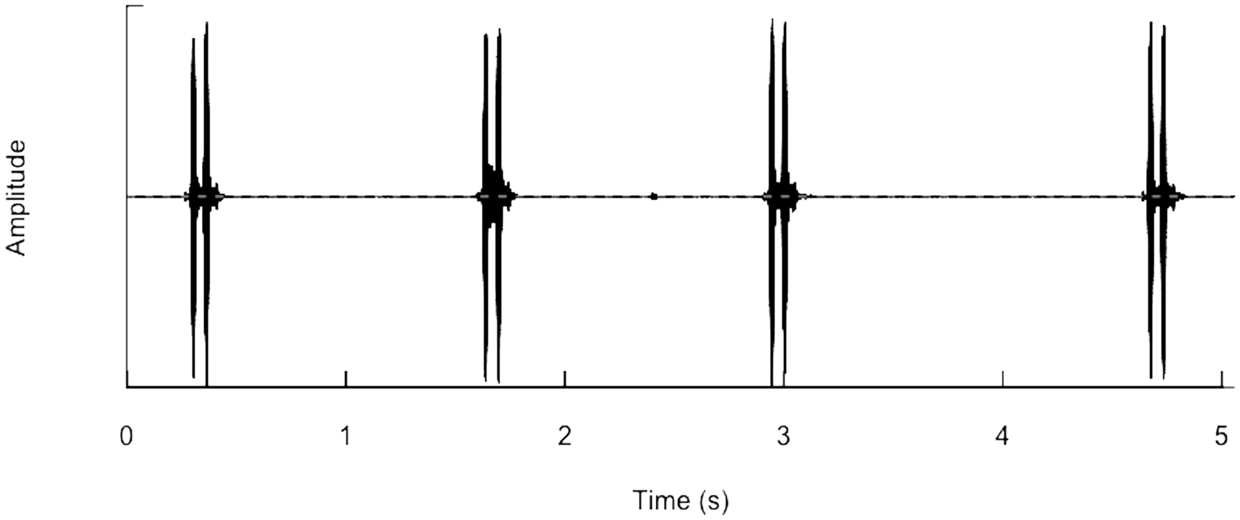

FIGURE 8. Five second waveform of calling song of *A. domesticus*: (R11-133) Telegraph Pass, AZ (S11-94), at 24°C;

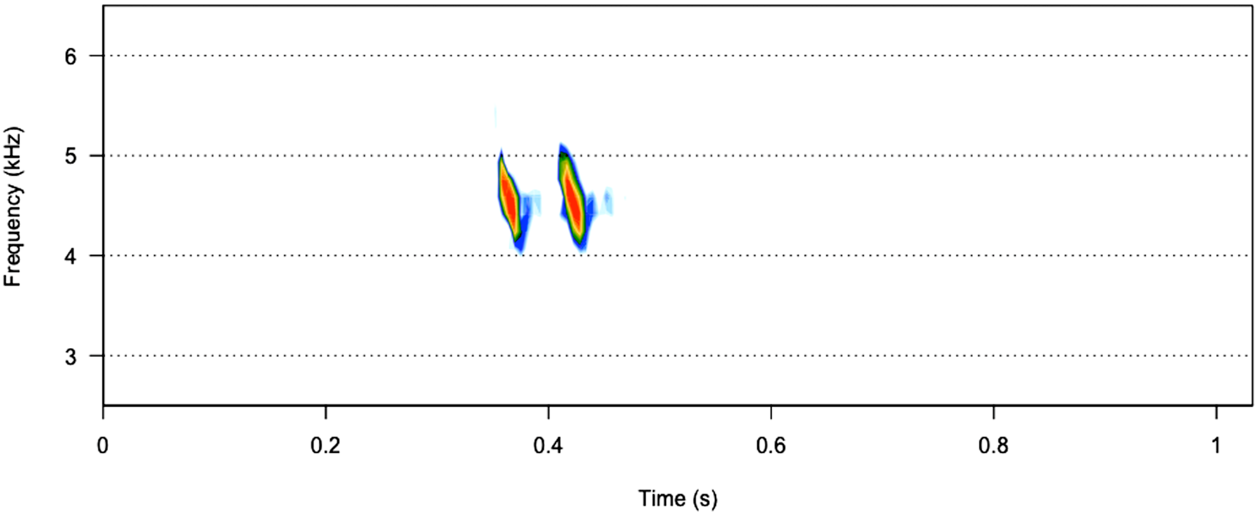

FIGURE 9. One second spectrogram of *A. domesticus*, same male as in Fig. 8.

Recognition characters and song. Usually straw colored (but some individuals dark—see Fig. 7), always with long hind wings, unless apterous (Weissman & Rentz 1977b, Walker 1977), and a distinctive, irregular, dark transverse bar extending between the eyes. A similar bar is seen in introduced *Gryllodes sigillatus* but this other cricket always has short hind wings, longer cerci, more flattened appearance, and quicker evasive movements. *Song* (Figs. 8, 9; R11–133), in *A. domesticus,* 2–4 (usually 2–3) pulses/chirp delivered at 40–200/minute, dominant frequency 4500–5000 Hz. Compare with the more rapid chirp rate of *G. sigillatus* on SINA (Walker 2019).

Geographic range. Fig. 10.

Specimens examined. **Arizona.** *La Paz Co.*, Quartzite, 26-vi-1980 (S80-46); 27-vii-1981 (S81-33); 14-ix-2011 (S11-89). *Maricopa Co.,* Buckeye, gas station, 840', 18-ix-2011 (S11-102). Gila Bend, 712', 1-viii-2009 (S09-103); 30-vii-2015 (S15-111). Goodyear, 31-vii-1981 (S81-46). Scottsdale, 22-iv-1985 (S85-41). Hwy 85 10.5 m N Ajo, 1240', 20-viii-1998 (S98-73). *Pima Co.,* Ajo, 1720', 20-viii-1998 (S98-72, 98-74). Catalina, 2940', 18-viii-1998 (S98-65). Organ Pipe National Monument, 1-ix-1961, D.C. Rentz. Outskirts Tucson on Saguaro Rd., 31-vii-1981 (S81-35). *Yuma Co.,* Telegraph Pass, 676', 15-ix-2011 (S11-92, S11-94). **California.** *Imperial Co.,* Algodones Dunes 2.6 m NW Glamis off Ted Kipf Road, 240', 15-ix-2011 (S11-91). El Centro, 27 & 28-i-1959, Kirschbaum, D.C. Rentz. *Inyo Co.,* Death Valley National Park, Furnace Creek, 5-vi-1983 (S83-60); 5-v-2003 (S03-36). *Kern Co.*

Bakersfield near Cal State Bakersfield, 5-viii-1980 (S80-70). *Los Angeles Co.,* CSU Northridge campus, 8-v-2003 (S03-47). Westlake Village, 22-v-1982. *Orange Co*., Crystal Cove, 7-vii-1976. Tustin, 20-vii-1975; 12-vi-1976. *Riverside Co.,* Blythe, 26-vi-1980 (S80-47). Corn Springs, 1-ix-2001; 18-iv-2010, 3-ix-2012; 10-iv-2015. Joshua Tree National Monument, Cottonwood Springs, 3000', 7-viii-1988 (S88-78). Palm Springs, 2-iv-1989 (S89-8). UC Riverside campus, 15-vii-2001 (S01-96). Box Canyon Rd 10.9 m E Mecca, 800', 7-viii-1988 (S88-76). *San Bernardino Co.,* Baker, 1000', 4-viii-1991 (S91-72). Barstow, 2300', 22-vii-2016 (S16-28). Havasu Lake, 460', 13-ix-2011 (S11-84). Newberry Springs, 2160', 16-viii-1998 (S98-59). Route 66 at intersection I40, truck stop. 2103' 23-vii-2016 (S16-32). Ludlow exit off I40, 2060', 16-viii-1998 (S98-60). San Bernardino Mts., Mill Creek Ranger Station, 2800', 25-vii-1981 (S81-27). *San Diego Co.,* Borrego Springs, 8-viii-1988 (S88-83). *Santa Clara Co.,* Los Gatos, 10-ix-1990. Stanford University, Lake Lagunita, 26-viii-1983 (S83-113). *Shasta Co.,* Shasta Lake, Bridge Bay Road yacht area, 4-viii-1980 (S80-67). **Kansas.** *Sedgewick Co.,* Wichita, 9-viii-1980. **Nebraska.** *Red Willow Co*., McCook, 28-viii-1989 (S89-74). **Nevada.** *Clark Co.,* Cottonwood Cove, 750', 24-vi-1980 (S80-36); 26-vii-1981 (S81-31). **Oregon.** *Benton Co*., Corvallis, 18-i-1969, Tao. **Utah.** *Utah Co.,* Provo, 1-ii-1965, A.T. Whitehead. **Texas.** *Brewster Co.,* Big Bend National Park, Rio Grande Village, 1860', 28-v-2016 (S16-12). *Tarrant Co.,* Grapevine Lake Dam, 23-v-2001 (S01-48). *Tom Green Co.,* San Angelo, 11-vi-1988 (S88-30). *Val Verde Co.,* Del Rio, 1000', 27-vi-1986 (S86-48).

DNA. Multilocus 2017-045 (Gray *et al.* 2019) shows that *A. domesticus* is more closely related to *Nigrogryllus* than to *Teleogryllus*.

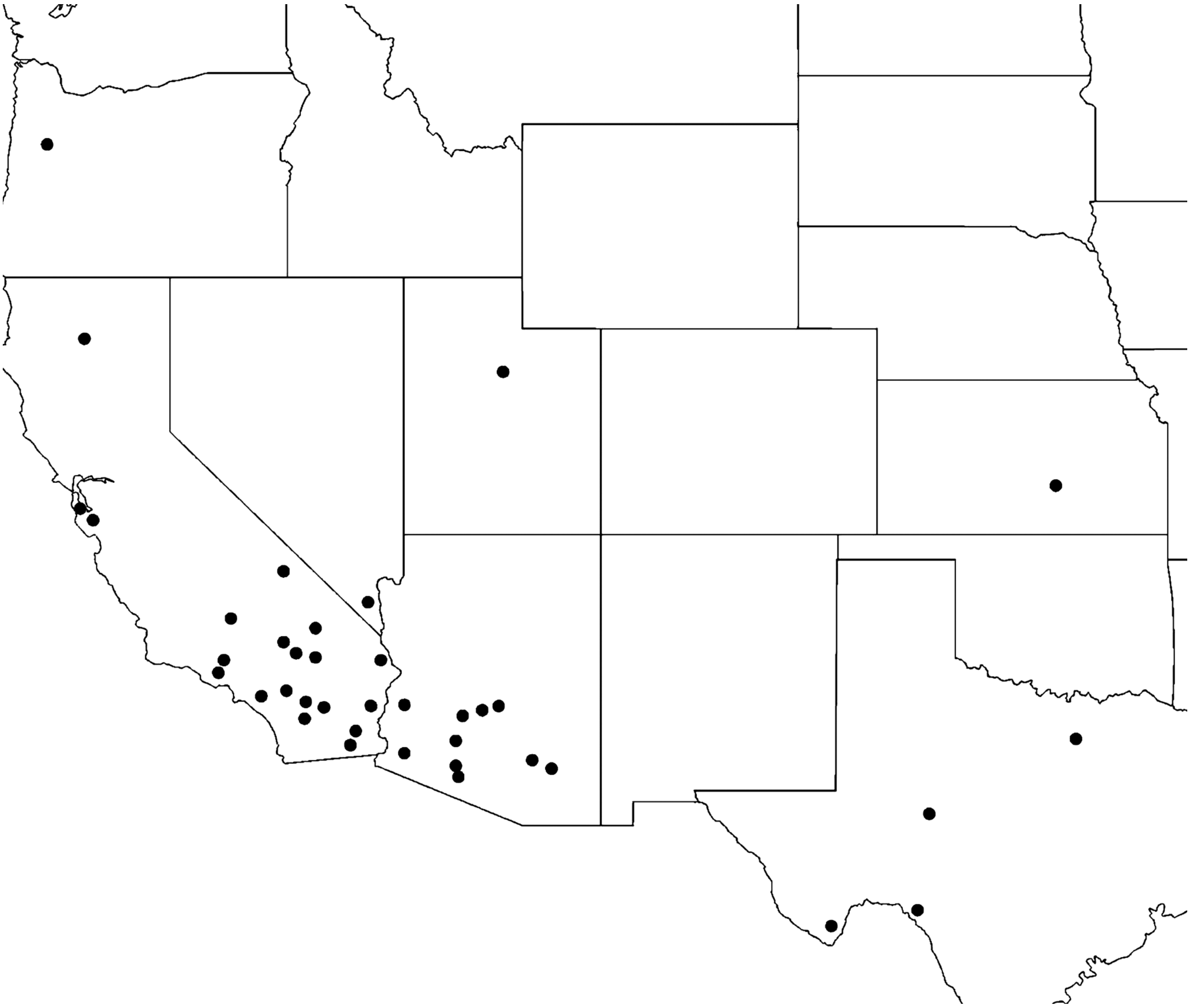

FIGURE 10. Populations of *Acheta domesticus* that we studied.

Discussion. Several of the above localities are natural habitats away from human disturbance—e.g. Algodones Dunes (S11-91), Telegraph Pass (S11-92), Box Canyon Road (S88-76), 10.5 m N Ajo (S98-73), which is why we recommended (Weissman *et al.* 2012) a switch to *Gryllodes sigillatus* by the pet-feeder industry, because the latter does not appear to readily exist away from human disturbance. Olzer *et al*. (2019) compared behavior of feral and commercially reared *A. domesticus*.

Gryllus bimaculatus De Geer

Two Spotted or Black Field Cricket
Figs 11–13

1773. *Gryllus bimaculatus* De Geer. Mémoires pour servir à l'histoire des insectes 3:521. Type locality: Africa, West Tropical Africa, Mali, Mourdiah. Type deposited in ANSP.

Recognition characters and song. Apparently the most widely, naturally distributed *Gryllus* species found from the tip of South Africa north into Europe and east as far as Thailand (Otte & Cade 1984). This is a medium-large sized, short hind femur, usually pure black, short or long hind winged cricket with a shiny pronotum. Most males have a pale, yellowish area (Fig. 11a) at the base of each tegmen where they attach to the pronotum. Adult females may be without or have a slight indication of pale tegminal areas (Fig. 11b). Brown males are known (see Fig. 11a, and Otte and Cade 1984). *Song* (Figs. 12, 13; R12–14) with 2–6 pulses/chirp, usually 3–5 chirps/second, pulse rate 21–28 at 25°C, dominant frequency 4633–5816 Hz in pet store specimens.

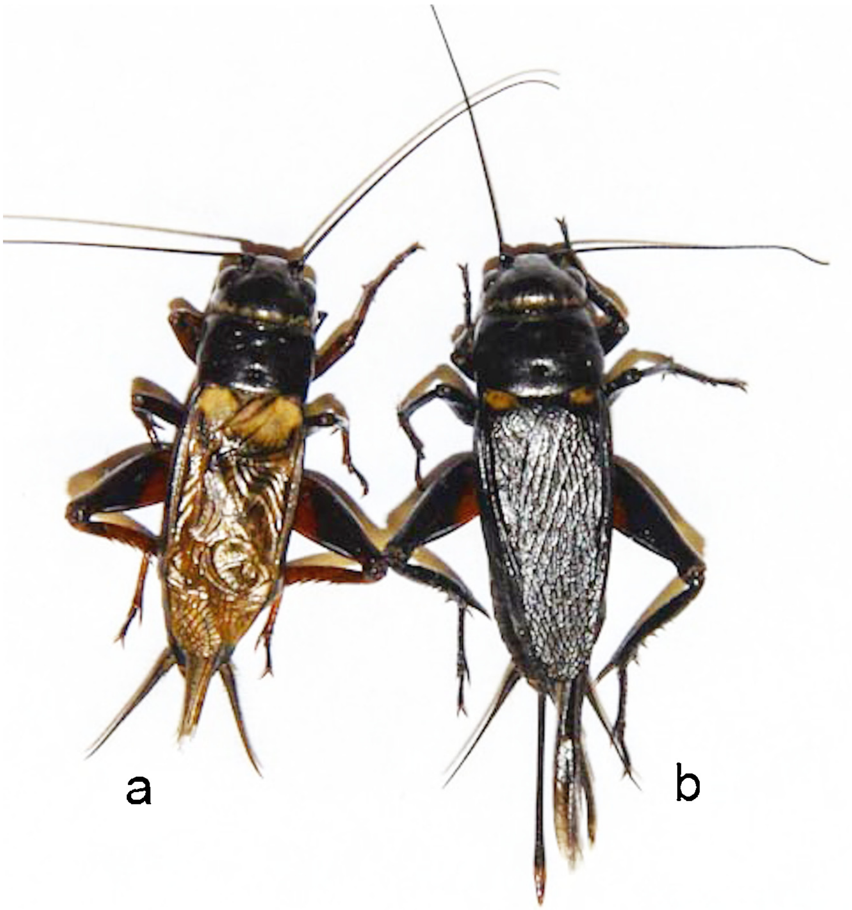

FIGURE 11. Male (a) *G. bimaculatus* with obvious bilateral, pale-yellowish area at base of tegmina. Female (b) with similar, but smaller areas. Both specimens from commercial pet store.

Discussion. As discussed in Weissman *et al*. (2012), this is one of two non-native US *Gryllus* (the other being *G. locorojo*) that was being commercially raised in 2012 and shipped to US pet food stores for sale to the general public. Such activities will invariably result in the release, either by accident or on purpose, of this species into the environment, similar to what has probably occurred with *Acheta domesticus* (Weissman *et al*. 1980). The effect of such releases is unknown, as is whether or not these crickets can survive and multiply outside of commercial farms. We discussed (Weissman *et al.* 2012) why regulatory oversight by federal and state regulatory agencies has been inadequate and suspect that such surveillance has only gotten worse, since 2012, given continued tightening US federal budgets and malaise from both state and federal regulators. Additionally, we have no idea what the current commercial status is for these two species because they are more aggressive and cannibalistic than the replaced *A. domesticus*, and tend to bite the lizard they are usually being fed to. Thus, the pet-food industry may be voluntarily replacing *G. bimaculatus* with the ecologically preferred (Weissman *et al.* 2012) *Gryllodes sigillatus*. We present *G. bimaculatus* here in case they establish feral populations encountered by an inquiring biologist.

DNA. Multilocus 1999-101, from Zimbabwe, maps closest to Old World *G. campestris* Linnaeus, and at the base of the *Gryllus* tree along with several other *Gryllus* taxa (Fig. 6, p. 28). This position agrees with that seen in more limited 16S mapping (see Fig. 6 in Weissman *et al*. 2012).

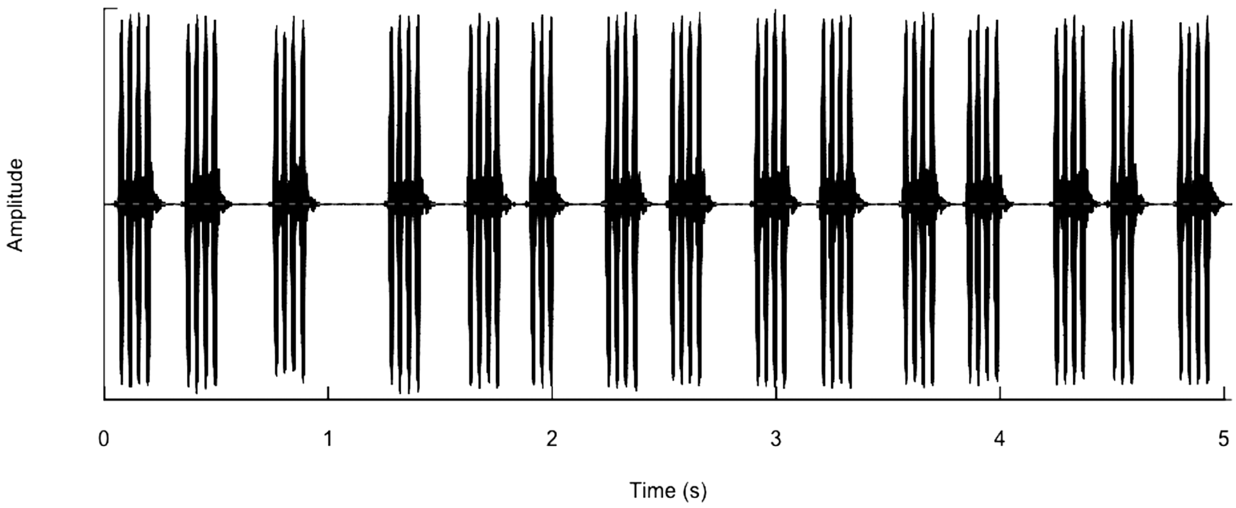

FIGURE 12. Five second calling song of *G. bimaculatus* (R12-14) commercial pet store, at 25°C.

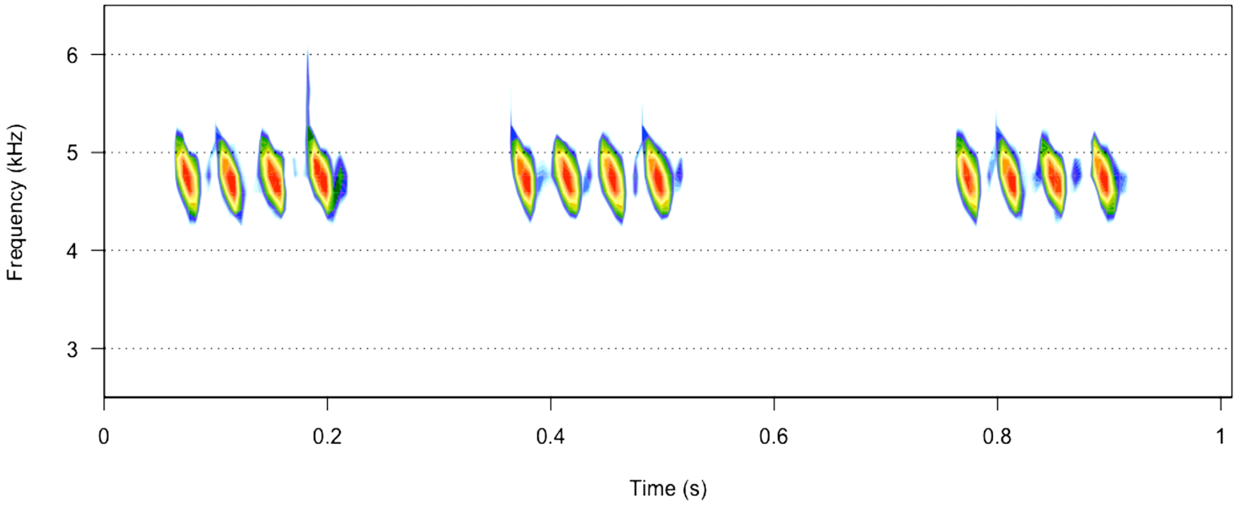

FIGURE 13. One second spectrogram of *G. bimaculatus*, same male as in Fig. 12.

Gryllus locorojo Weissman & Gray

Crazy Red Field Cricket
Figs 14–16, 54, 62, Table 1

2012 *Gryllus locorojo* Weissman & Gray. Zootaxa 3504: 67–88. Type locality: USA: California, Los Angeles Co., Compton, Rainbow Mealworms. Type deposited in CAS, Entomology type #18657.

Distribution. Known only from pet food stores and commercial cricket farms in North America, Europe, and western Asia. Original locality still unknown, but most likely somewhere in South America, perhaps Ecuador (Weissman *et al.* 2012).

Recognition characters and song. Body size medium-large, long or short hind wings, reddish/brownish colored (Fig. 14), head frequently with three or four longitudinal stripes. *Song* variable (Figs 15, 16; R12–3), usually 2 (range 1–3) p/c, less than 1 chirp/second, PR 25–42 at 25°C.

FIGURE 14. Head on view of male *G. locorojo* showing head stripes.

Discussion. We repeat here the same concerns as under *G. bimaculatus.* As discussed in Weissman *et al*. (2012), this is one of two non-native *Gryllus* (the other being *G. bimaculatus*) that was being commercially raised in the US, in 2012, and shipped to US pet food stores for sale to the general public. Such activities will invariably result in the release, either by accident or on purpose, of this species into the environment, similar to what has probably occurred with *Acheta domesticus* (Weissman *et al.* 1980). The effect of such releases is unknown, as is whether or not these crickets can survive and multiply outside of commercial farms. We discussed (Weissman *et al*. 2012) why oversight by federal and state regulatory agencies is inadequate and suspect that such surveillance has only gotten worse, since 2012, given continued tightening US federal budgets and malaise from both state and federal regulators. Additionally, we have no idea what the current commercial status is for these two non-native species because they are more aggressive and cannibalistic than the replaced *A. domesticus*, and tend to bite the lizard they are being fed to. Thus, the pet-food industry may be voluntarily replacing *G. locorojo* with the ecologically preferred (Weissman *et al*. 2012) *Gryllodes sigillatus*. We present *G. locorojo* here in case they establish feral populations encountered by inquiring biologist. Similar concerns were presented by Barranco (2012), who discussed the possible invasive situation of "*G. assimilis*", which was being sold for pet food in Spain. As discussed in Weissman *et al*. (2012), this is probably *G. locorojo*, although inquiries to P. Barranco, in 2013 and 2014, as to the number of p/c in the calling song of their cricket, which would easily distinguish true *G. assimilis* from *G. locorojo,* went unanswered. *G. locorojo* has been used for studies on calling song and phonotactic selectivity (Rothbart & Hennig 2012) as well as courtship song (Vedenina & Pollack 2012).

DNA. Multilocus G2159, from a commercial pet food store, maps (Fig. 6, p. 28) this species closest to *G. assimilis* and *G. multipulsator*, despite very different calling songs between *G. locorojo* and the other two species.

However, as noted in Weissman *et al.* (2019), courtship songs of these three species are similar in having a double-tick structure unlike any other US *Gryllus* for which courtship song is known to us.

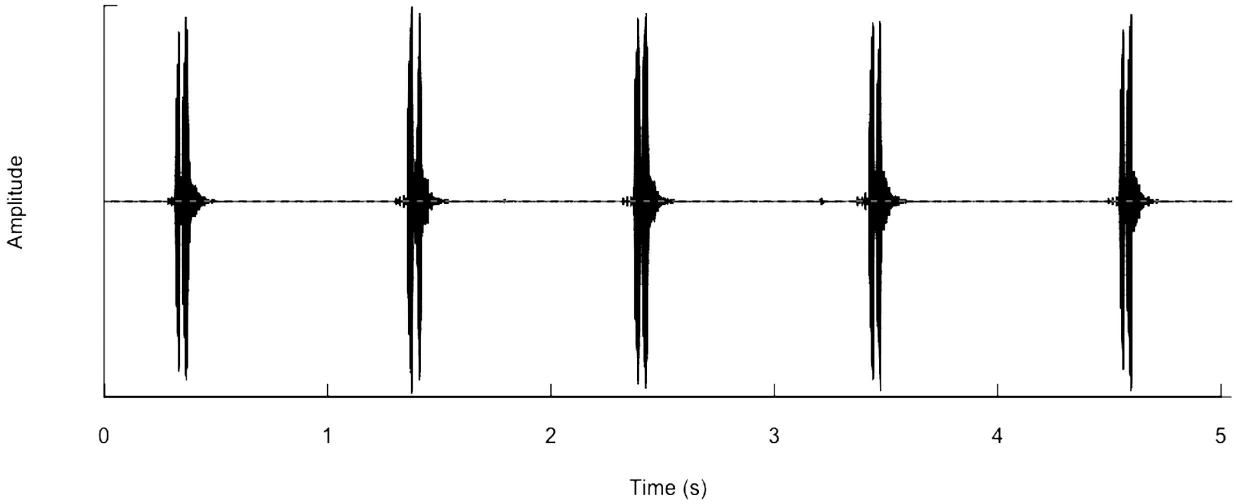

FIGURE 15. Five second calling song of *G. locorojo*: (R12-3) commercial pet store, at 22°C.

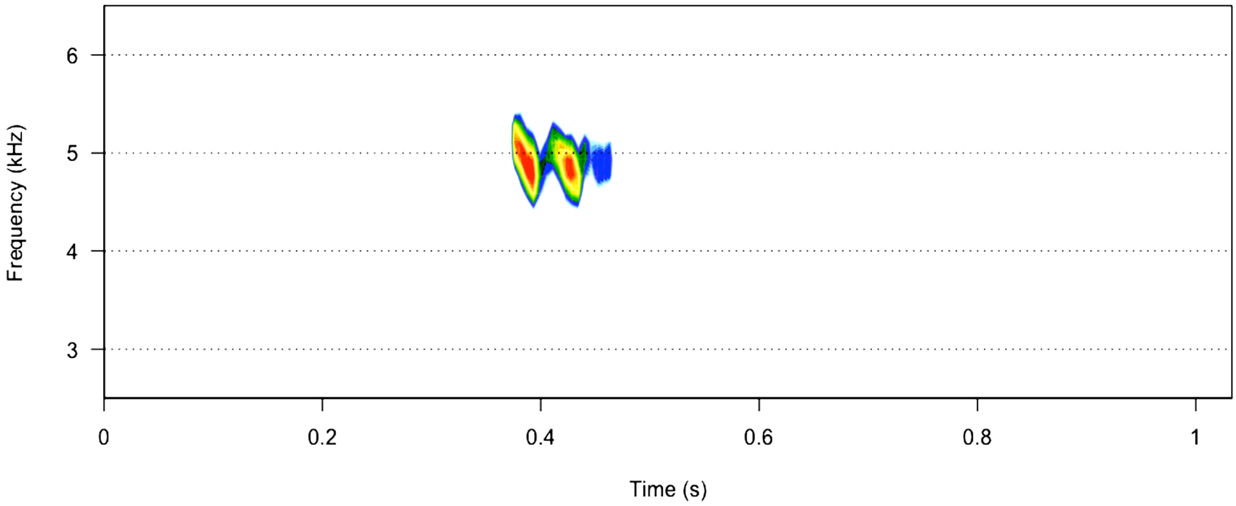

FIGURE 16. One second spectrogram of *G. locorojo,* same male as in Fig. 15.

The Brevicaudus Group

G. brevicaudus Weissman, Rentz, and Alexander

Within the US, *G. brevicaudus* is the only representative; however three other island-inhabiting endemic species (*G. insularis*, *G. alexanderi*, and *G. bryanti*) are close relatives (Fig. 6, p. 28). These island species are all flightless, short winged, slow chirpers. While loss of flight capability is common in many island taxa (Carlquist 1974, Darlington 1938), these 3 dispersed island endemics still generate interesting biogeographical questions. *G. bryanti* is discussed here (p. 40), but treatment of *G. alexanderi* and *G. insularis* will be included in future work on the *Gryllus* of Mexico.

Gryllus brevicaudus Weissman, Rentz, and Alexander

Short-Tailed Field Cricket

Figs 17–21, Table 1

1980 *Gryllus brevicaudus*. Weissman et al. 1980, p. 338. Holotype male (Fig. 18): California, Santa Clara Co., Palo Alto, Type deposited at CAS, Entomology type #13219.

1977 'Gryllus VIII', Weissman & Rentz (1977a).

'Gryllus #8' of DBW notebooks.

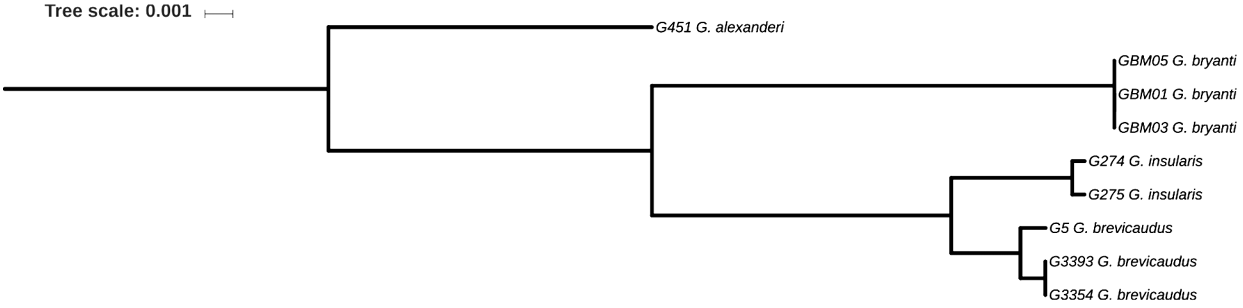

FIGURE 17. ITS2 gene tree. ***G. brevicaudus*** samples: S03-8 (G5); S16-1 (G3354, G3393); ***G. insularis*** samples: Guadalupe Island, Baja California Norte, Mexico; ***G. bryanti*** samples: Andros Island, Bahamas; ***G. alexanderi*** sample: Clarion Island, Colima, Mexico.

FIGURE 18. Holotype male, and labels, of *G. brevicaudus.*

Distribution. California only. Restricted to areas of central California usually surrounding the Central Valley.

Recognition characters and song. A small to medium sized, always short hind-winged cricket (see measurements Table 1, p. 18) that when alive or recently killed, is immediately recognizable because of contrast between totally black body and legs versus unique tegmina that have an area, especially in males (see Fig. 19), of yellow-orange tinge on the lateral field and anteriorly where the tegmina attach to the body. When alive, usually with golden pubescence on pronotum and hind femurs. Ovipositor shortest of any described *Gryllus* (Fig. 19)*,* even shorter than those of smallest *G. veletis* from Mirror Pool, North Dakota. Hind femur longer than cerci, cerci usually longer than ovipositor in situ. Song (Fig. 20; R03–8) 3–6 p/c, PR usually 20–30. Song similar to *G. veletisoides* but never microsympatric (although individuals synchronic) and *G. brevicaudus* separable from the latter by its longer cerci, shorter ovipositor, tegmina with a yellow-orange tinge.

Derivation of name. "brevicaudus" or "short tailed" in reference to having the shortest known ovipositor in the genus *Gryllus*.

Geographic range. Fig. 21.

FIGURE 19. Top: Live male (Jasper Ridge, S92-44) *G. brevicaudus* showing distinctive yellow-orange markings that contrast with rest of black cricket. Bottom: Female from Palo Alto, CA (S87-33) showing short ovipositor.

Habitat. Always in open grasslands, both sandstone and serpentine, below 610 m elevation. When ground wet and saturated from winter and spring rains, under rocks (SE Paicines, S03-8; Clayton, S19-3). As grasslands dry out and soil cracks form, individuals then move into these deep cracks (Jasper Ridge, S93-26; W Springville, S09-37) where they can be difficult to flush with water. Often at moderate to high density, when found within appropriate habitat, as gauged by the number of singing males.

Life cycle and seasonal occurrence. One generation/year. No egg diapause. Along with *G. lineaticeps,* probably the earliest maturing *Gryllus* species in central California with first adults singing in mid-winter when males can be heard during warm, early-March days. Latest known collection date is 27 August, but usually no males heard in most populations well before then. We wonder if some August collected adults represent areas where they can retreat into deep, cool soil cracks, which prolongs survival. This is one species where we have been able to do multiple surveys during the season—on Jasper Ridge, San Mateo Co., there is clearly only one generation. Nymphs from laboratory hatched eggs do not grow well and most stop developing as middle/late instars, perhaps indicating the presence of an obligate winter diapause.

Variation. **Size:** San Luis Obispo Co. specimens average larger body size, have longer ovipositors, and longer stridulatory file than individuals from more northern localities. **Color:** After death, the yellow-orange tegmina areas (especially of males) darken with drying and time (see Fig. 18 of holotype).

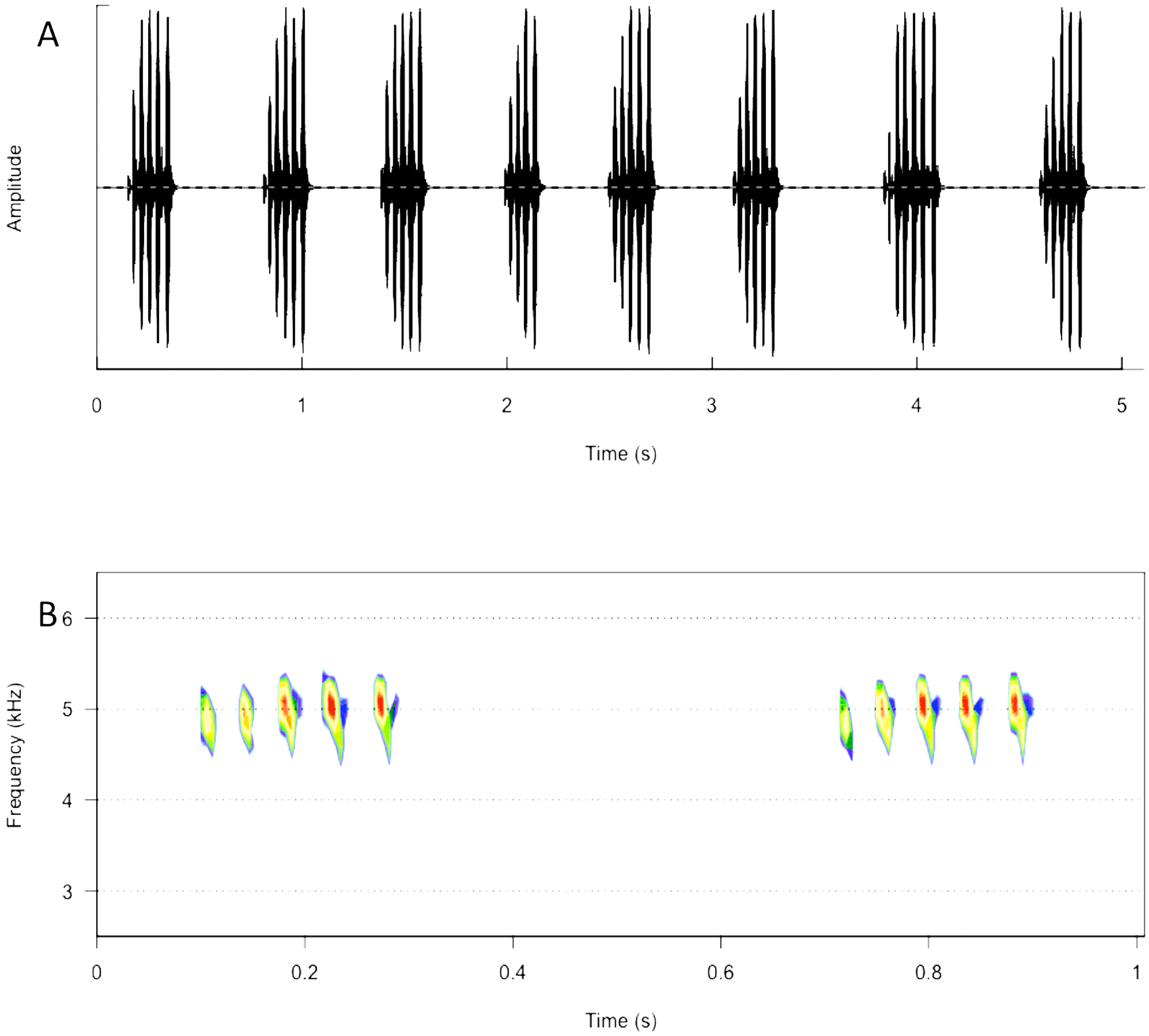

FIGURE 20. Five second waveform (A) and one second spectrogram (B) of calling song (R03-8) of *G. brevicaudus* from San Benito Co., CA (S03-8), recorded at 24.5°C.

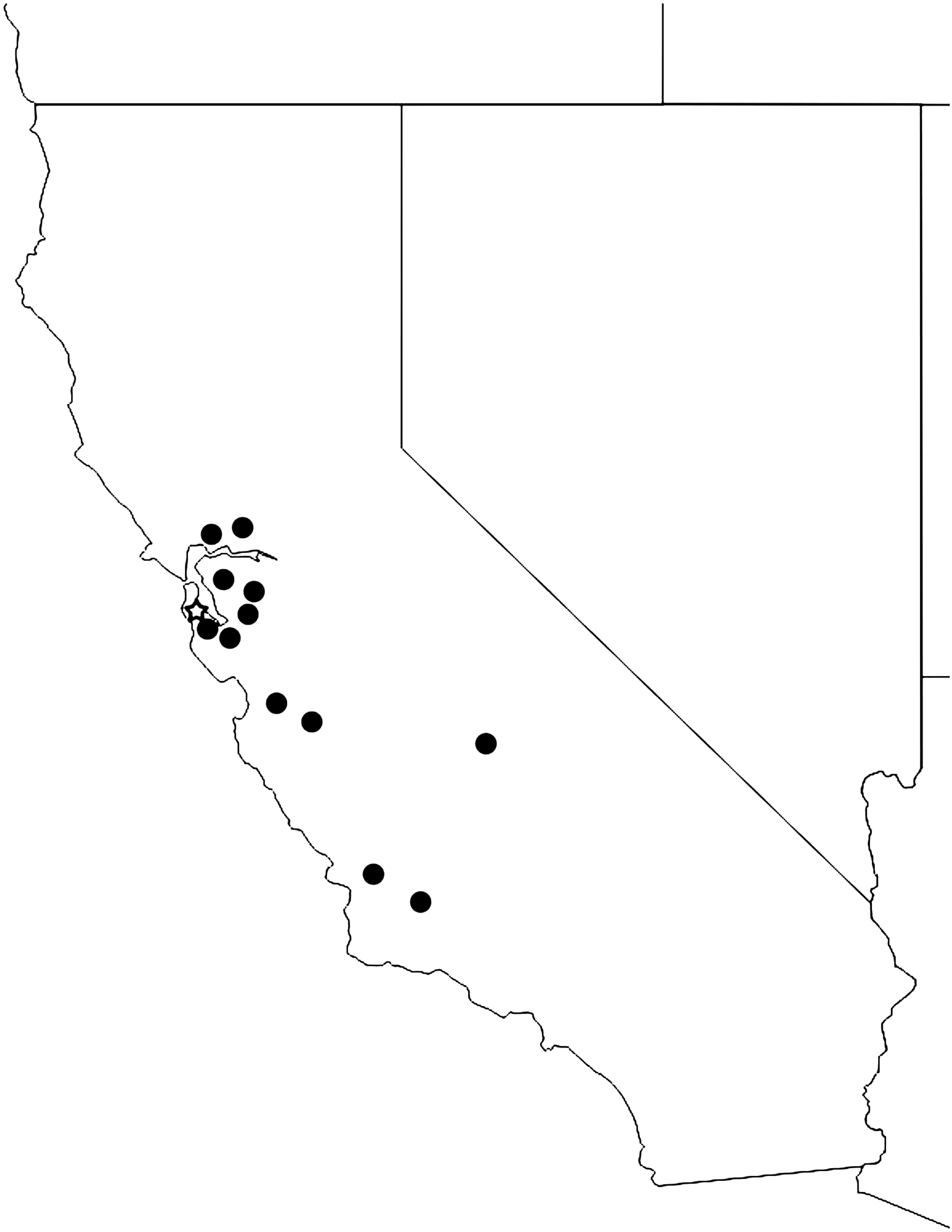

FIGURE 21. Known distribution for *G. brevicaudus.* Star shows type locality.

Specimens examined. **California:** *Contra Costa Co.* Clayton, Russelmann Park Road, 252m, 12-iv-2019, 37° 54’ 56.98” -121° 54’ 17.95” (S19-3). Lafayette, 21-vi-1965 (CIS). Marsh Creek, 28-iv-1957 (CIS). Mt. Diablo, 750’, 29-iv-1923; 21-vi-1940 (CIS); 13-vii-1982, (S82-39). *San Benito Co.* Hollister, 1-viii-1980 (S80-55). 18 m SE Paicines, 1480’, 21-iii-2003 (S03-8). *San Luis Obispo Co.,* Carrizo Plain National Monument, 2-3 m N Caliente Range, 700m, 27-iii-2002, 35° 10’ 30” -119° 51’ 50” P. Schiffman (DAG 2002-010). San Luis Obispo 14-v-1967; 27-viii-1967. 1 km E Santa Margarita 14-v-1967. El Chorro Regional Park Campground, 307’, 13-vii-2017, 35.33163 -120.73091°. *San Mateo Co.* Stanford University Jasper Ridge, 21-iii-1970, 2-v-1992 (S92-44), 2-v-1993 (S93-26), 18-v-2016 (16-1). *Santa Clara Co*. Mountain View, 9-vi-1981 (S81-13); Palo Alto, field at Foothill Expressway and Stanford Avenue, 24-vii-1974, 23-v-1987 (S87-33). *Solano Co.* 20 m NW Rio Vista 6-v-1978, N. Corey (CIS). *Tulare Co.* 10 m W Springville, 700’ 29-v-2009 (S09-37).

DNA. Multilocus G3393 Jasper Ridge, S16-1, closest extant relative may be *G. insularis* Scudder from Guadalupe Island, Baja California Norte, MX; ITS2 also shows a close relationship between *G. brevicaudus* and *G. insularis* (Fig. 17).

Discussion. This species is one of the few *Gryllus* that can be morphologically recognized in museum collections. Nevertheless, it is rarely collected perhaps because it matures in winter/spring, and males sing from the edges of deep cracks from which they are difficult to flush with water. Once days warm up, males sing only at night. Oatmeal trails through known populations can attract females and occasionally males.

We wonder if this species’ short ovipositor is associated with egg laying deep in cracks, where humidity may be higher, that are so prevalent in grassy fields during California’s dry spring and summer.

We have flushed individuals of *G. lineaticeps* from the same soil cracks (Mt. View, S81-13; Mt. Diablo, S82-39; Clayton, S19-3) in which *G. brevicaudus* males were singing. *G. integer* can also be singing at such localities.

One adult male (Jasper Ridge, S93-26) parasitized by unidentified tachinid.

Gryllus bryanti Morse

Bahama Island Field Cricket
Figs 17, 22, Table 1

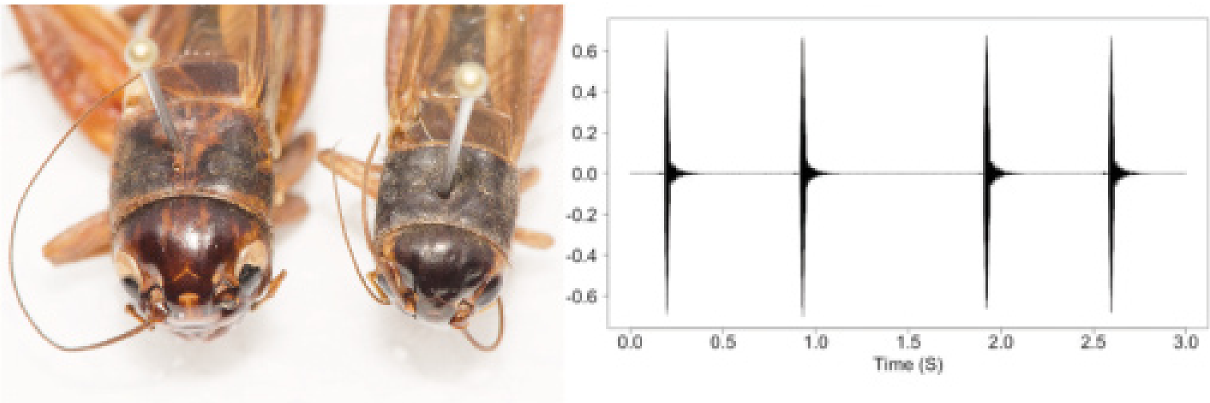

FIGURE 22. Left Panel: *G. bryanti* (on left) vs. sympatric *G. assimilis* (right), both from Bahamas. Note head wider than pronotum in *G. bryanti.* Right Panel: Three second waveform of typical single-pulse chirp calling song of *G. bryanti* (neotype male, GBM08, Andros Island, at 25 °C).

Although not known from the United States, this cricket is endemic to the Bahama Islands, which are less than 80 km away from the closest US location along the Florida coast. Since our earlier publication (Weissman *et al.* 2019), we have documented this cricket on a third island in the Bahamas: San Salvador, 24.122279° -74.45678°, 23-i-2019, 1♂, N. Lee, deposited CAS.

Recognition characters and song. Known only from 3 islands in the Bahamas. Body color as in Fig. 22. *Song* (Fig. 22) at 25°C typically with widely spaced single pulses delivered at 7–15/10 seconds at a pulse rate of 0.8–2.1.

DNA. GBM05, from Andros Island, multilocus appears (Fig. 6, p. 28) to be one of several *Gryllus* near the base of a continental North American species group, distinct from the Afro-Eurasian *G. bimaculatus* and *G. campestris* Linnaeus. We interpret this result cautiously, however, as we lack DNA samples for other geographically nearby species *G. jamaicensis* Walker, *G. mandevillus* Otte & Perez-Gelabert, and *G. bermudensis* Caudell (probably most closely related to *G. firmus* [Kevan 1980]).

The Ovisopis Group

Gryllus ovisopis Walker and *Gryllus thinos* Weissman and Gray, n. sp.

These two species are distributed in far allopatry on opposite sides of the Gulf of Mexico: *G. ovisopis* in Florida, Georgia, and South Carolina, and *G. thinos* in coastal Texas. They differ in several major ways: *G. ovisopis* is a wood cricket, with an obligate egg diapause, and lacks a functional calling song. In contrast, *G. thinos* is a beach cricket without an obligate egg diapause and has a 4–7 pulse chirp calling song. Nonetheless, multilocus DNA places them as sister species.

Gryllus ovisopis **Walker, 1974**

Taciturn Wood Cricket

Fig. 23

Gryllus ovisopis Walker, 1974 Florida Entomologist 57:13. Holotype male, Florida, Alachua County, deposited in USNM, type #72970. Holotype male and allotype female both listed on USNM type webpage and specimens located and photographed by Floyd Shockley and Kayla Kramer (Fig. 23).

Recognition characters and song. This species is an egg overwintering, obligate egg diapausing, fall maturing species where adults first appear in September, and whose documented US distribution includes 3 states (Florida, Georgia, and South Carolina) but may include as many as 6 southeastern states: Florida, Georgia, South Carolina, Alabama, Mississippi, and Louisiana (Capinera *et al*. 2004, Walker 2019). Head is narrower than pronotum. Males produce no calling song, but do naturally produce both aggressive and courtship songs, and can be chemically induced to produce a feeble 3–5 pulse chirp structurally similar to *G. pennsylvanicus* and *G. firmus* songs (Gray *et al.* 2018).

DNA. Multilocus 2018-001 and 2016-035, courtesy of Kevin Judge's cultures, from samples originally from the type locality of Gainesville, FL., show (Gray *et al.* 2019) that nearest multilocus relative is non-taciturn, non-egg diapausing *G. thinos,* the latter known only from coastal Texas. In the absence of genetic sequencing data, Walker (1974) believed *G. fultoni,* and perhaps *G. firmus,* to be the nearest relatives. Harrison & Bogdanowicz (1995) showed a single clade of *G. ovisopis, G. pennsylvanicus,* and *G. firmus* with 1.3% separation for the whole group; Huang *et al.* (2000) found similar results.

Discussion. With the exception of a single male nymph caught 22-vii-2002 (DAG FLA02-311) in Yulee, Nassua Co., FL, we have no field experience with this species. Therefore, the interested reader is referred to Walker (1974, 2019) and Capinera *et al*. (2004).

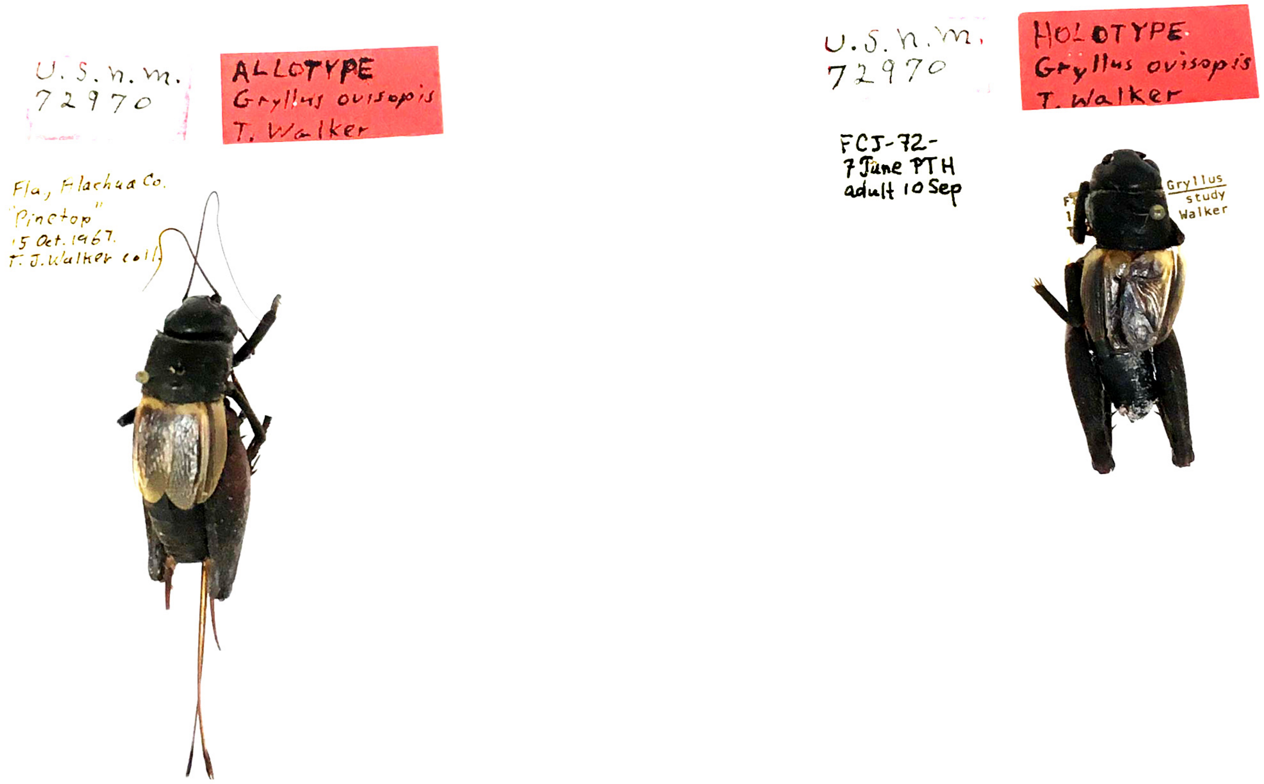

FIGURE 23. Male holotype (right) and female allotype (left) *G. ovisopis*.

Gryllus thinos Weissman & Gray, n. sp.

Texas Beach Field Cricket
Figs 24–27, Table 1

'Gryllus #21' and 'near #21' of DBW notebooks.

Distribution. Texas—restricted to Texas Gulf coast and up to 8 km inland.

Recognition characters and song. Small to medium sized (Fig. 24) , always short hind wings, medium length cerci, almost always in sandy habitats, males frequently sing from up in vegetation. *Song* (Fig. 25; R07-125) a slow chirp, CR usually < 90, 4–7 p/c, PR 20–35. Can be distinguished from only other Texas Gulf coast, sandy-environment field cricket, *G. firmus* (Texas), by DNA, non-overlapping file teeth, teeth/mm and a generally lower PR (Table 1, p. 18). Singing males of *G. thinos* also easier to approach than singing, microsympatric *G. firmus*. Females of the two taxa can be difficult to separate although *G. firmus* ovipositor length is generally longer in that larger species (see Table 1).

Holotype. Male (Fig. 24). USA, Texas, Kleberg Co., Padre Island National Seashore around Malaquite Visitor Center, 11-vi-2011, 15'. 27° 25' 23.2" -97° 18' 07.7". D.B. Weissman. S11-35, R11-8, DNA sample G2018. 16S GenBank accession #MK446632. BL 17.28, HF11.53, LC 10.76. Right tegmen removed: 119 teeth, file length 3.1, TL 10.0, TW 4.6. Type deposited in CAS, Entomology Type #19274.

Paratypes. (Total: 67♂ 14♀) **Texas**. *Aransas Co*., Business 35 near Rockport, 10', 12-vii-2013, 27° 57' 32.7" -97° 06' 14.4" (S13-55) 1♂. Texas 188 0.2 m SE Hwy 35, 19', 12-vii-2013, 27° 57' 56.1 -97° 07' 13.7" (S13-54) 2♂. *Cameron Co*., Boca Chica State Park, 10', 25° 59.827" -97° 09.146" 3-vi-1991 (S91-36) 5♂ 1♀; 10-vi-2007 (S07-25) 6♂ 4♀. South Padre Island, Isla Blanca Park, 5', 10-vii-2013, 26° 04" 09.3' -97° 09" 41.7 (S13-41) 3♂. *Kleberg Co*., Padre Island National Seashore, near Park entrance, 11-vi-2011, 27° 28" 39.9' -97° 16" 28.7' (S11-34) 1♂. Malaquite Visitor Center, 11-vi-2011 (S11-35) 2♂ 3♀; 3 m N Malaquite Visitor Center, 2-vi-1991 (S91-33) 11♂ 5♀; South Beach, 2-vi-1991 (S91-34) 2♂. *Matagorda Co*., Hog Island, 21', 13-vii-2013, 28° 36' 17.4" -95°

57’ 34.8” (S13-60) 4♂. *Nueces Co*., Corpus Christi near 10421 S. Padre Island Dr., 27° 40’ 02.5” -97° 16’ 54.4”, 29-vi-1986 (S86-57) 20♂ 1♀; 12-vii-2013 (S13-53) 1♂. Mustang Island State Park, 5’, 12-vii-2013, 27° 40’ 25.9” -97° 10’ 30.1” (S13-51) 7♂. Hwy 361 2 m S Port Aransas, 12-vii-2013, 15’ (S13-52) 2♂.

FIGURE 24. Holotype male (left), *G. thinos*. Female (right) from type locality showing typical, linear head stripes.

Derivation of name. “thinos” is Greek for beach, shore, or strand in recognition of where this cricket occurs.

Geographical range. Fig. 26. Known only from coastal and barrier island areas of Texas and inland for no more than 8 km. May get into adjacent coastal Mexico but areas not checked due to limited access. We did find suitable sandy areas just south of Tampico, Mexico, and around Galveston, Texas, but no *G. thinos* at either site.

Habitat. Almost always on sandy substrate in open, low rolling coastal dunes. In Corpus Christi (S86-57 and S13-53), somewhat sandy-substrate vacant field with grasses, forbs, and small shrubs (all three vegetation types from 10 to 40 cm tall), males almost always singing from vegetation (but never at top of plants) and initially visible on triangulating but quickly climbed (not jumped) down. Also heard throughout town of Corpus Christi in 1986 in road median areas, mowed lawns, etc. At Padre Island National Seashore (S91-33), common, with some in plants, but many just along mowed edges of road in vegetation 5 cm tall and singing with females also walking around. At Padre Island National Seashore (S11-34), nymphs and one adult male collected under boards just above high tide line. At Mustang Island State Park (S13-51), several reddish/pale mid instar nymphs under boards on low rolling dunes during daytime. At night at Mustang Island, all 7 singing males 15 to 46 cm up in grass, dead twigs, and *Yucca* spp. Two of those males quickly climbed down and retreated into nearby holes in the sand and were easily flushed with water.

Life cycle and seasonal occurrence. No egg diapause: Corpus Christi (S86-57). Probably one generation/year but many late spring and early summer mid-instar nymphs, at Padre Island National Seashore (S91-33) and Mustang Island State Park (S13-51), either represent a second generation or, more likely, show that maturation occurs over several months. Mid instar nymphs from those two localities molted to adults in August.

Variation. **Color:** tegmina almost equally divided between brown and black. Rear leg femur and tibia usually tan/orange but also black. **Head**: 13 adult males (out of 67) and 3 adult females (out of 14) with defined linear head stripes (Fig. 24), a character also seen in some late instars.

DNA. Multilocus G1209 (Boca Chica State Park, TX, S07-25) maps (Gray *et al.* 2019) with 2 males from Corpus Christi, TX (G2018, G2022 from S11-35). Surprisingly, the single, fall generation, egg diapausing *G. ovisopis* appears to be the sister species.

Much DNA variation between habitats although no morphologically corresponding characters. When South Padre Island specimens (S11-35) were genetically compared with those from Boca Chica (S07-25), less than 200 km south and in a similar habitat, we found, for CO1, 17 fixed nucleotide differences in 700+ base pairs; and for 16S, 6 fixed nucleotide differences in 500+ base pairs. We are concerned, however, that the COI variation might be an artifact of pseudogenes (see general DNA discussion, pages 16 & 17). ITS2 also shows very slight separation within *G. thinos* from these localities (Fig. 27). Further analysis might support species status for these genetically very different populations but in a comparison of their morphological characters (see Table 1, p. 18), nothing stands out. Plus, all 3 individuals are each other's nearest neighbor in multilocus tree. The Boca Chica habitat, while appearing very similar to Padre Island, is somehow ecologically different in that the former locality is also inhabited by microsympatric *G. firmus*, while no other *Gryllus* species occurs on Padre Island.

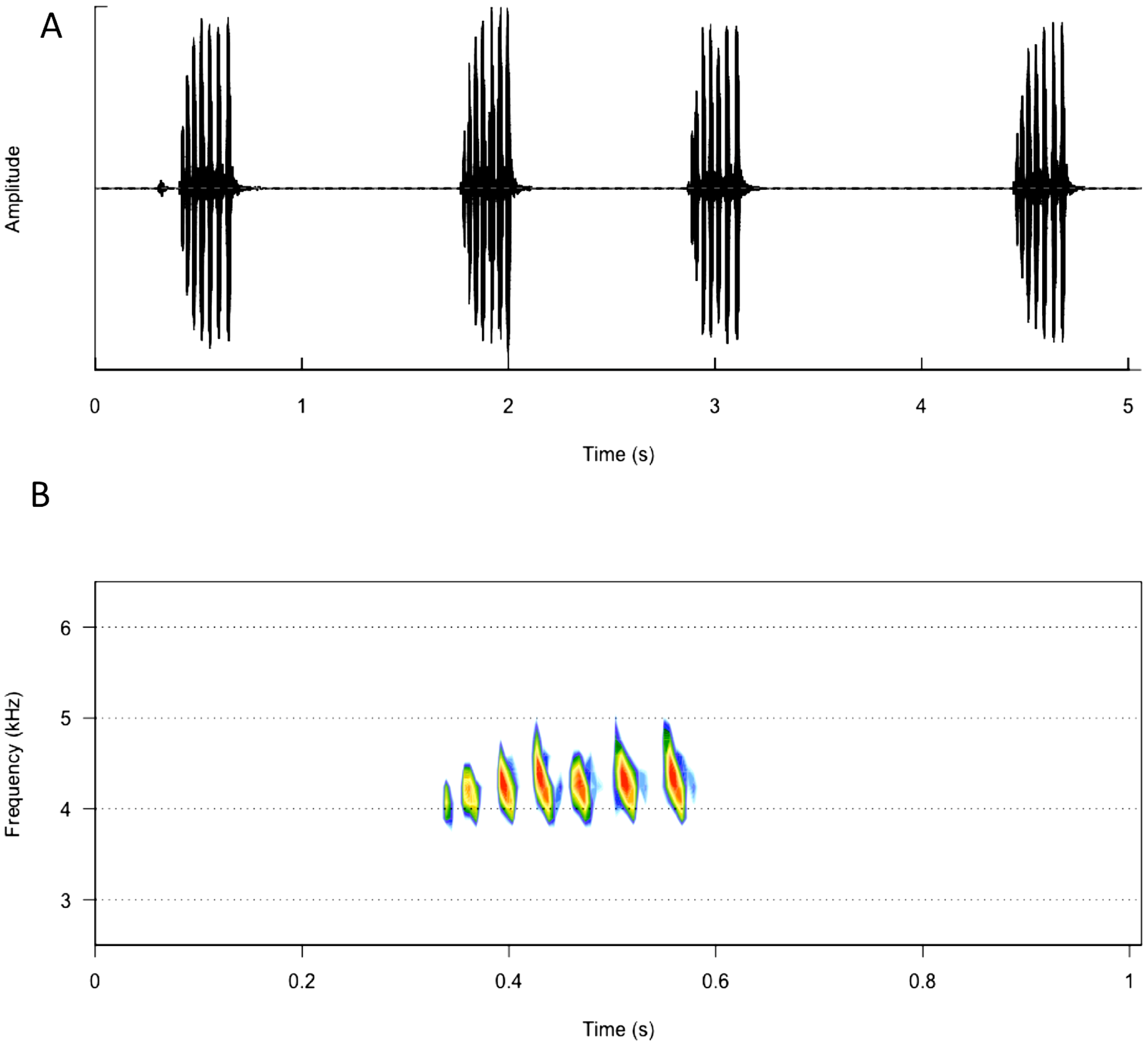

FIGURE 25. Calling song of *G. thinos* (R07-125) Cameron Co., TX (S07-25), at 25°C: (A) five second waveform, (B) one second spectrogram.

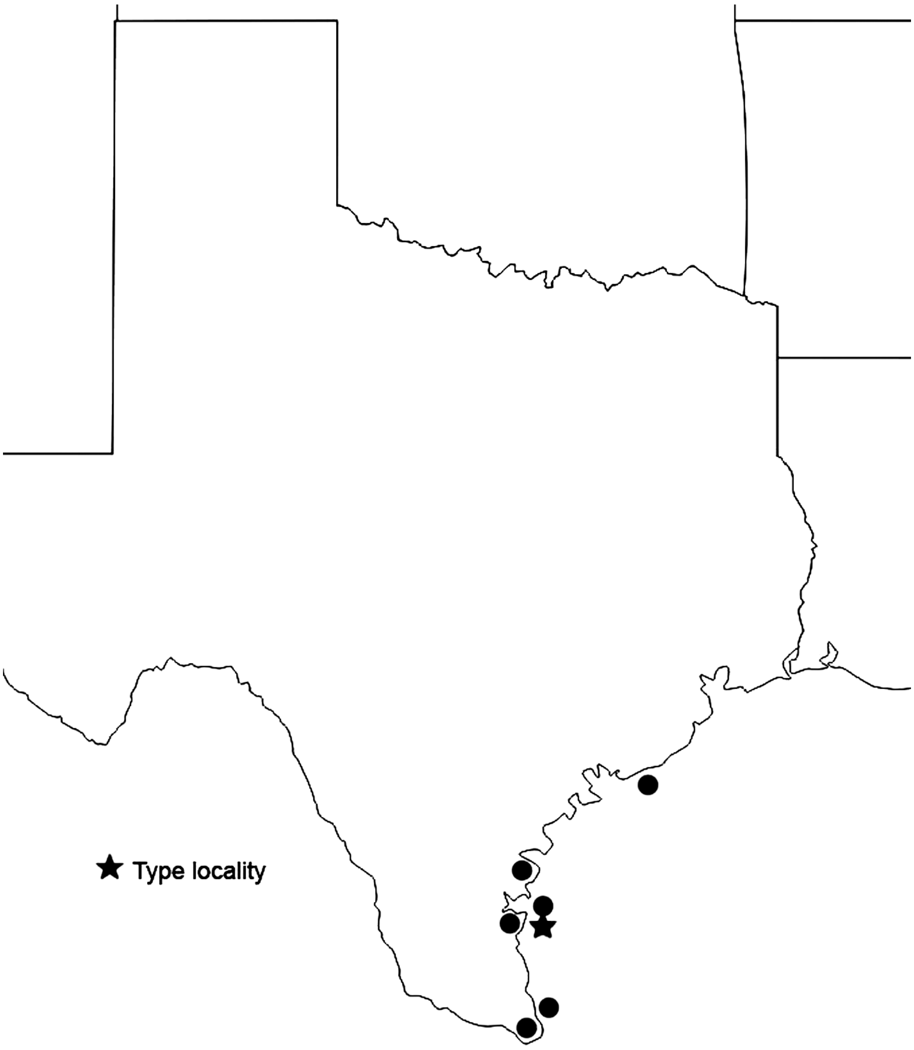

FIGURE 26. Known distribution of *G. thinos*.

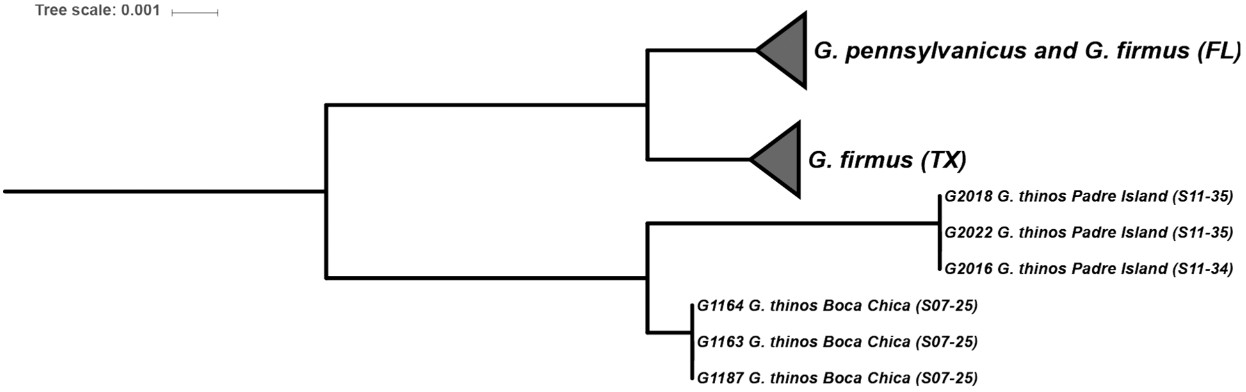

FIGURE 27. ITS2 gene tree showing some separation between Padre Island and Boca Chica samples of *G. thinos*.

The Texas beach inhabiting crickets, *G. thinos* and *G. firmus* (Texas), are clearly genetically distinct: Tamura-Nei genetic distance within *G. thinos* ITS2 samples is low (N = 6, mean ± SD, 0.0044 ± 0.0037), similar to variation within *G. firmus* (Texas) samples (N = 12, mean ± SD, 0.0034 ± 0.0040), but an order of magnitude greater between *G. thinos* and *G. firmus* (Texas) (0.0240 ± 0.0027 mean ± SD).

Discussion. Singing males easy to approach. On 10-vi-2007, males not singing well until 21:45, considerably after sunset, and without a significant moon. Oatmeal trails in dunes helped to attract wandering individuals.

Besides finding *G. thinos* microsympatric with *G. firmus* at Boca Chica, we also found them together near Port Aransas (S13-52), and Mustang Island State Park (S13-51). Singing males of the two species are easily separated in the field by the slower pulse rate in *G. firmus.*

The Pennsylvanicus Group

Gryllus pennsylvanicus Burmeister and *Gryllus firmus* Scudder.

Sister species of 3–5 pulse chirping field crickets (Figs 28, 29). *G. pennsylvanicus* widespread distribution throughout the colder more northern US and into Canada; *G. firmus* coastal Texas and southeastern US (including Atlantic seaboard) inland for variable distances. With post-mating, but pre-zygotic, genetic incompatibility in hybrid crosses of *G. firmus* females with *G. pennsylvanicus* males (Larson *et al.* 2012), but nonetheless difficult to separate morphologically. Both ITS2 (Fig. 30) and multilocus analyses (Gray *et al.* 2019) suggest that Texas and Florida populations of *G. firmus* are distinct.

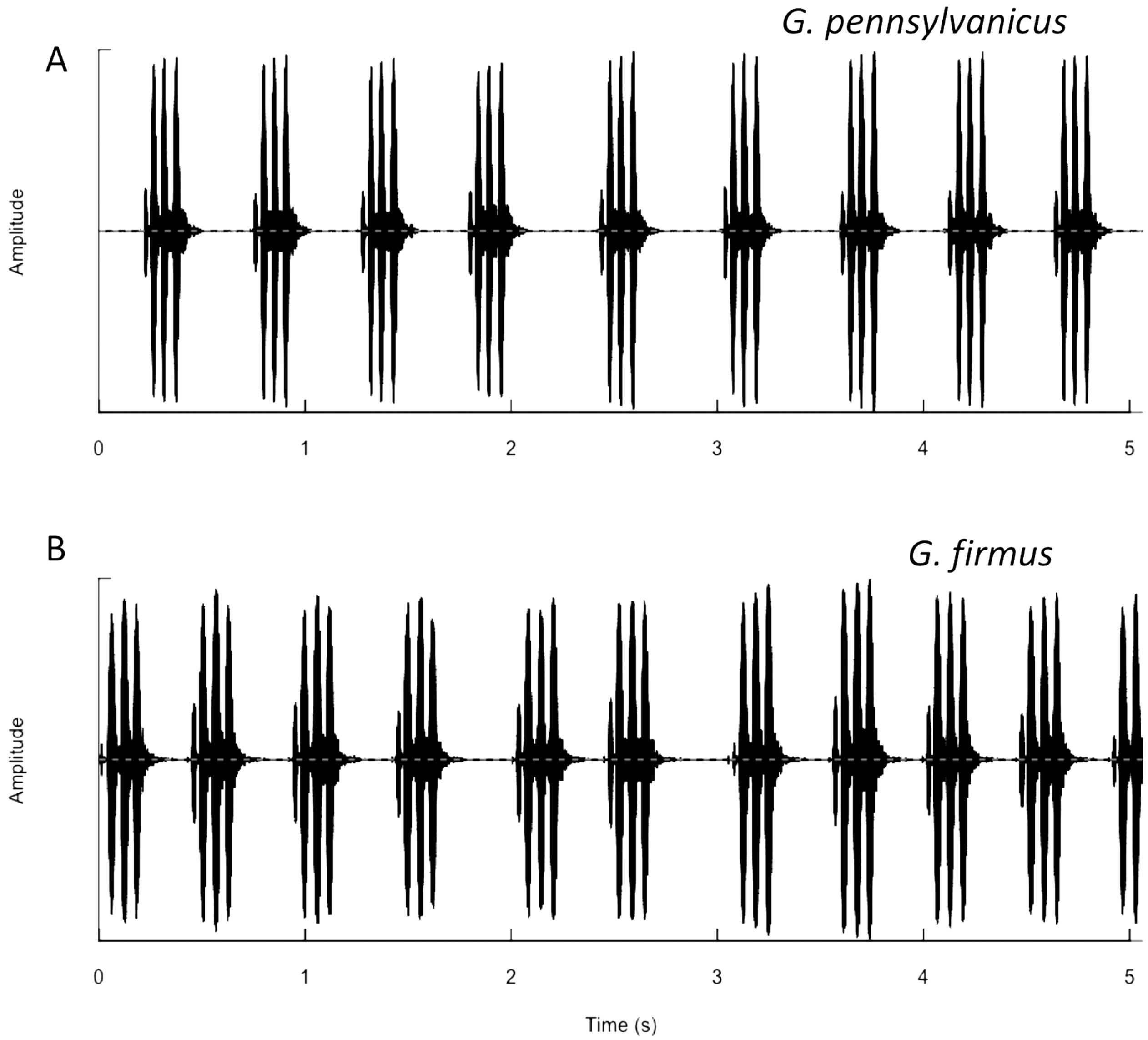

FIGURE 28. Five second waveforms of calling songs of (A) *G. pennsylvanicus* and (B) *G. firmus*. *G. pennsylvanicus* (R04-110) Whatcom Co., WA (S04-91), at 25°C. *G. firmus*: (R03-255) Gainesville, FL (S03-85), at 25°C.

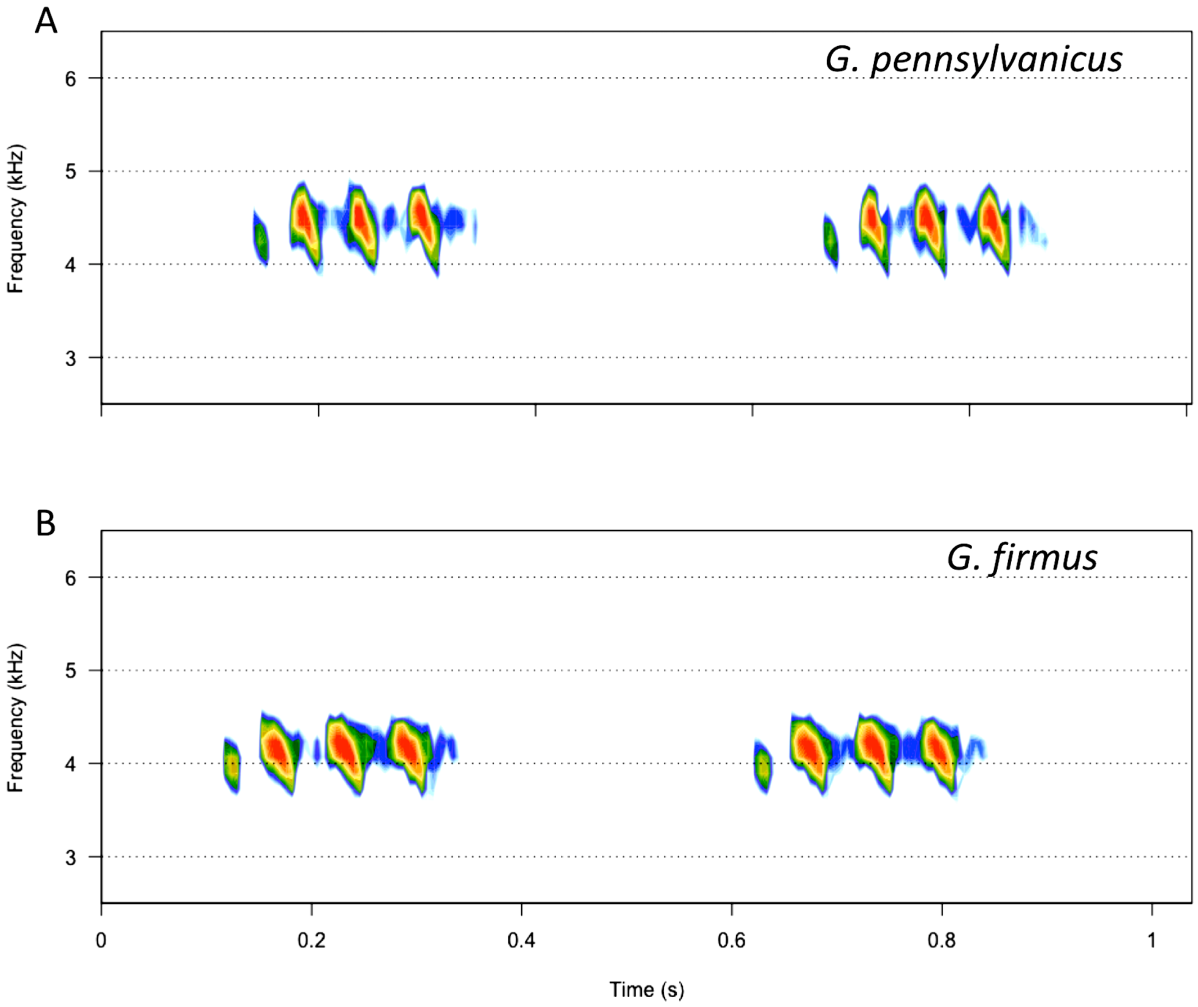

FIGURE 29. One second spectrograms of (A) *G. pennsylvanicus* and (B) *G. firmus*; same males as in Fig. 28.

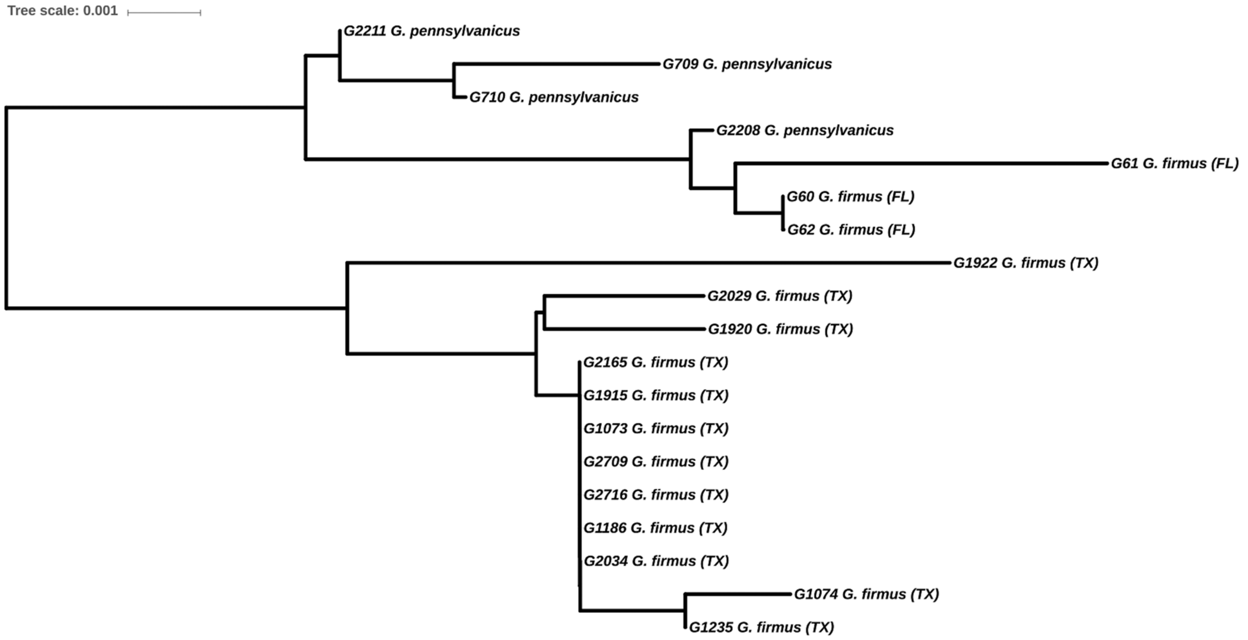

FIGURE 30. ITS2 gene tree. ***G. firmus*** samples: S03-85 (G60, G61, G62); S07-25 (G1073, G1074); S07-26 (G1186, G1235); S10-63 (G1920, G1922); S10-67 (G1915); S11-29 (G2165, G2029, G2034); S13-41 (G2709); S13-59 (G2716); ***G. pennsylvanicus*** samples: S08-74 (G709, G710); S11-107 (G2208); S11-108 (G2211).

Gryllus pennsylvanicus Burmeister

Fall Field Cricket

Figs 28–37, 45–50, 52, 53, 139, Table 1, 2

1838 *Gryllus pennsylvanicus* Burmeister. Handb. Ent., II, p,734. Lectotype male designated by Alexander, 1957, p. 586. "North America." Burmeister's original description (last paragraph under 13. Gr. Campestris) reads: "A similar species (Gr. pennsylvanicus*) is found in North America; it is somewhat smaller, the tegmina shorter than the body, without yellow base, but with brown main longitudinal vein." According to Michael Ohl (pers. comm. to DBW May, 2003) of the Museum of Natural History of Humboldt-University in Berlin (ZMB), entry #983 of the historic catalogue of the ZMB says (catalogue columns separated by slashes): "Gryllus abbreviatus Serv./ 4 [specimens; subsequently corrected to 3]/ Pennsylvan. Zimmerm./ Types of Gryllus pennsylvanicus Burm.*" These 3 specimens are still in the collection and include the male lectotype labeled by R.D. Alexander and 2 females. Sigfrid Ingrisch (pers. comm. to DBW May, 2003) believes that although the "…original description reads only North America, …one might guess from the name [and the catalogue entry] that it was from Pennsylvania." Lectotype male and labels illustrated on OSF website (Cigliano *et al*. 2019).

1957 *Acheta pennsylvanica.* Alexander. Ann. Entomol. Soc. Amer. 50: 586.
1964 *Gryllus pennsylvanicus*. Randell. Can. Entomol. 96: 1592.
'G. eastern and western pennsylvanicus', 'G. hanksville' and 'G. near hanksville' of DBW notebooks.

Distribution. Widespread across the US although absent from the Southwest and Southeast.

Recognition characters and song. We apply this name to any US *Gryllus* with the following constellation of characters: obligate (winter) egg diapause, one generation/year, adults first appearing mid to late summer (usually after August 1st), slow chirping (2–3 c/s; Fig. 31; R04-110), 3–5 p/c, black crickets with short cerci, a relatively long ovipositor and generally not living on sandy substrates. Morphologically most similar to *G. firmus* and we discuss elsewhere (see Hybrid Zones, p. 61) the problems associated with separating the two species. Must also be separated from *G. veletis* which occasionally overlaps in distribution and time of occurrence. Where *G. pennsylvanicus* and *G. veletis* are synchronic in Nebraska, South Dakota, Oklahoma, Missouri, and Kansas, clear field differences (see Table 2, p. 144) in pulse rate and tooth count, with *G. pennsylvanicus* having a lower pulse rate and higher tooth count, are apparent, although such song differences appear absent in Michigan (Alexander & Meral 1967). Also, *G. pennsylvanicus* overwinters in an egg diapause while *G. veletis* overwinters as a late instar since the eggs have no diapause. In northwestern Oregon, *G. pennsylvanicus* can be distinguished from morphologically similar looking, black, short cerci, non-egg diapausing spring and early summer adult *G. veletisoides* compared to the late summer adults of *G. pennsylvanicus* with different DNA. We suspect that the 2 taxa may be synchronic in northwestern Oregon in late July–early August but have no collections to document.

Derivation of name. Apparently in reference to the type series being collected in Pennsylvania (see discussion above).

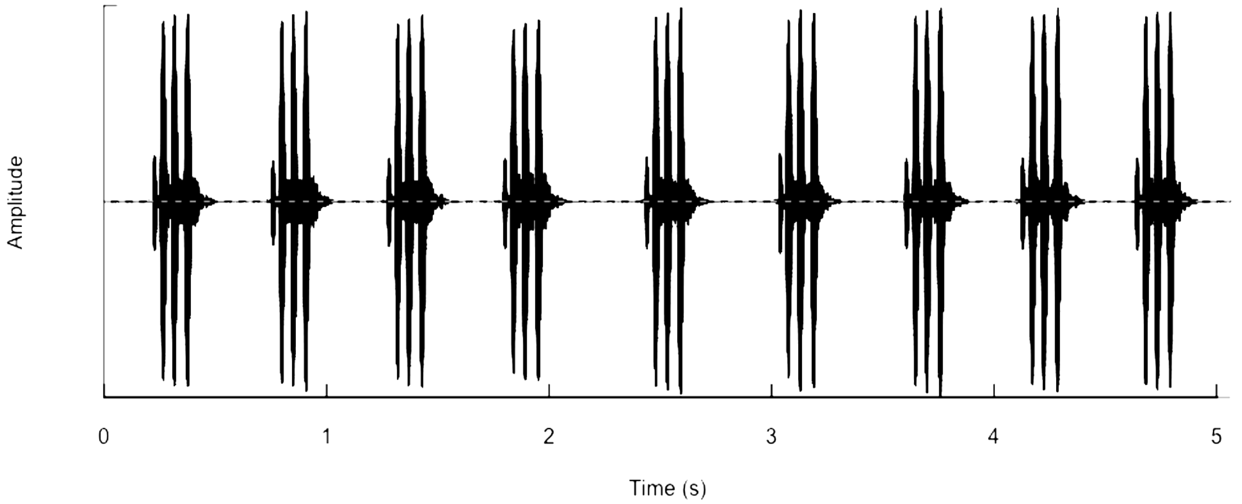

FIGURE 31. Five second calling song of *G. pennsylvanicus* (R04-110) Whatcom Co., WA (S04-91), at 25°C.

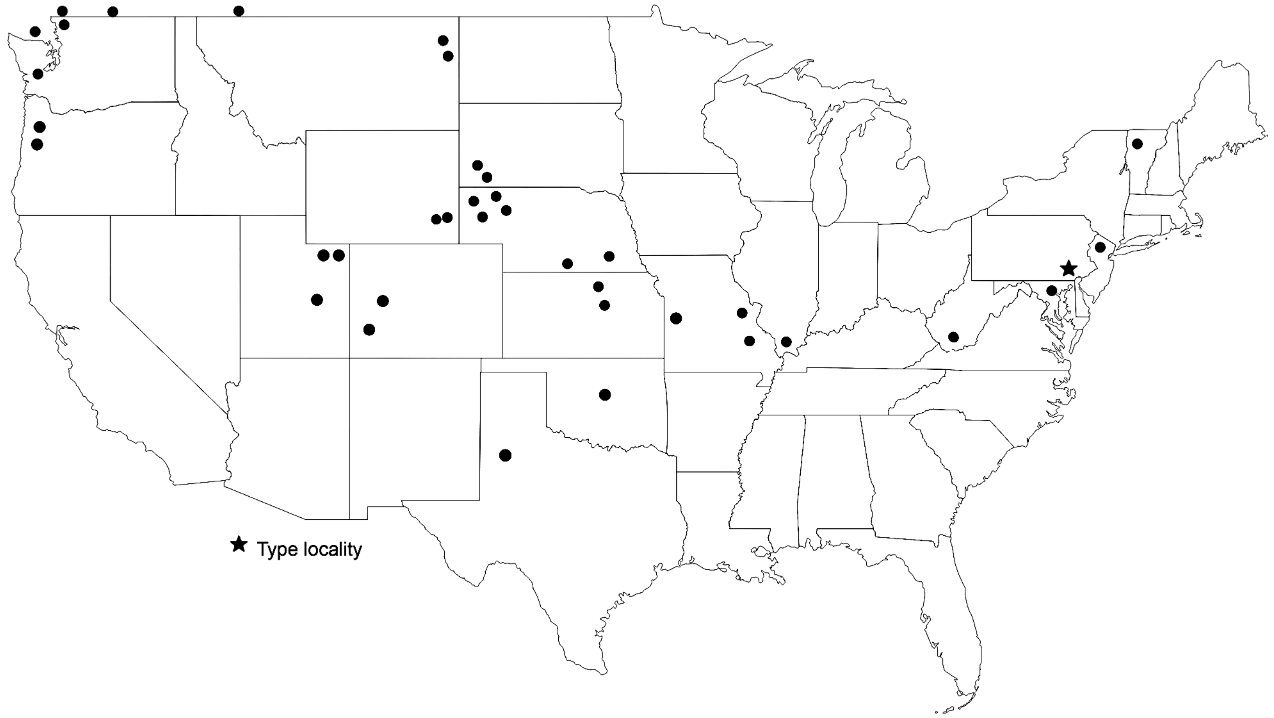

FIGURE 32. Populations of *G. pennsylvanicus* studied by us.

FIGURE 33. Size differences, in *G. pennsylvanicus*, between northern (right) from Berrien Co., Michigan, and southern (left) from Saline Co., KS [S02-49]).

Geographic range. Fig. 32. More eastern localities are presented in Walker (2019) and Capinera *et al*. (2004). An egg-diapausing cricket in Cuatrocienegas, Mexico may also be *G. pennsylvanicus*, and will be addressed in our Mexico *Gryllus* paper. California localities listed in Weissman *et al*. (1980) are actually *G. saxatilis.* We believe that a fall (18-ix-2013), long ovipositor (18.42 mm) adult female collected in the Texas Panhandle, in Lubbock (S13-80), is *G. pennsylvanicus*, despite no associated song, tooth count or egg diapause data, given the elevation of 990 m and 33° N latitude. This female (G2708) mapped in the multilocus tree (Gray *et al.* 2019) with other individuals of *G. pennsylvanicus* and *G. firmus*, without clearly resolving which. If indeed *G. pennsylvanicus*, this would represent the most southerly range limit (excepting the unconfirmed Cuatrociénegas samples).

Habitat. In towns in cracks, under objects, in grassy vegetated areas and also in clay badlands in Alberta, Canada (S05-72, 73) and Nebraska (S97-83).

Life cycle and seasonal occurrence. One generation/year. Obligate egg diapause present: Vancouver, Canada (S00-54), Scottsbluff, Nebraska (S99-144), Sidney, Montana (S97-95), Guernsey, Wyoming (S97-78, S99-138 & 99-139), Concordia, Kansas (S02-50), Corvallis, Oregon (S83-39), Hanksville, Utah (S04-128). Overwinter as eggs in diapause (Rakshpal 1962) with first adults appearing in late July–early August. Field collections in early August typically yield a few adults with most of the population late instars. In early summer, it is not unusual to find adult *G. veletis* microsympatric with early-mid instar *G. pennsylvanicus*; while in August, it is not unusual to find adult *G. pennsylvanicus* microsympatric with early to mid-instars of *G. veletis*.

Variation. **Body length:** Northern specimens (Michigan) considerably smaller than those from Kansas (Fig. 33). **Hind wing length:** Rare adults of both sexes with long hind wings, including two of five females from Lincoln, NB (S02-52). **Number of file teeth** (see Fig. 34): Range from 124–223 with more northern and smaller males having shorter files and fewer total teeth. Teeth/mm also higher where tooth number highest in Nebraska, Colorado, Kansas, Missouri, and Oklahoma. In 13 males from Salina, Kansas (S02-49), teeth ranged from 161–215, or a 54-tooth range. This parameter usually varies by <30 teeth over an entire species' range (Weissman, unpublished). **Ovipositor length:** Range from 10.43 to 22.29 mm (Lincoln, Nebraska, S02-52) with larger females having longer ovipositors (for example, Fig. 35, S02-49). **Pulse rate:** Varies from 10.4–25.0, with males with higher number of teeth having lower pulse rates (see Fig. 52 in Hybrid Zones, p. 68).

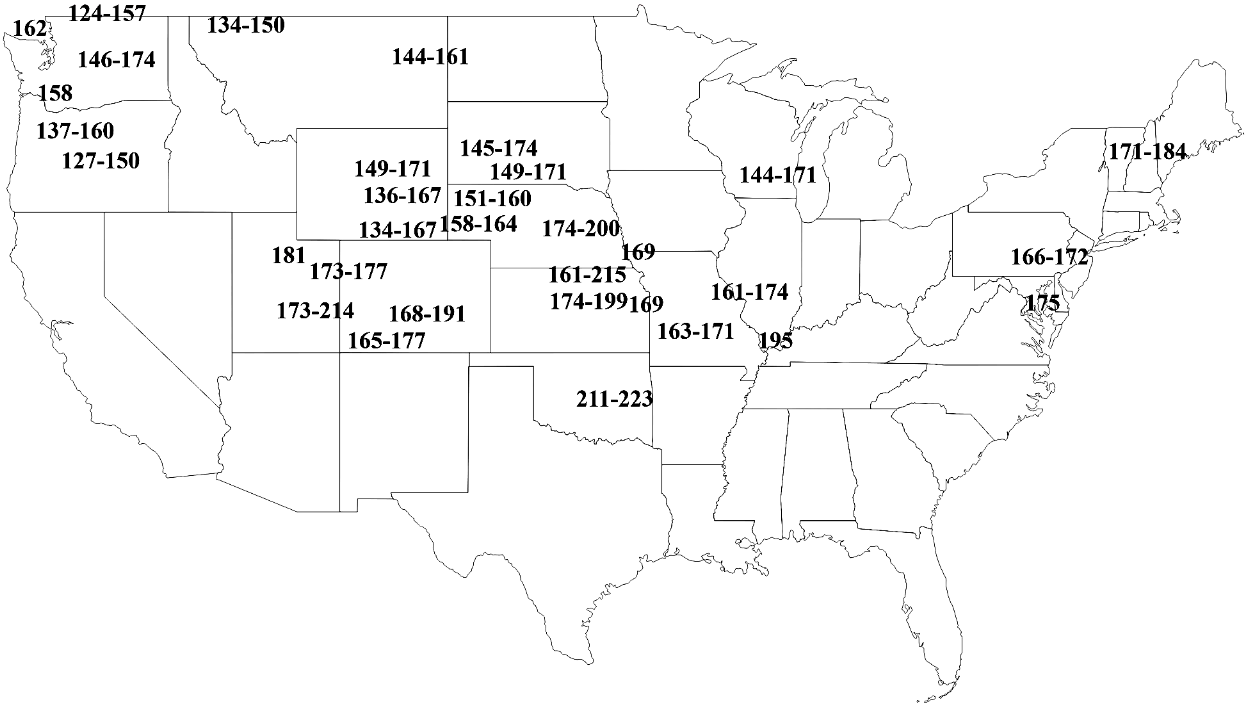

FIGURE 34. Map of *G. pennsylvanicus* showing variation in file tooth number across the United States. File teeth range from 124 (Vancouver, S00-54)) to 223 (Oklahoma City, S02-48).

FIGURE 35. Long ovipositor *G. pennsylvanicus* from Saline Co., KS (S02-49).

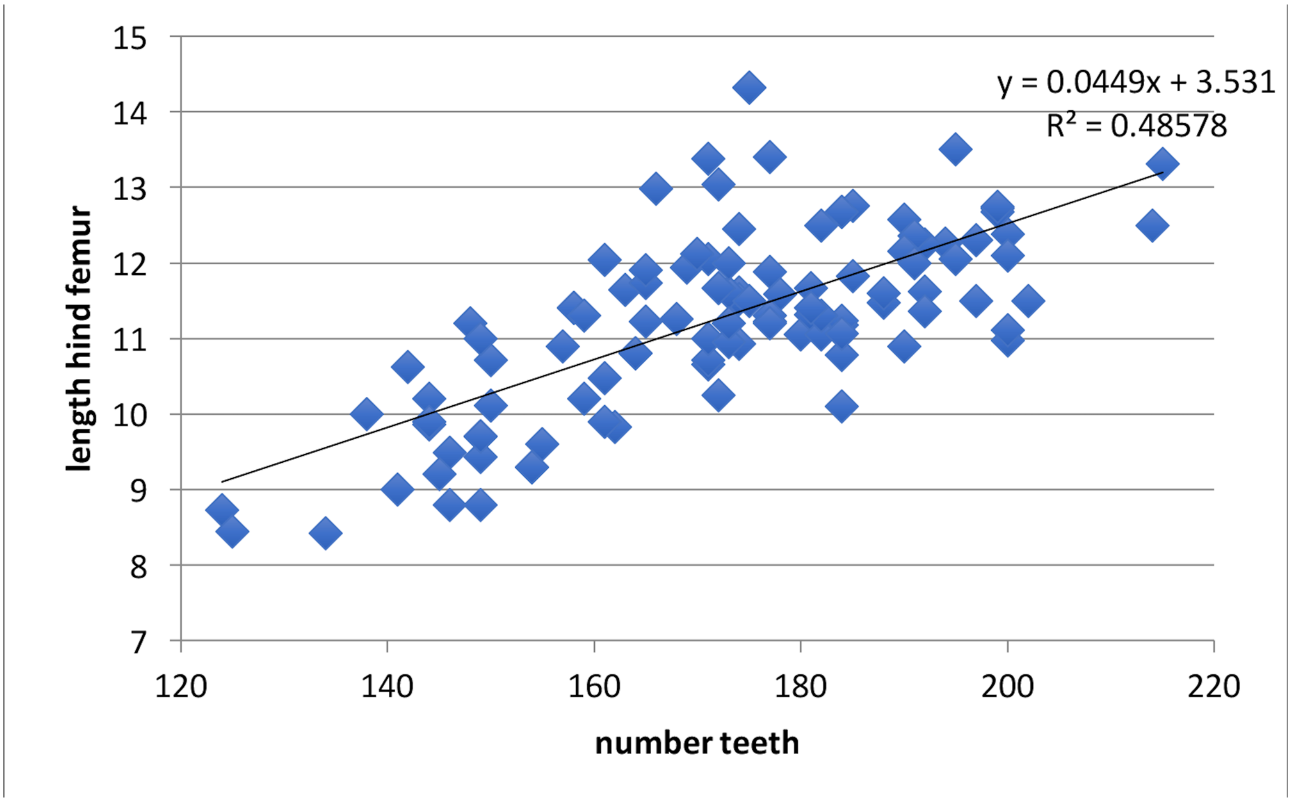

FIGURE 36. Regression *G. pennsylvanicus* showing a weak correlation between number of file teeth and hind femur length, the latter a proxy for body size.

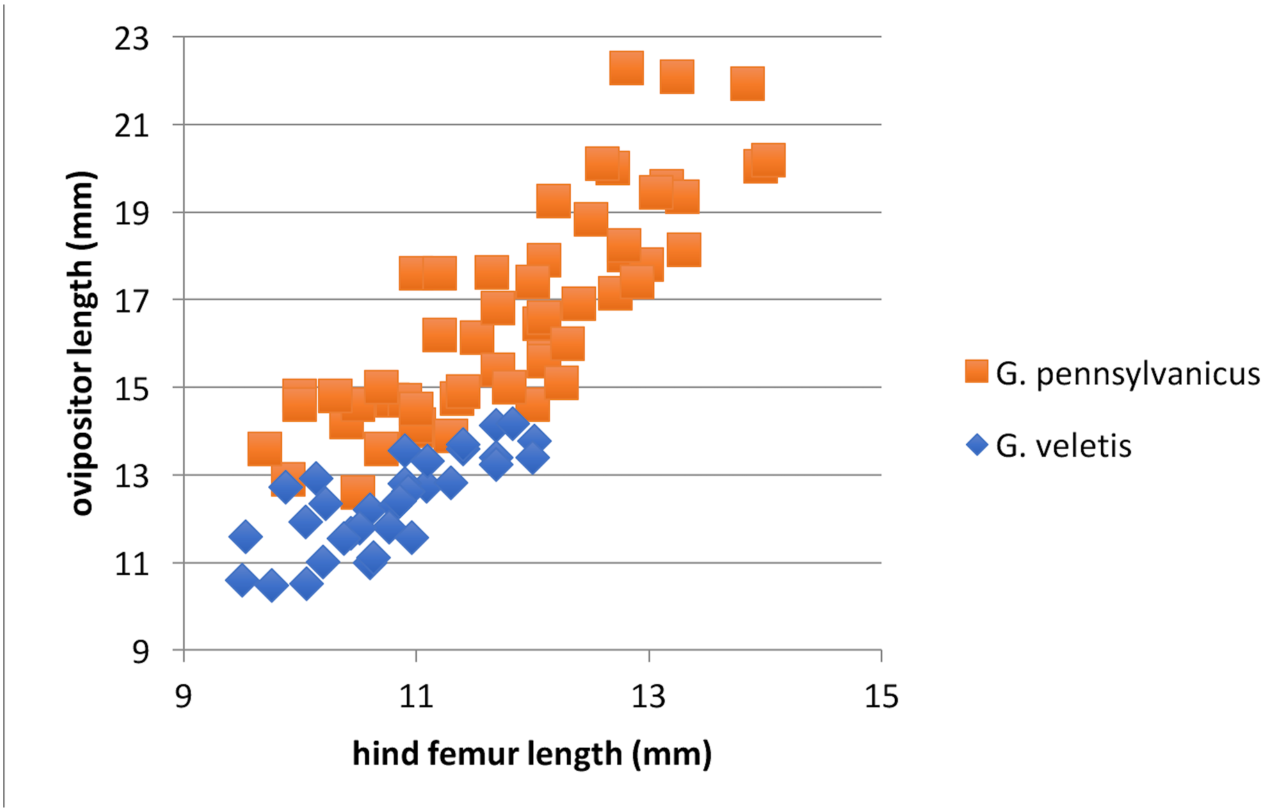

FIGURE 37. Regression *G. pennsylvanicus* vs. *G. veletis* demonstrating longer ovipositors in the former taxa. Specimens from only the 6 localities discussed in text.

Specimens examined. **CANADA**. **Alberta:** Drumheller Municipal Airport, 2470', 15-viii-2005, 51° 29.028' -112° 43.235' (S05-73). Horseshoe Canyon 14km W Drumheller, 15-viii-2005, 51° 25.128' -112° 52 (S05-72). **British Columbia:** 3 m N Osoyoos, Haynes Ecological Reserve, 1200', 26-viii-2000 (S00-27). Vancouver, 15-viii-1983 (S83-125) S. Tanaka; 22-ix-2000 (S00-54). Vancouver Island, near Butterfly Zoo in Saanich, 16-ix-2007 (S07-90). **USA. Colorado:** *Garfield Co.,* Rifle, 5140', 15-viii-2009 (S09-109). *Mesa Co.,* Fruita, 4420", 16-viii-2009 (S09-114). **Illinois:** *Madison Co.,* 10-viii-2002 (S02-60). **Kansas:** *Cloud Co.,* Concordia, 1100', 7-viii-2002 (S02-50). *Saline Co.,* Salina, 1100', 7-viii-2002 (S02-49). **Maryland:** *Prince George Co.,* College Park, 500' 30-v-2004 (adult molt 6-viii-2004) S04-35. **Missouri:** *Cape Girardeau Co.,* Millersville, 9-viii-2002 (S02-58). *Jackson Co.,* Kansas City, 8-viii-2002 (S02-54). *St. Louis Co.,* St. Louis, 10-viii-2002 (S02-61). **Montana:** *Richland Co.,* Sidney, 1840', 31-vii-1997 (adults and late instars) (S97-95). Hwy 23 5 m SE Sidney, 1920', 31-vii-1997 (adults and late instars) (S97-94). **Nebraska:** *Dawes Co.,* Hwy 385 ~4 m S Hwy 20. 3680' 13-ix-1999 (S99-143). 3 m W and 13 m S Chadron near Coffee Grinder Butte, 3680', 28-vii-1997 (S97-84). 4 m W and 4 m S Chadron, 3100", 28-vii-1997 (S97-83). *Fillmore Co.,* Geneva, 1420", 7-viii-2002 (S02-51). *Lancaster Co.,* Lincoln, 940" 7-viii-2002 (S02-52). *Scotts Bluff Co.,* Scottsbluff, 3960', 13-ix-1999 (S99-144). *Sioux Co.,* Agate Beds National Monument, 4500', 13-ix-1999 (S99-141). **New Jersey:** *Morris Co.,* Pequannock, 13-ix-1987 (S87-100). **Oklahoma:** *Oklahoma Co.,* Oklahoma City, 1000', 6-viii-2002 (S02-48). **Oregon:** *Benton Co.,* Corvallis, 15-viii-1983 (S83-122), S. Tanaka. *Lane Co.,* Eugene, 14-x-2006 (S06-128). **Pennsylvania:** *Chester Co.,* New London, 406', August, 2011, 39.767099° -75.897706° (S11-107), D.H. Funk. **South Dakota:** *Jackson Co.,* Badlands National Park, 2200-2400', 30-vii-1997 (S97-90). Kadoka, 2200' 30-vii-1997 (S97-87). **Texas:** *Lubbock Co.,* Lubbock, 18-ix-2013 (S13-80). **Utah:** *Uintah Co.,* Jensen, 4740', 10-ix-1999 (S99-127). Naples, 5200', 10-ix-1999 (S99-126). *Wayne Co.,* Hanksville, 4500', 1-viii-1992 (S92-109); 11-ix-1998 (S98-88); 9-ix-1999 (S99-119); 12-ix-2004 (S04-128). **Vermont:** *Addison Co.,* Middlebury, 6-x-2006 (S06-117); 5-x-2008 (S08-74). **Washington:** *Mason Co.,* Shelton, 16-viii-1983 (S83-123) S. Tanaka. *Skamania Co.,* Mt St Helens, 3800', 16-ix-2015, 46° 15' 59" -122° 04' 50", pit fall trap, D.C. Lightfoot. *Whatcom Co.,* Birch Bay State Park, 5', 17-viii-2004, 48.54407° -122.45758° (S04-91). **West Virginia:** *Mercer Co.,* Camp Creek State Park, 2025', 19-vii-2011 (adult molt 9-ix-2011), 37.504477° -81.134305° (S11-108), D.H. Funk. **Wyoming:** *Platte Co.,* Guernsey, 4300', 12-ix-1999 (S99-138). Road 270 3.9 m N Hwy 26, 4300', 28-vii-1997 (mid-instars) (S97-82); 12-ix-1999 (S99-139).

DNA. Multilocus G710 Middlebury, Vermont (S08-74); G368 Hanksville, Utah (S04-128); and G2708 Lubbock, Texas (S13-80) map (Gray *et al.* 2019) closest to Florida G62 Gainesville (S03-85), and Texas G1915 Bastrop State Park (S10-67); G1917 Schulenburg (S10-65); G1920 Brackettville (S10-63); G2029 Sea Rim State Park (S11-29); and G2715 Matagorda Island (S13-59) *G. firmus.*

Discussion. We initially considered western US *G. pennsylvanicus* to be several species given the range of file tooth counts and the geographic isolation of some populations. Because further collecting has not made the situation any clearer, combined with the multilocus DNA tree indicating close relatedness between these populations, we treat them as one species, although we believe further investigation is indicated.

Only *G. veletis* has a more widespread US distribution than *G. pennsylvanicus.* It thus seems prudent to compare the two taxa over their ranges since both may represent groups composed of several sister species. Fig. 34 suggests a clear north to south cline in increasing tooth count in files of *G. pennsylvanicus.* Northern males from Vancouver may have as few as 124 teeth while a male in Oklahoma had 223 teeth, a difference of 99 teeth. Regressing number teeth vs. hind femur length (Fig. 36) (the latter a good measurement of overall body size—see p. 17) we demonstrate that this cline in number of teeth is weakly related to body size (R^2=0.486). In contrast, while males of *G. veletis* similarly double in size over their north to south distribution, number of teeth only increase from 116 to 175 (a difference of 59) in going south (Fig. 141, p. 140).

Where *G. pennsylvanicus* is sympatric and synchronic with *G. veletis*, as at Kadoka, South Dakota (S97-87); Jensen, Utah (S99-127); Concordia, Kansas (S02-50); Kansas City, Missouri (S02-54); and Geneva (S02-51) and Lincoln, Nebraska (S02-52), then ovipositor length in *G. veletis* considerably shorter than *G. pennsylvanicus* (Fig. 37).

As an example, the two collected female *G. pennsylvanicus* from Kadoka, SD (S97-87), both had ovipositors of 17.6 mm and hind femurs of 11.0 and 11.2 mm. A single female *G. veletis*, from the same locality, had an ovipositor of 11.7 mm and a hind femur of 10.6 mm. Both species sang from deep grass where individuals were difficult to collect. When synchronic and at the same temperature, field differences in PR between the two taxa are also easily appreciated as pulses in *G. pennsylvanicus*, at 20–25°C, are countable (as also seen in *G. longicercus* and *G. firmus)* especially when males have more than 170 file teeth. Pulses in *G. veletis* are not countable by ear at 20–25°C and the chirp rate is noticeably faster. For instance, we could hear a PR difference in Lincoln, Nebraska (S02-52) when a *G. veletis* male, with 148 teeth, was singing at 5 AM adjacent to a *G. pennsylvanicus* male with 169 teeth. We wonder if these two species, in such areas of synchronicity, may display character displacement in pulse rate as evidenced by some of the highest numbers of file teeth seen in any *G. pennsylvanicus* males? In other words, having more teeth in the file could result in a slower pulse rate since more teeth are being struck. We suspect that synchronicity between these two taxa is also more common than we document (also see Alexander & Meral 1967) because most of our field collecting was done in early summer since that is when most other *Gryllus* species are adult.

G. pennsylvanicus has been used for studies on pest potential (Carmona *et al.* 1999), calling and courtship (Zuk 1987, Harrison *et al*. 2013) and behavior (French & Cade 1987, 1989), as well as an extensive study of Hybrid Zones done in the R. Harrison lab—see discussion starting on p. 61.

Mermithids (Poinar & Weissman 2004) present in one male from Sidney, MT (S97-95).

Gryllus firmus **Scudder**

Sand Field Cricket
Figs 28–30, 38–51, 53, Table 1

1902 *Gryllus firmus* Scudder. Psyche 9:295.

1957 *Acheta firma* (Scudder). Alexander 1957. Ann. Entomol. Soc. Amer. 50:586. Lectotype male designated, "Pungo" Bluff, North Carolina. Three labels as follows: 1. Dingo Bluff, N. C. Nov. 15, 1876 Parker Maynard. 2. Gr. firmus Scudder's type, 1901. 3. Red type label 14064. File with 175 teeth (per D. Otte, pers. comm. to DBW by J. Weintraub, 5/10/2018). Type in ANSP (see Fig. 38). Despite Scudder (1902) clearly stating Dingo Bluff, Rehn & Hebard (1915, p. 295) listed the locality as Pungo Bluff, without explanation. This change was repeated by Alexander (1957). Checking various geography name sources, we find no official place names of Dingo Bluff or Pungo Bluff but we do find, in North Carolina, a Pungo River, Pungo Creek, Pungo Swamp, and Pungo Lake as well as a coastal town of Pungo. A Google search for both 'Dingo Bluff' and 'Pungo Bluff' yielded both of these collection localities assigned to many other North Carolina insect specimens.

1964 *Gryllus firmus.* Randell, 1964 Canadian Entomologist 96: 1592.

'Gryllus #19', 'near #19, #35, #45' of DBW notebooks; Thompson *et al*. (2012) used 'G. #45' in their paper.

Distribution. From south coastal Texas (near Brownsville) east to the Atlantic coast and inland for variable distances. In Texas (Fig. 39), found a maximum of 350 km inland (Brackettville).

Recognition characters and song. A small to large cricket usually with black head, pronotum and tegmina, short hind wings, long ovipositor, >160 file teeth, and frequently associated with sandy substrate. *Song* a slow chirp (2–3 c/s) with 4p/c (range 2–5), and pulse rate usually <15 at 25°C (Fig. 40; R03-255). One generation/year (except along the southeastern US seaboard and continuous coastal areas along the Gulf of Mexico) because of an egg diapause, late summer maturing adults (although present year around in Florida [Capinera *et al.* 2004]). Generally light colored tegmina and individuals can have longitudinal head stripes (Fig. 41) when living on coastal beach or lowland sandy substrate habitats. Both dark (Fig. 41) and light-colored specimens from coastal and southern areas of Texas, whose eggs have no or variable egg diapause, such as from Brackettville or Schulenburg, are placed here. Those in coastal dunes also frequently with lighter colored body (as all 3♂ and 6♀ from Boca Chica State Park [S91-37]) and legs. Nickle & Walker (1975) note that, in Florida, the lateral portion of the tegmina is diagnostically dark with many distinctive cross veins there, a condition also typical of Texas *G. firmus* specimens but not diagnostic there because several other Texas taxa also have this character. Within our study area, *G. firmus* must only be distinguished from the closely-DNA related *G. pennsylvanicus*, with which it forms a long hybrid zone (Larson *et al*. 2013) along the eastern slopes of the Appalachian and Blue Ridge Mountains. We discuss this complex situation elsewhere in this paper (see Hybrid Zones, p. 61). But, for now, we consider any population in central and SE Texas with a high tooth count, low pulse rate and no egg or a variable egg diapause to be *G. firmus*. If *G. pennsylvanicus* occurs in this area, then all their eggs should have a diapause. We realize the cumbersomeness of this distinction but, at present, without further investigations, we cannot separate the two taxa except based on geography (compare maps p. 49 vs. p. 56). *G. longicercus* from western Texas also has >160 file teeth and a slow pulse rate but is distinguished from *G. firmus* in having longer cerci, associated with rocks, and different DNA.

Derivation of name. "firmus" is Latin for strong, stout, and durable perhaps in reference to its being the largest known US *Gryllus* when it was described in 1902.

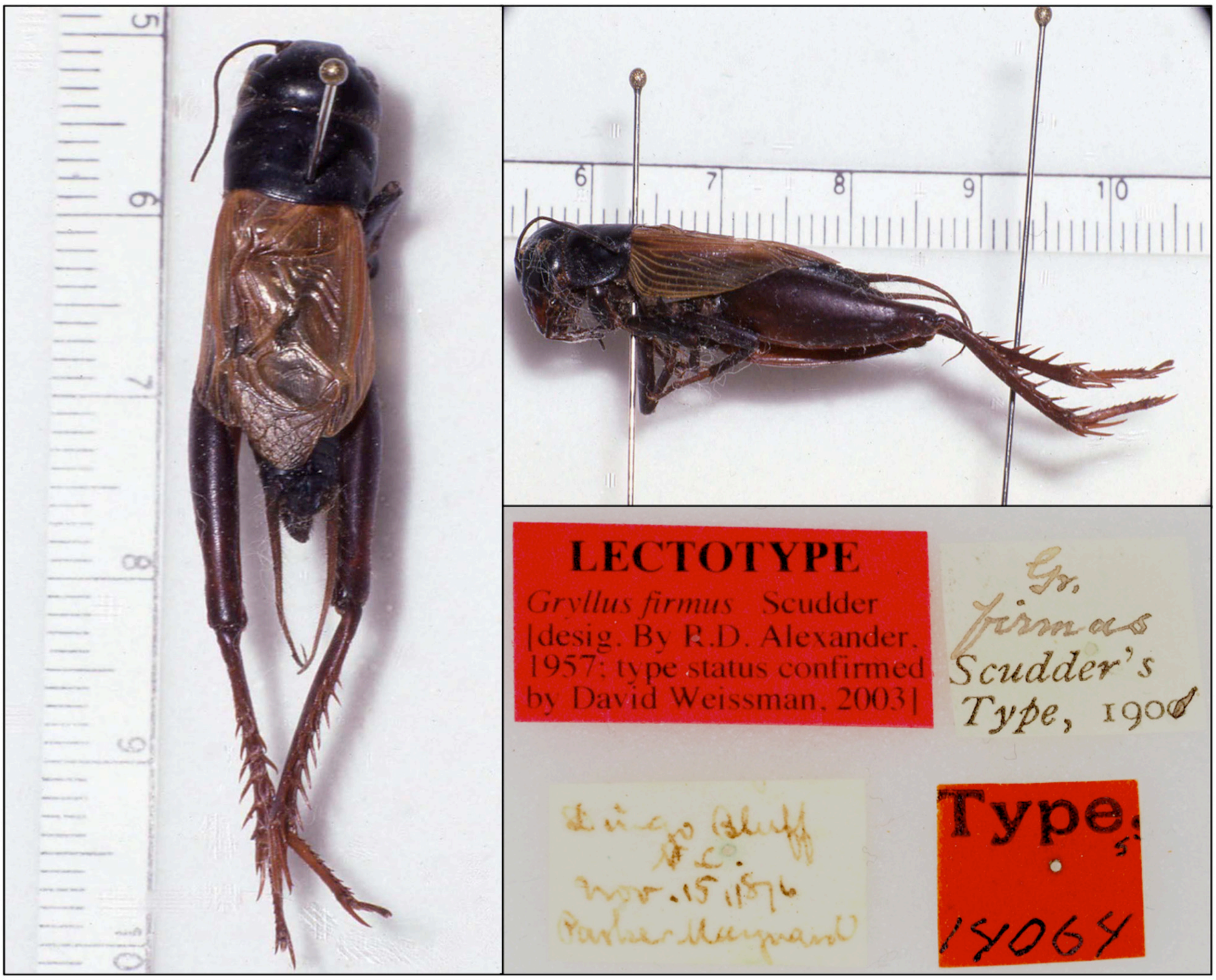

FIGURE 38. Lectotype male, *G. firmus,* specimen and labels.

Geographical range. Fig. 39. East of Texas, see Walker (2019) and Capinera *et al.* (2004). T. J. Walker has looked for *G. firmus* in Louisiana without finding it (pers. comm. to DBW, May, 2014). R. D. Alexander (unpublished 1964 notes given to DBW, by RD Alexander in ~1990) state *G. firmus* as abundant on the islands off Texas and Louisiana, although Fig 4. in Alexander (1968) shows only two collection localities for *G. firmus* in Louisiana. We thus assume that one taxon occurs along coastal sandy habitats of the Atlantic and Gulf of Mexico coasts, but see discussion from multilocus DNA analysis on p. 59. Not known from Tampico, Mexico (although coastal, sandy Mexican areas closer to the US/Mexico border not checked because of poor access).

Habitat. Coastal sand dunes, sandy habitats and barrier islands, and inland off of sand, always below 365m. In Texas, in Western Gulf Coastal Plain and East Coast Texas Plains ecoregions (Griffith *et al*. 2004). Also associated with ocean tidal surge areas (near Boca Chica S91-37; Sea Rim S11-30); open, grassy fields (Schulenburg S10-65); eastern oak woodlands (Brenham S92-123 & S01-51; Bastrop State Park S10-67)); dense overgrown lots (Brackettville), and irrigated lawn areas (Alice S13-49). Coastal paved road at Sea Rim State Park, Texas (S91-28, S11-30) washed out by Hurricane Jerry in 1989 and road rebuilt. Area subsequently hit by Hurricane Rita in 2005 and Hurricane Ike in 2008 and road not rebuilt by 2011 but *G. firmus* present under objects in area of tidal wash in 2011. These are tough crickets!

Life cycle and seasonal occurrence. Life cycle of *G. firmus* studied in detail only in the northern Florida area around Gainesville (Ibrahim & Walker 1980, Walker 1980, Masaki & Walker 1987) where continuous generations occur with some eggs laid by a single female having a diapause and others no diapause. Walker (1980) also documents mixed diapausing eggs from females from Carolina Beach, North Carolina. Starting somewhere north of Carolina Beach, one generation/year with most (all?) eggs having a diapause and adults first appearing in late summer or early fall. *G. firmus'* life cycle has not been studied in southern Florida (Walker, pers. comm. to DBW, 2014) although Capinera *et al*. (2004) note its occurrence there as year around.

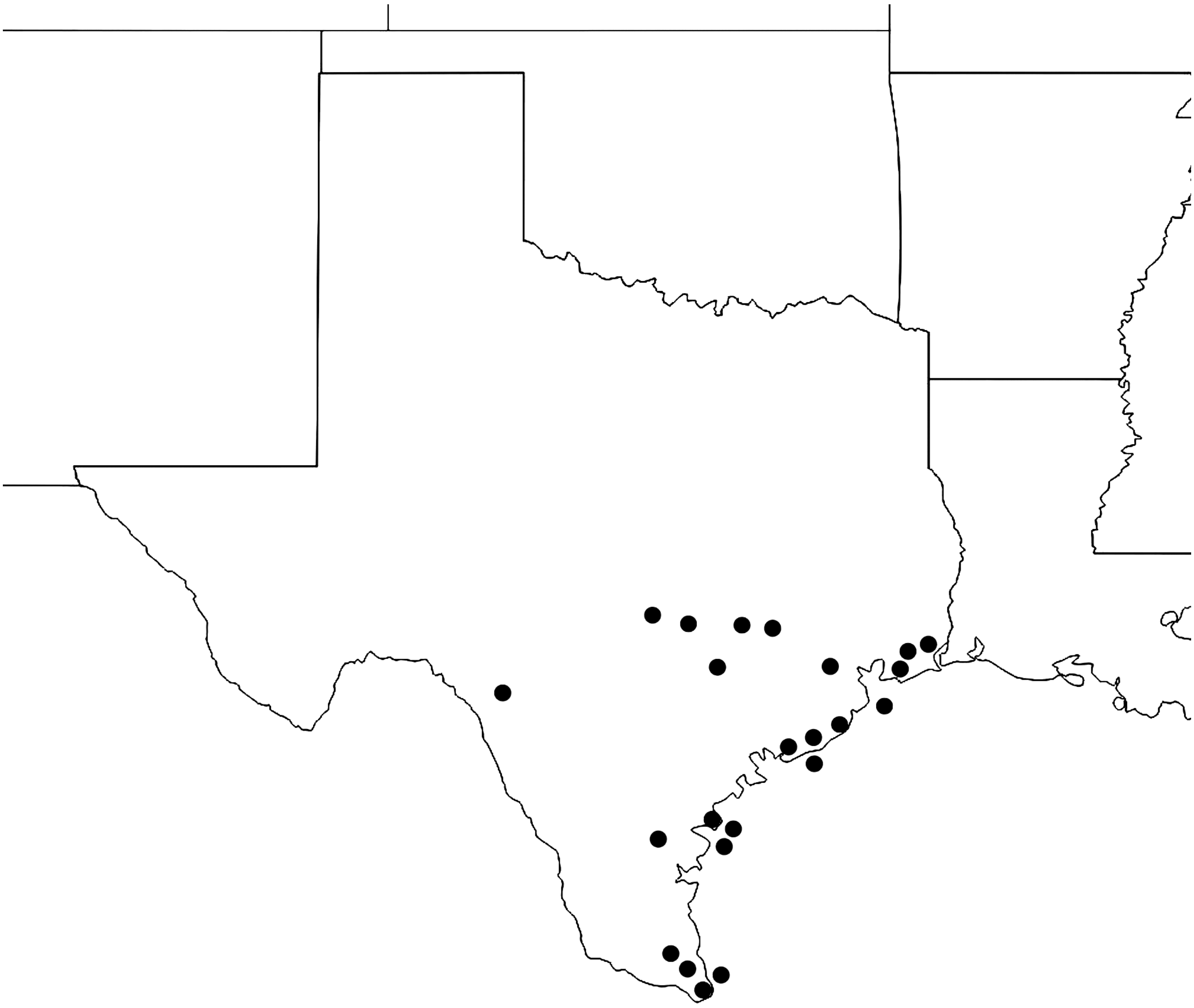

FIGURE 39. Populations of *G. firmus* that we studied.

We find a complicated life cycle situation along the Texas coast. Coastal populations appear to have 1 generation/year, without an egg diapause (Boca Chica S91-37, Sea Rim S11-30), where the majority of the collected individuals are late instars in early June (Sea Rim S91-28, S11-29 S11-30; Boca Chica S91-36, S91-37, S07-25, and S07-26) with nymphs usually molting to adults from mid-June to early July. But field collected individuals from some of these same coastal populations (Isla Blanca Park, S13-41; Egret Island, S13-59; Boca Chica State Park, DAG 2010-117) matured from mid-August to mid-September and may represent a second generation or eggs that hatched with a delay when compared with those eggs that hatched within 3 weeks after oviposition. These June/July maturing coastal dune individuals are also smaller, as adults, than those microsympatric ones maturing in August/September and those maturing away (and warmer?) from the immediate coast. More inland, no egg diapause (Alice, TX, S13-49; Brackettville, TX, S85-61) and probably 2 generations/year even though 2 males and 4 females collected at Brackettville (S91-40) on June 4, were last instars and molted to adult between 15-vi and 18-vii. Singing adults collected from some 10 m W Brenham, TX, on 24-v-2001 (S01-51) and 6-ix-1992 (S92-123); Brackettville on 10-vi-1985 (S85-61), 4-vi-1991 (S91-40) and 7-ix-2010 (S10-63); and from stops in Fayette Co. (S10-65), Bastrop Co. (S10-67) also probably indicate 2 generations/year at these inland sites.

Interestingly, we collected a mated adult female from Schulenburg, TX (multilocus G1917, collected 13-vii-2013, S13-65) that laid some 460 eggs over eight days (27-vii to 4-viii-2013). The first eggs hatched 27-viii, which is a normal incubation period for non-diapausing eggs kept between 20-25°C. But eggs from this one female continued to hatch over the next 5.5 months (see Fig. 42), a pattern more typical (see discussion on p. 9) of an egg diapausing *Gryllus* species and similar to what Walker (1980) found for *G. firmus* from Gainesville, FL. Two other adult females from Schulenburg (S10-65), collected 9-ix-2010, appeared to have mostly non-diapausing eggs but they were not followed in as much detail as the 2013 female. An adult female from Bastrop State Park (S10-67) also had some eggs hatch quickly, after oviposition, but most rotted and did not hatch.

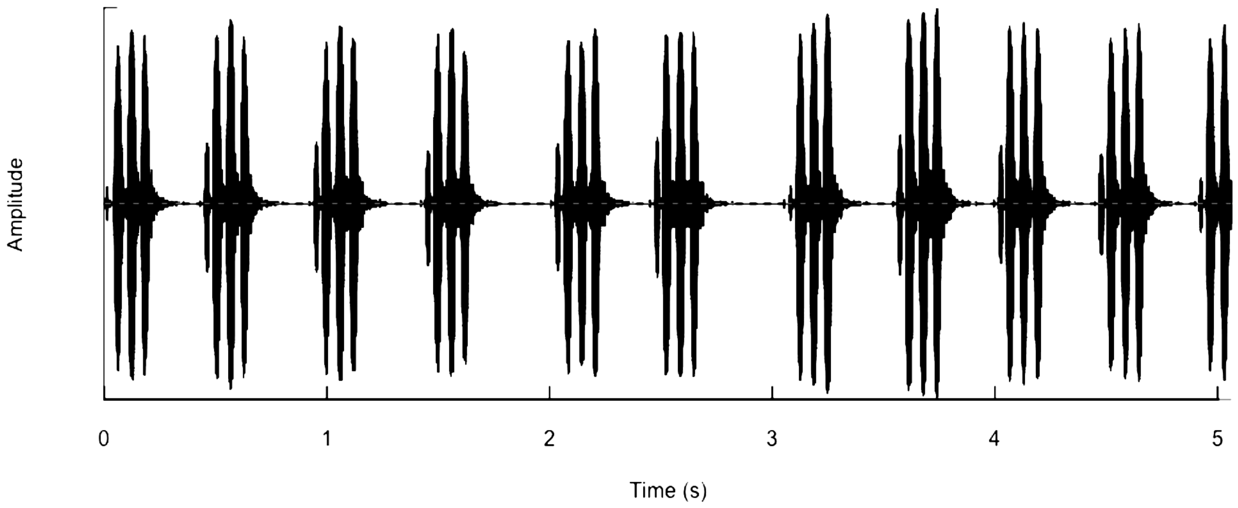

FIGURE 40. Five second calling song in *G. firmus*: (R03-255) Gainesville, FL (S03-85), at 25°C.

Variation. **Body color:** Coastal individuals, especially females, usually light in color, although 7 of 12 females from Brackettville also light colored, some with head stripes. **Body size:** Inland specimens from Texas are bigger with more teeth and longer ovipositors. Measured immediately after killing, we collected, from around Schulenburg, both our longest male at 26.96 mm (S10-65), and the longest female at 26.01 mm (S13-65). Our shortest male and female are 16.44 and 15.53 mm, respectively, both from Sea Rim State Park (S91-28). T. J. Walker writes (pers. comm. to DBW, July, 2014) that "field-collected *firmus* in Gainesville are more variable in size than any other Florida *Gryllus.* The smaller ones are nearly the average size of *G. rubens* and the bigger ones compare well with *G. ovisopis.*" **Head patterns:** Coastal females more likely than coastal males to have head stripes (as in Fig. 41), most notably 3 of 7 females from Sea Rim State Park (S11-30). **Hind wing length:** Of 174 Texas specimens, only 19 (10.9%) have long hind wings. Veazey *et al.* (1976) presented pitfall trap data from northern Florida where 15% of adults collected during the summer peak were long winged and 3% collected during the fall peak were long winged. Typically, adults collected at sound traps will all be macropterous because they have to be capable of flight to get into the traps. **Ovipositor length:** The 1914 Maryland female and the 1938 Alachua, Florida, female have the longest ovipositors seen in any US *Gryllus* species: 25.62 and 23.19 mm, respectively. Larson *et al.* (2013) lists 2 female *G. firmus* having 23.5 and 23.6 mm long ovipositors. Long ovipositors are generally associated with one of two different natural histories: species that overwinter as eggs in diapause and those inhabiting coastal sandy habitats. In the former situation, eggs laid deep in the ground have a better chance to survive freezing winter temperatures while in the latter, eggs laid deep have a better chance to survive periods of decreased or absent rainfall (Walker 1980). Both parameters apply to *G. firmus* in parts of its range, although we note that egg depth is not entirely determined by ovipositor length (Réale & Roff, 2002).

Specimens examined. **Florida:** *Alachua Co.,* Alachua, 20-x-1938, 1♀. Gainesville, 17-ix-1987 (S87-102); 10-ix-2003 (S03-85) 11♂ 10♀ (T.J. Walker). *Osceola Co.,* Intercession City, 1-viii-2002 (WG3, WG4) 1♂ 1♀. **Maryland:** *Cecil Co.,* "Cheapk BCH" (Chesapeake Beach?), 17-ix-1914, 1♀. **Texas.** *Aransas Co.,* near Rockport, 12-vii-2013 (S13-55) 4♂. *Bastrop Co.,* Bastrop State Park, 9-ix-2010 (S10-67) 1♂ 1♀. *Brazoria Co.,* 1 m SE Surfside Beach, 13-vii-2013 (S13-62) 1♂. *Calhoun Co.,* Magnolia Bay, Indian Point Historic Park, 4-viii-2002 (S02-36) 2♀. Rio Hondo, 10-vii-2013 (S13-44) 2♂. *Cameron Co.,* Boca Chica State Park, 3-vi-1991 (S91-36) 8♂ 1♀; 10-vi-2007 (S07-25) 3♂ 1♀; 18-ix-2010 (DAG 2010-117) 2♂ 3♀, all late instars. Hwy 4 3.1 m W Boca Chica State Park, 3-vi-1991 (S91-37) 3♂ 6♀; 10-vi-2007 (S07-26) 4♂ 1♀. Isla Blanca Park on South Padre Island, 10-vii-2013 (S13-41) 4♂. *Fayette Co.,* Schulenburg, 4-viii-2002 (S02-38) 5♂ 1♀; 14-vii-2013 (S13-65) 6♂ 1♀. 2.3 m S Schulenburg, 9-ix-2010 (S10-65) 6♂ 3♀. *Galveston Co.,* Galveston Island, 13-vii-2013 (S13-63) 2♂ 1♀. *Harris Co.,* Cypress, 13-vii-2013 (S13-64) 2♂. Hwy 290 0.5 m W Cypress, 1-vi-1991 (S91-27) 2♂. *Jefferson Co.,* Port Arthur 10-vi-2011 (S11-32) 1♂. O.5 m NW Sabine Pass 1-vi-1991 (S91-30) 2♂. Sea Rim State Park 1.7 m SW of Park entrance, 10-vi-2011 29° 40' 32.9" -94° 02' 34.5" (S11-29, 30) 4♂ 7♀; 6.2 m SW of Park entrance, 1-vi-1991 (S91-28) 8♂ 3♀. *Jim Wells Co.,* Alice 28-vi-1986 (S86-53) 2♂ 1♀; 11-vii-(S13-48, 49, 50) 4♂ 2♀. *Kinney Co.,* Brackettville, 10-vi-1985 (S85-61) 6♂ 5♀; 27-vi-1986 (S86-47) 2♂ 3♀; 4-vi-1991 (S91-40) 6♂ 8♀; 7-ix-2010 (S10-63) 2♂. *Matagorda Co.,* Matagorda, 13-vii-2013 (S13-58) 7♂ 1♀. Egret Island, 13-vii-2013 (S13-59) 6♂ 3♀. *Nueces Co.,* Mustang Island State Park, 12-vii-2013 (S13-51) 4♂. 2 m S Port Aransas along Texas 361, 12-vii-2013 (S13-52) 4♂. *Travis Co.,* Austin, U. Texas Brackenridge Field Lab, 10-ix-2004 (DAG 2004-122) 1♀. *Washington Co.,* 10 m W Brenham, 6-ix-1992 (S92-123) 1♂; 24-v-2001 (S01-51) 2♂; mid-July (S01-95) 1♂. *Willacy Co.,* FR 1420 0.3 m S FR 1018, 10-vii-2013 S13-45) 2♂.

FIGURE 41. Color variation in Texas *G. firmus*: lighter, coastal specimens, with head stripes (2 upper photos and lower left), Cameron Co., TX, S07-26 vs. darker, inland specimen (lower right, Schulenburg, TX, S10-65).

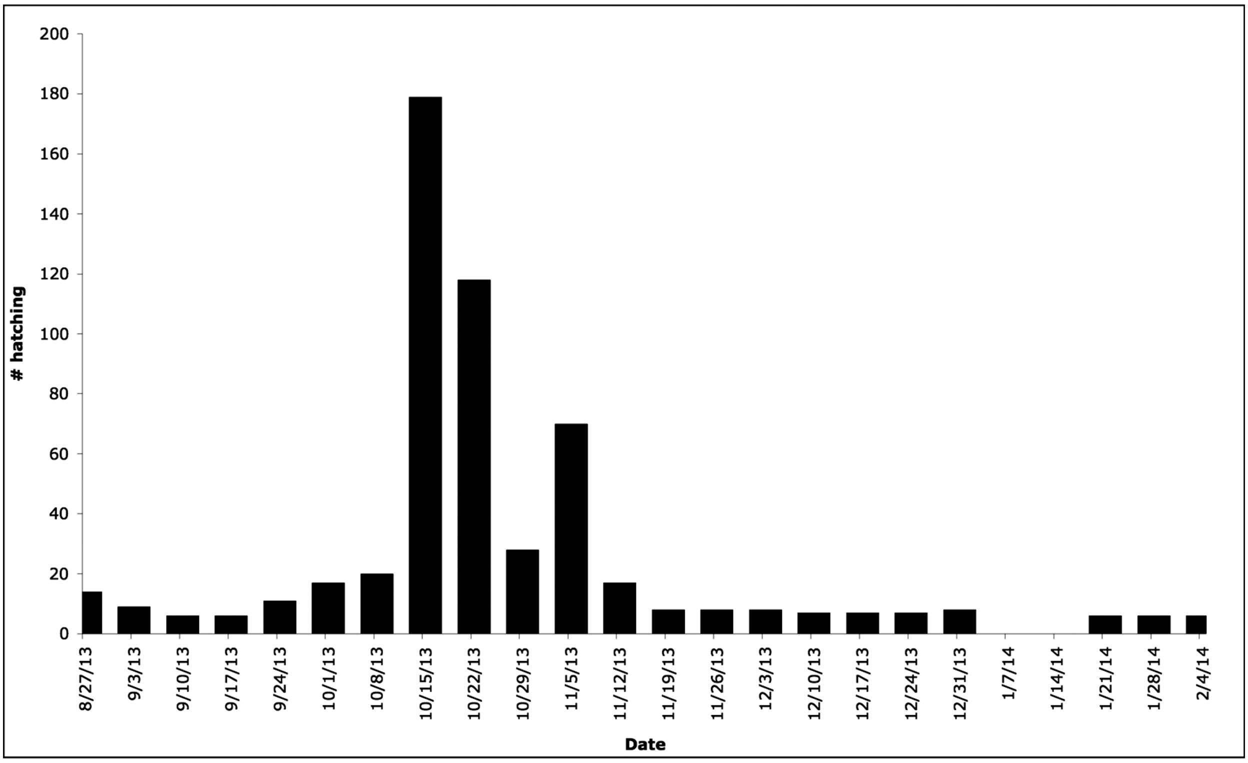

FIGURE 42. Egg hatch from single field collected *G. firmus* (S13-65) from near Schulenburg, TX, showing a mixed egg diapause pattern.

DNA. Multilocus sequences checked (Gray *et al.* 2019) from 5 Texas populations of what we consider *G. firmus* (i.e. no egg diapause): G2029 (Sea Rim State Park, S11-29); G2715 (Matagorda Island, S13-59); G1920 (Brackettville, S10-63); G1915 (Bastrop State Park, S10-67); and G1917 (Schulenburg, S10-65). These were compared to presumptive (because we don't have egg diapause data) *G. pennsylvanicus* from Lubbock, TX (G2708, S13-80); definite *G. pennsylvanicus* from Vermont (G710, S08-74) and Hanksville, Utah (G368, S04-128) against definite Florida *G. firmus* (G62, S03-85). For 16S, our mapping agrees with Harrison & Bogdanowicz (1995, 1997) who showed a single clade for *G. ovisopis, G. pennsylvanicus,* and *G. firmus*, with 1.3% total separation. For ITS2, we show that all Texas populations (*G. ovisopis* and Lubbock *G pennsylvanicus* not run) map together, but separately from Florida *G. firmus* and Pennsylvania, Vermont, and West Virginia *G. pennsylvanicus*. Both ITS2 and multilocus analyses (Gray *et al.* 2019) suggest that Texas and Florida populations of *G. firmus* are distinct.

Discussion. We initially divided Texas *G. firmus* into four species. We detail those impressions here so that future researchers can investigate further since we are not completely convinced that our current taxonomic decisions are correct.

(1) 'Gryllus #19' (multilocus G1920) was only found in Brackettville, on the southern edge of the Edwards Plateau and some 270 km farther inland from the nearest population of *G. firmus* in Austin. No egg diapause (S85-61). '*G.* #19' is distinguished by geographical isolation and habitat differences from other populations of *G. firmus* because it is always associated with areas of dense vegetation (overgrown baseball field and the vacant lot adjacent to "Burgers and Shakes" off Hwy Business 90). Males also have more file teeth when compared to hind femur length (Fig. 43) and females in Brackettville have longer ovipositors vs. hind femur length (Fig. 44). All adults from there were medium sized whereas other inland Texas *G. firmus* are usually larger, although these Brackettville males did have the higher tooth counts (range 179-212) seen in inland populations of *G. firmus.* Adults known June through September.

(2) 'Gryllus near #19' (multilocus G2029—Sea Rim State Park) was found in Harris and coastal Jefferson Co., Texas, as small to medium sized crickets that are never dark. They had no egg diapause (S11-30), probably one generation/year and differed from coastal 'Gryllus #35' in almost no overlap, in females only, in hind femur and ovipositor lengths (Table 1, p. 18). At Sea Rim State Park (S11-29), singing males and nymphs under various objects (such as hay bales) in tidal surge area. In town of Sabine Pass (S11-31) and Port Arthur (S11-32), males singing from areas of mowed, roadside grass.

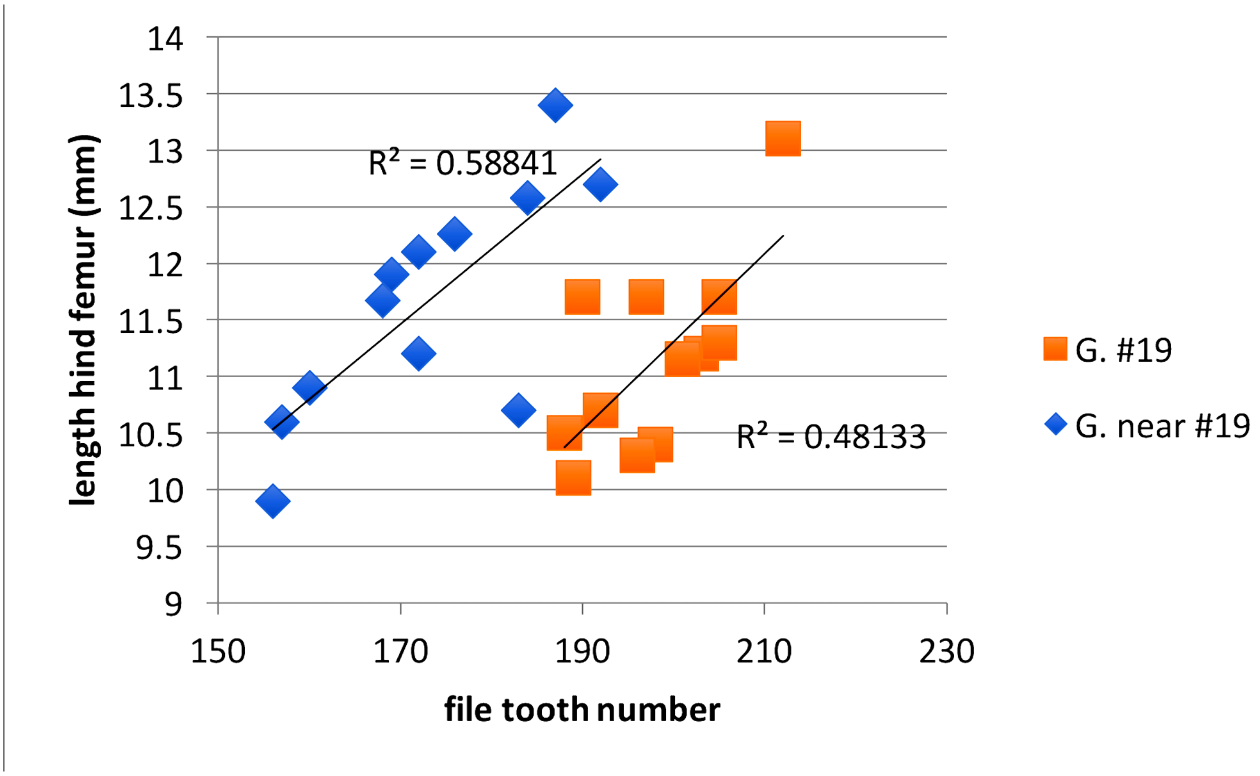

FIGURE 43. Regression file tooth number vs. length hind femur in 'G. #19' vs. 'G. near #19.'

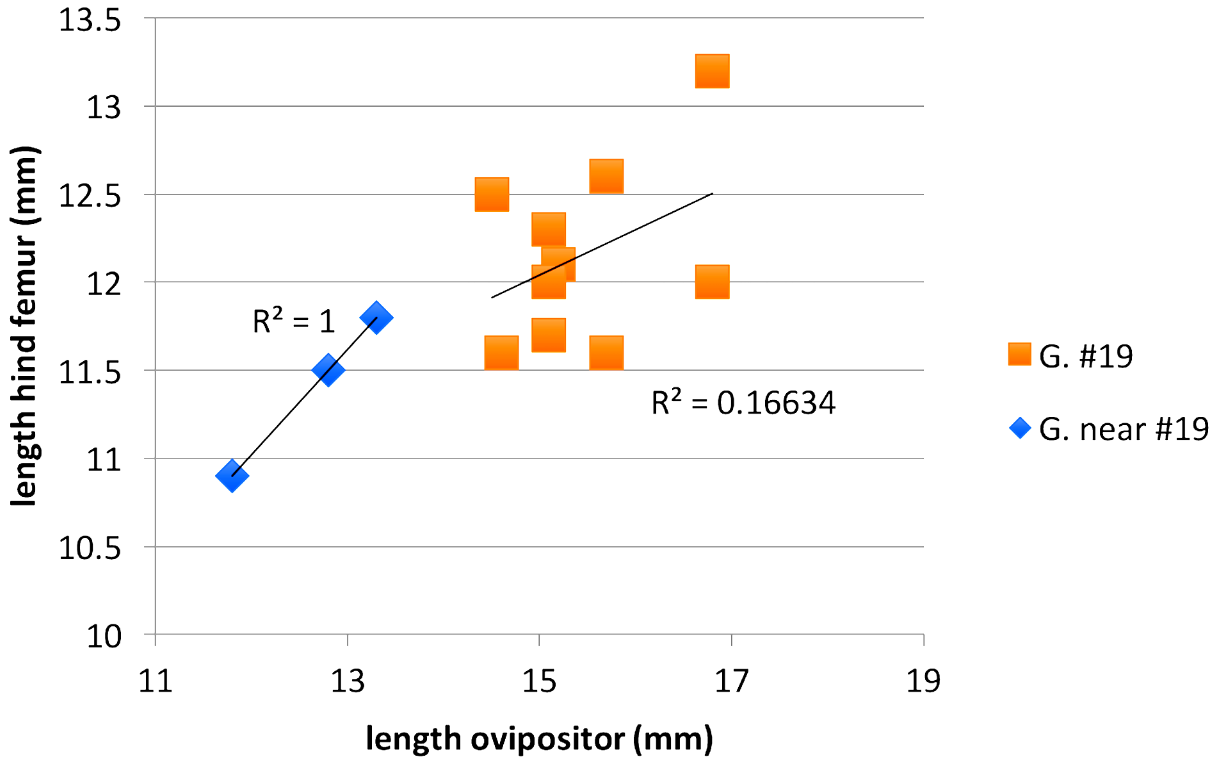

FIGURE 44. Regression length ovipositor vs. length hind femur in 'G. #19' vs. 'G. near #19.'

(3) 'Gryllus #35' (multilocus G2715, Matagorda Island) was found only in south eastern, Gulf of Mexico coastal Texas areas, as medium to large sized crickets, with shorter tegmina than in Florida. They had no egg diapause (Boca Chica, S91-37), probably one generation/year and differed from (1) as discussed above. 'G. #35' can vary from tan/brown forms with head stripes to dark ones.

(4) 'Gryllus #45' (multilocus G1915, Bastrop State Park) are always dark colored and found more inland near forest edges, open grasslands, and watered areas but never associated with sandy areas. No egg diapause (Bastrop State Park, S10-67) and 2 generations/year (S92-123 and S01-51). Likes to climb (10 m W Brenham, TX, S92-123). Corresponds to 'G. #45' of Thomson *et al*. 2012.

In 2013, we conducted an extensive transect along the Texas coast with both forms (2) and (3) found within 3.5 km of each other, on July 13th, in Matagorda Co., at Matagorda (S13-58) and on Egret Island (S13-59). The former site is a semi-residential area where 8 adults (7♂ 1♀) were collected. Of those 7 males, 4 were singing 8 cm above ground on small plants. The ground surface was covered with short annual vegetation and the soil was more loam than sandy. At S13-59, in a dry water channel with clay substrate, we collected 5 adults (2♂ 3♀) and several mid to late instars. From the instars, we raised 1female (adult molt 25-vii) and 5 males (adult molts 5-ix to 30-ix). Four of these September molting males were much larger than the 2 adult males collected there in July but one male was similar in size to those July males.

Given the differences discussed above between (2) and (3), why are we grouping them as one species? For starters, the differences between them as related to no overlap in female cerci, hind femur, and ovipositor lengths, can all be explained by total body size differences, i.e. larger crickets have larger physical characters. When these measurements for femur, ovipositor and cerci length in addition to pronotum width, number of file teeth, and teeth/mm are linearly regressed against each other, the points all fall on or near the same line. Likewise, those differences in when individuals molt to adult might be partially explained by larger females taking more time to mature and/or these later maturing females were the result of continuous generations with variable maturation times. Plus, Walker (1998) has shown that different generations of the same species can have different song properties. In any case, given the similar DNA and song properties, we find no consistent way to separate the two. We do add another unsettling finding to our taxonomic conclusion, even given our limited sample sizes: both (2) and (3) differ in file tooth density, without overlap, between Matagorda (S13-58, range 54.7-58.4, n=7) and Egret Island (S13-59, range 49.5-52.7, n=6), a character that we generally find to be size independent in *Gryllus* species. Clearly more fieldwork is required to determine if two, or more, sister species are microsympatric in this area or if continuous generations, as a result of variable egg diapauses, are responsible for this complicated life cycle picture. Additionally, since northern Florida *G. firmus* have mixed diapause eggs while northern Atlantic coast populations may all have an egg diapause, where does this transition occur and over what geographic distance? Plus examining southern Florida populations might uncover areas where no eggs have a diapause, given their year-round presence (Alexander, 1957; Capinera *et al*., 2004).

G. firmus has been the subject of much work on hind wing length polymorphism (e.g. Roff 1984; Mitra *et al*. 2011; Roff & Fairbairn 2012); flight muscle physiology (e.g. Zera *et al*. 1997; Zera 2005; Jiang *et al.* 2012); biology (Réale & Roff 2002); and mating systems, calling behavior, and female phonotaxis (e.g. Doherty & Storz 1992; Mitra *et al*. 2011; Maroja *et al*. 2014), besides those references mentioned in the section on Hybrid Zones (p. 61).

G. firmus appears to be the only *Gryllus* species where file length is consistently <1.0 mm shorter than tegmina width. *G. firmus* is a confirmed natural host of the tachinid *Ormia ochracea* in Florida, but rates of parasitism are very low (Walker & Wineriter 1991). We recovered one *Ormia ochracea* tachinid from a male from Matagorda Co., Texas (S13-58).

HYBRID ZONES, and other issues between *G. pennsylvanicus* and *G. firmus*.

In the following discussion, we apply the name *G. pennsylvanicus* to any US *Gryllus* population with the following properties: One generation/year because of an obligate winter egg diapause, late summer maturing adults, slow chirping calling song, generally overall black coloration, including tegmina, living on loam substrate (not sand), in inland and upland habitats.

In the following discussion, we apply the name *G. firmus* to any US *Gryllus* population with the following properties: One generation/year (except along the southeastern US seaboard and continuous coastal areas along the Gulf of Mexico) because of an egg diapause, late summer maturing adults (although present year around in Florida [Capinera *et al*. 2004]), slow chirping calling song, generally light colored tegmina (beach individuals can also have longitudinal head stripes), living on coastal beach or lowland sandy substrate habitats. Both dark and light-colored specimens from coastal and southern areas of Texas, whose eggs have no or variable egg diapause, such as from Brackettville or Schulenburg, are placed here. Even so, we have reservations, discussed below, about whether or not what we are calling *G. firmus* in Texas is truly the same species as *G. firmus* along the southeastern US seaboard. For clarity, in the following discussion we denote the western, Texas populations of *G. firmus* as 'TX *G. firmus'*.

From the onset, we state that we do consider *G. firmus* and *G. pennsylvanicus* to be distinct species, but we find diagnostic separation more difficult than previous authors have indicated. We are most persuaded that two species are involved because reciprocal crosses producing viable and fertile offspring can only be made in one direction: male *G. firmus* x female *G. pennsylvanicus* (Harrison 1983; Larson *et al*. 2012). We review below additional evidence based on habitat, morphology and song that suggests that more than one taxon is involved, but we emphasize that despite almost 40 years of research on these taxa and their hybrid zones by the R. G. Harrison lab, the phylogenetic and taxonomic situation between them is not entirely resolved. The statement by Harrison and Arnold (1982) "… that there is still considerable uncertainty about the distributional and evolutionary relationships…" between these two taxa is possibly truer today than more than 37 years ago when first written, since, with this report, a much larger area of the US has now been sampled.

We start with a year-of-publication literature review, mostly from studies along the eastern US, to place subsequent discussions in proper context. Fulton (1952) first appreciated, in North Carolina, the occurrence of a late season, light colored "beach" cricket. Alexander (1957) formally re-assigned Scudder's 1902 name *G. firmus* to Fulton's beach cricket [as *Acheta firma* (Scudder)], and also noted the occurrence of similar light-colored crickets in sandy areas around Lake Michigan and Lake Erie and along the Illinois and Mississippi Rivers. These Midwestern light-colored crickets were able to cross with more commonly encountered, darker-colored specimens of *G. pennsylvanicus*. Alexander (1957, Fig. 18) also noted a complete morphological separation in *G. firmus*, from other Eastern US taxa, when ovipositor length was regressed against body length: he documented that *G. firmus* are large crickets with ovipositors typically longer than 19 mm while *G. pennsylvanicus* are smaller crickets with ovipositors shorter than 18 mm and always shorter than body length. These observations have also been addressed elsewhere by Lutz (1908), Alexander (1968), and Rand & Harrison (1989b), who discussed edaphic factors of body and tegminal color and ovipositor length associated with sandy habitats. The two-species had no overlap (Alexander 1957, Fig. 15 and Table 1) in pulse rates at 85°F: 17-19 in *G. firmus* vs. 22-29 in *G. pennsylvanicus* (repeated in Capinera *et al*. 2004; but see Doherty & Storz 1992, Fig. 3b, for overlap in "far allopatric populations."), although number of file teeth were not noted (see discussion below). Interestingly, of the 9 early mating trials attempted with *G. firmus* males x *G. pennsylvanicus* females, none produced offspring (Fulton 1952; Alexander 1957). These results are different than those subsequently achieved by the Harrison lab.

In the late 1970s, R.G. Harrison and his laboratory began extensive investigations looking at a hybrid zone, along the US east coast, involving *G. firmus* and *G. pennsylvanicus*. They found (Harrison & Arnold 1982) that the most reliable morphological character to separate these two similarly sounding species was ovipositor length. Also *G. firmus* had more file teeth, larger body size and paler tegmina. And while both pulse rate and chirp rates differed between the species, there was overlap. They also found no diagnostic genetic differences. In 1983, Harrison documented that Virginia and Connecticut male *G. firmus* could hybridize with female *G. pennsylvanicus* but not the reverse (but see Rand & Harrison 1989b, p. 443 [and repeated in Mandel *et al*. 2001]; and Maroja *et al*. 2008, for limited exceptions). Significant differences in adult maturation times between the two taxa were noted (Harrison 1985) in Virginia but not in Connecticut, implying possible, but incomplete, temporal separation in Virginia. Harrison (1986) documented that their hybrid zones were a mosaic of populations, and that electrophoresis for three loci provided the most useful markers for distinguishing populations/species. He also noted (Harrison 1986) that ovipositor length in *G. pennsylvanicus* is always <16 mm and >16 mm in *G. firmus*.

Rand & Harrison (1989a, p. 552) noted that mtDNA is the single best genetic character and used (Rand & Harrison 1989b) an electrophoretic index, as part of a broader character index, to separate the two taxa. Ross & Harrison (2002) noted that "ovipositor length is the character that most clearly differentiates the two species." Broughton & Harrison (2003) identified their crickets using "differences in body length, hind wing length, ovipositor length, and tegminal color." Mandel *et al*. (2001) and Maroja *et al*. (2008) determined that the intracellular bacteria *Wolbachia* is not responsible for the one-way hybridization incompatibility seen between these two species, and that soil type preference (Mandel *et al.* 2001) and calling songs (Maroja *et al*. 2008) are slightly different. Andrés *et al.* (2013) examined patterns of transcriptome divergence in male accessory gland proteins. Larson *et al*. (2013) found pronotum width and tegminal hue best for classifying males while ovipositor length and body size were most useful for classifying females. They (Larson *et al*. 2013) also found that "percent sand was only a marginally significant predictor of ovipositor length."

Maroja *et al*. (2014) examined cuticular hydrocarbons and found clear differences in profiles between males and females of both species, from four populations, that were raised in the laboratory during their last instars. The import of these differences is unknown as to whether or not they can be used to separate the two taxa. Maroja *et* *al.* (2009, 2015) list at least four barriers to gene exchange and demonstrate that most loci responsible for pre- and postzygotic barriers are apparently located on the X chromosome (further discussed in Gainey *et al*. 2018). Lastly, Harrison & Larson (2016) reiterate that soil type, in Connecticut, and habitat type and disturbance, in Pennsylvania, help determine the mosaic patchwork of populations of these two taxa.

In no paper to date, has a single morphological or ecological trait been described to unequivocally separate *G. firmus* from *G. pennsylvanicus*. Basically, live along or near the beach in Florida to Texas, and you are large, lighter colored without an egg diapause and called *G. firmus*. Live farther north or farther inland or at elevation, and you are smaller, black with an egg diapause and called *G. pennsylvanicus.* That such a reliable separation method is important, is well illustrated by Mandel *et al.* (2001), where they claim that incorrect assignment of crickets to species by Giordano *et al*. (1997) resulted in erroneous conclusions regarding *Wolbachia* compatibility studies between these two species. To quote Mandel *et al*. (2001, p. 707): "…we sampled [populations that] have been well characterized; based on morphology, allozymes, mtDNA and nuclear gene markers*, they appear* (our emphasis) to represent relatively 'pure' populations of *G. pennsylvanicus* and *G. firmus*." We think this represents circular reasoning: species' determinations were originally made based on variable characters, and then such species' determinations are cited in subsequent discussions as proving that the variable characters are reliable for species' separation.

We now discuss the various comparisons that we made between 'pure' populations of *G. firmus* and *G. pennsylvanicus* in areas of the US west of the Mississippi River and compare our results with what has been previously documented in the above cited publications. Unfortunately, we have also not found an accurate and definitive method to separate the two taxa and maintain that the relationship between these two entities still requires much investigation.

1. Body length and ovipositor length: It was claimed (Alexander 1957; Harrison & Arnold 1982; Harrison 1986; Ross & Harrison 2002; Broughton & Harrison 2003; Larson *et al.* 2013) that *G. firmus* adult females are larger and have longer ovipositors than *G. pennsylvanicus* females. As we discuss elsewhere (p. 17, "Results"), body length is a poor morphological character in field crickets, especially females, because of uneven shrinkage, after death, when specimens are pinned and air dried. Others have used pronotal width (Gray *et al*. 2016b) as a better gauge for body size but we find that hind femur length is even better (see below). In fact, using the supplementary data from Larson *et al*. (2013, available at https://datadryad.org//resource/doi:10.5061/dryad.rr387), from some 425 females of both species, we regressed body length against ovipositor length (Fig. 45, R^2=0.41211), pronotal width against ovipositor length (Fig. 46, R^2=0.62884), and femur length against ovipositor length (Fig. 47, R^2=0.68434).

The three regressions clearly display no separation between the two taxa, and merely show that larger female crickets, measured in several different ways, have longer ovipositors. In this instance, the lack of separation of taxa is not a surprise as the majority of the individuals were sampled from 'admixed' populations. But the regressions do indicate that hind femur length is a better predictor of ovipositor length than is body length or pronotum width given its higher R^2 value.

In our Texas study area (see Fig. 39, p. 56) along the coastal seaboard and low-lying flat plains of the Gulf of Mexico, we performed a similar series of regressions for 45 collected adult females, both light and dark colored, from sandy and non-sandy substrates, but always from presumed populations of TX *G. firmus* because of the absence of an egg diapause. (Note that we simultaneously compared these TX *G. firmus* with western US specimens of *G. pennsylvanicus*—those comparisons are discussed below). For these TX *G. firmus* populations, regressing hind femur length (Fig. 48, R^2=0.73448) against ovipositor length (range 11.8-21.39 mm), we find that larger crickets, as expected, have longer ovipositors. ANCOVA shows that the assigned species do statistically differ in ovipositor length after controlling for hind femur length (Femur $F_{1,\,158} = 229.83$, $P < 2e\text{-}16$; Species $F_{1,158} = 60.85$, $P < 7.8e\text{-}13$).

This seems promising, however the difference is clearly not diagnostic and, remarkably, for these western samples, *G. pennsylvanicus* have longer ovipositors for a given body size than do TX *G. firmus*, which is opposite the pattern observed by other authors studying populations farther east. Note that there is no circularity in our comparison of western samples: individuals were objectively assigned to species based on egg diapause characteristics, not ovipositor length, and were then tested for differences in ovipositor length. Interestingly, we found significant predictive value in TX *G. firmus* for cercus length versus ovipositor length (Fig. 49, R^2=0.66051), and cercus length versus hind femur length (Fig. 50, R^2=0.80151).

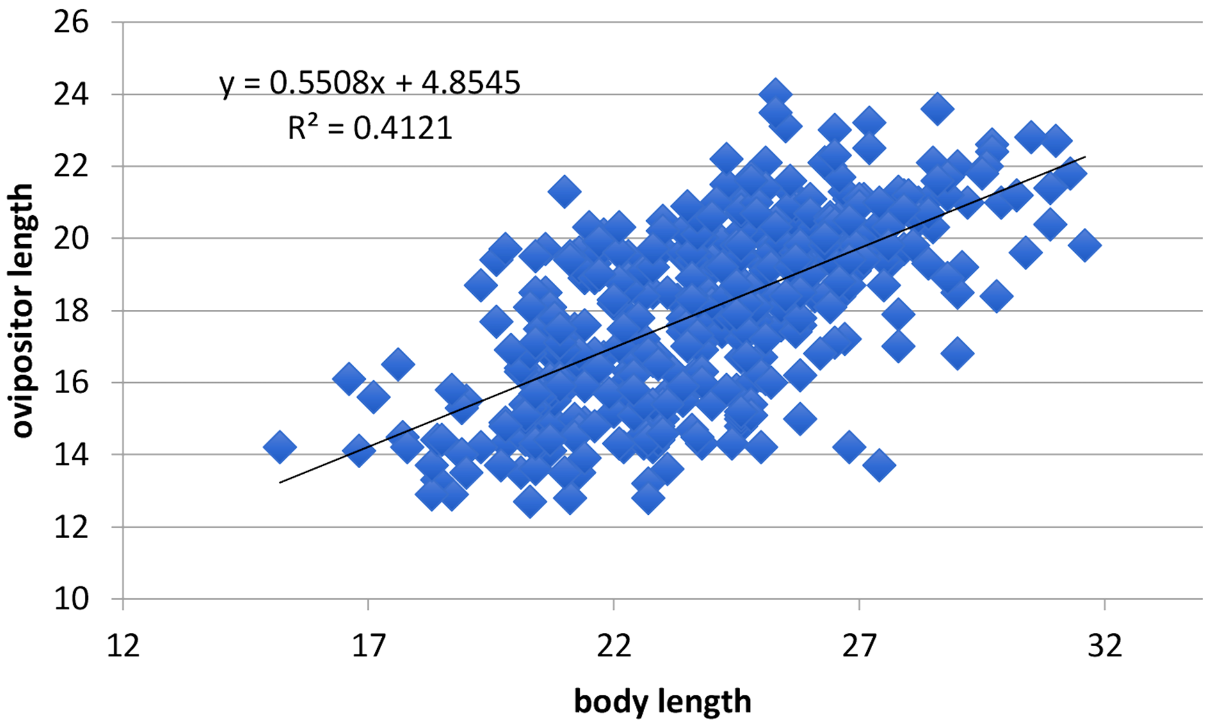

FIGURE 45. Regression body length vs. ovipositor length using combined data for *G. firmus* and *G. pennsylvanicus* from Larson *et al. (*2013).

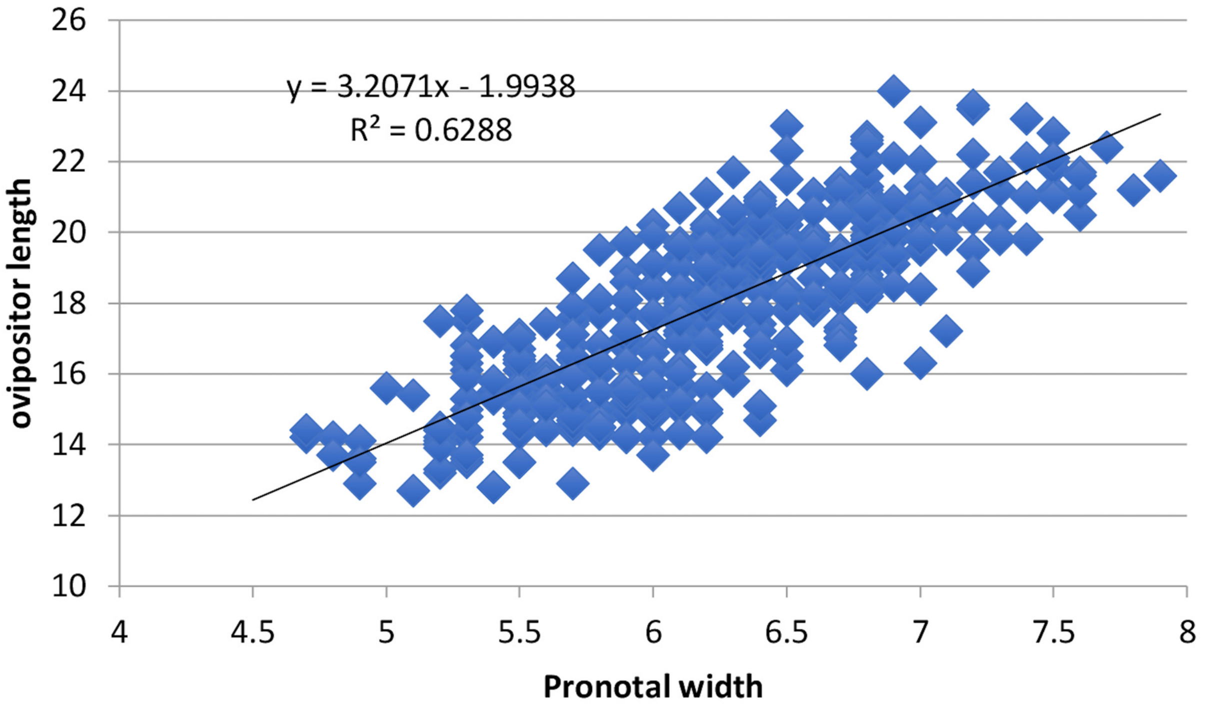

FIGURE 46. Regression pronotal width vs. ovipositor length using combined data for *G. firmus* and *G. pennsylvanicus* from Larson *et al.* (2013).

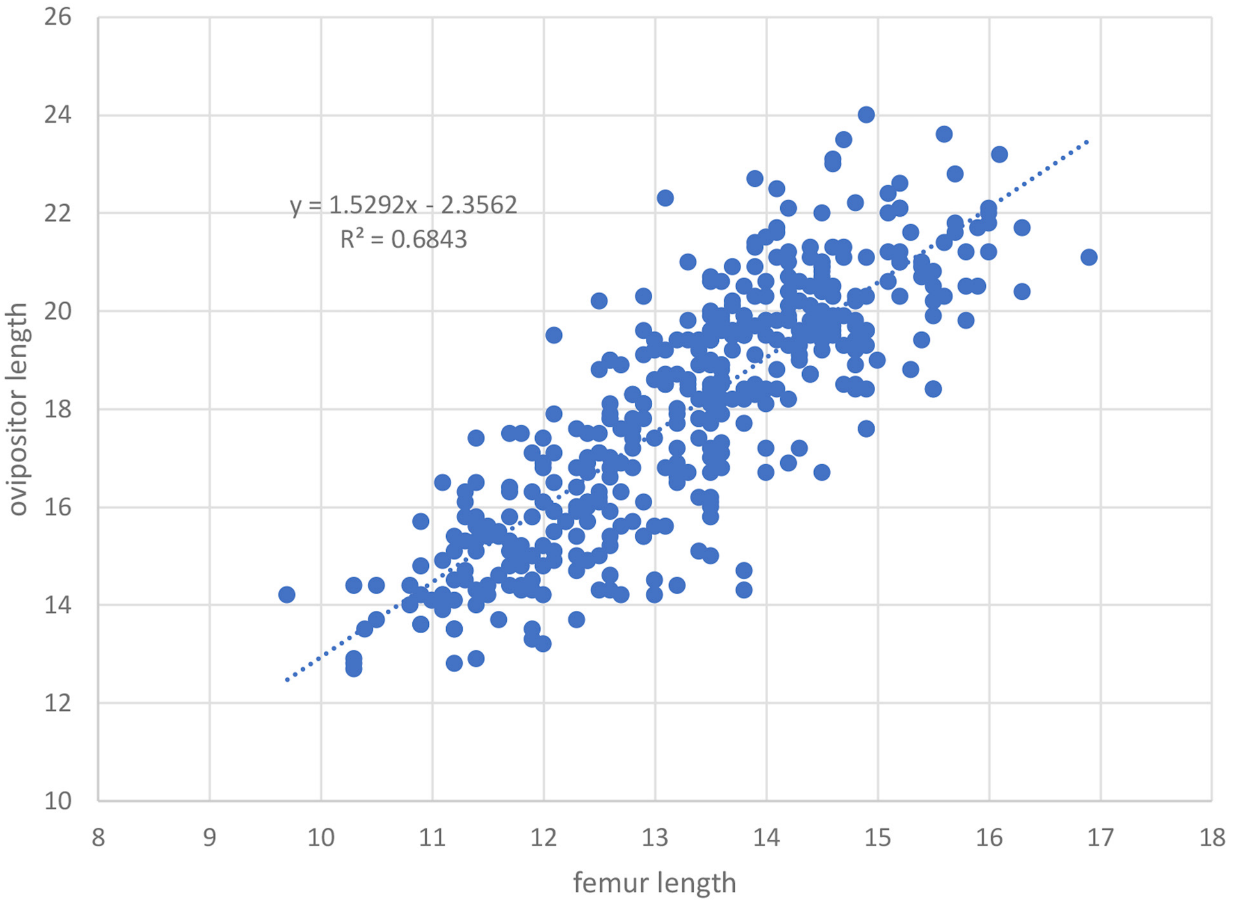

FIGURE 47. Regression hind femur length vs. ovipositor length using combined data for *G. firmus* and *G. pennsylvanicus* from Larson *et al.* (2013).

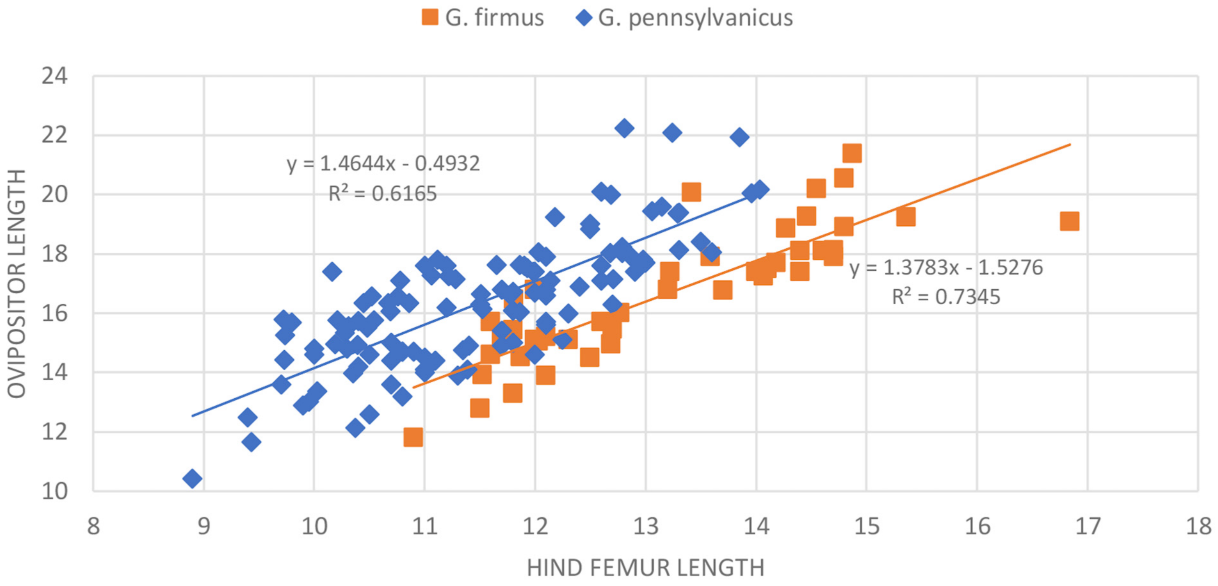

FIGURE 48. Regression hind femur length vs. ovipositor length in *G. firmus* vs. *G. pennsylvanicus.*

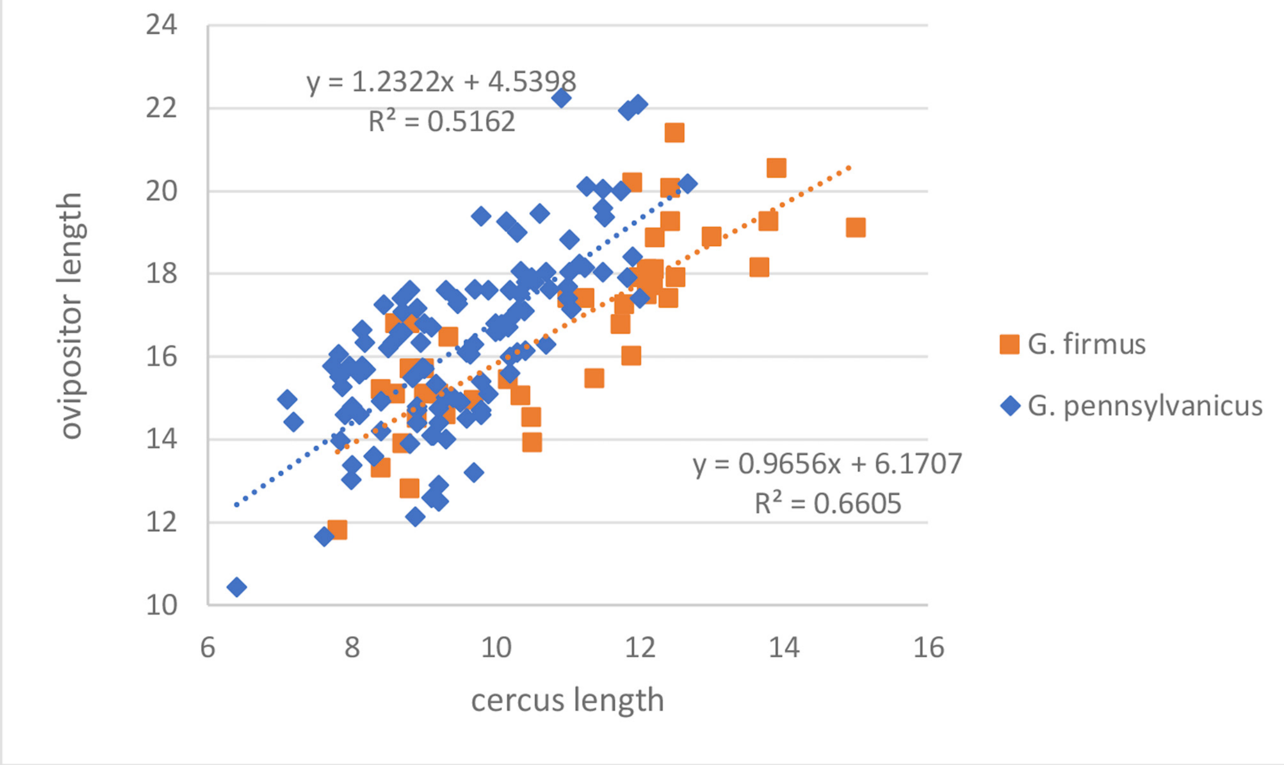

FIGURE 49. Regression cercus length vs. ovipositor length in *G. firmus* vs. *G. pennsylvanicus*.

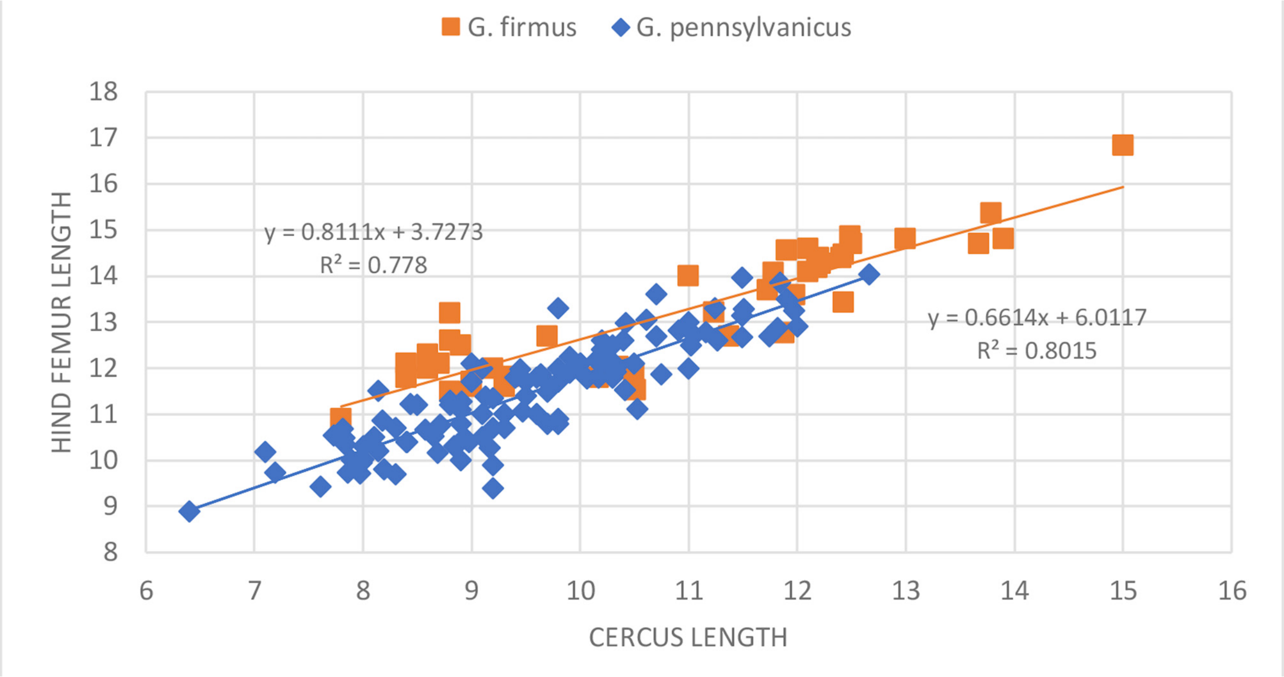

FIGURE 50. Regression cercus length vs. hind femur length in *G. firmus* vs. *G. pennsylvanicus*.

Such comparisons involving cercus length will probably only work well in those few taxa such as *G. pennsylvanicus* and *G. firmus* that have shorter cerci since, in species with longer cerci, these structures are more prone to breakage during molting, aging, and in cases of attempted predation. We also note that our multilocus genetic tree (Gray *et al*. 2019), utilizing some 500 loci, shows little or no separation between these western populations.

We made similar comparisons, (also shown on the previous 3 graphs), for inland and upland, univoltine populations of 116 adult female *G. pennsylvanicus* elsewhere in the western US (see Fig. 32, p. 49), where adults first start appearing in August and eggs have a diapause. We find the following relationships: For hind femur length versus ovipositor length (range 10.43-22.29) (Fig. 48, R^2=0.61648), cercus length versus ovipositor length (Fig. 49,

R^2=0.51623), and cercus length versus hind femur length (Fig. 50, R^2=0.77797). Once again, bigger crickets simply have larger body proportions. In summary, combining and comparing adult females of *G. pennsylvanicus* from the western US, with adult females of TX *G. firmus*, shows minimal separation between the two taxa for hind femur length vs. ovipositor length and no separation for cercus length vs. ovipositor length or hind femur length. The longest ovipositors in any population sampled by us, are found in *G. pennsylvanicus* from Nebraska, Kansas, and Illinois. We also have measured a singleton, large adult female of *G. firmus* from "Cheapk BCH", Maryland, (see p. 57) with an ovipositor exceeding 25.6 mm, and a *G. firmus* from Alachua, Florida, with a 23.19 mm ovipositor. But, in general, longer ovipositors are not diagnostic for *G. firmus*, as claimed for eastern US populations (Alexander 1957; Harrison & Arnold 1982; Harrison 1986; Ross & Harrison 2002; Broughton & Harrison 2003; Larson *et al.* 2013), when a more western US survey is conducted.

A combination of cold winters requiring deeply deposited eggs so as not to freeze, versus eggs laid in coastal sand dunes needing to be deeply deposited so as not to desiccate, raises the provocative possibility that these two 'species' are, in fact, the same? Such would be consistent with Ross & Harrison (2006) suggesting that soil type is not important in determining the success of crickets on different soils and Larson *et al*. (2013) finding that percent sand was only a marginally significant predictor of ovipositor length. So, one 'race' north of 30° latitude with an obligate egg diapause (as per Masaki & Walker 1987), a second 'race' with a variable egg diapause in the transition zone of one versus two generations/year (Walker 1980, in Gainesville, FL, at 29° 39' and Schulenburg, TX (this report, p. 56) at 29° 41', and a third 'race' in southern Florida with no egg diapause and continuous generations (Capinera *et al.* 2004). Although we are skeptical, might the eastern coast "hybrid zones" so well documented by Harrison and colleagues represent zones where climatic and habitat factors indirectly induce a one-way crossing incompatibility?

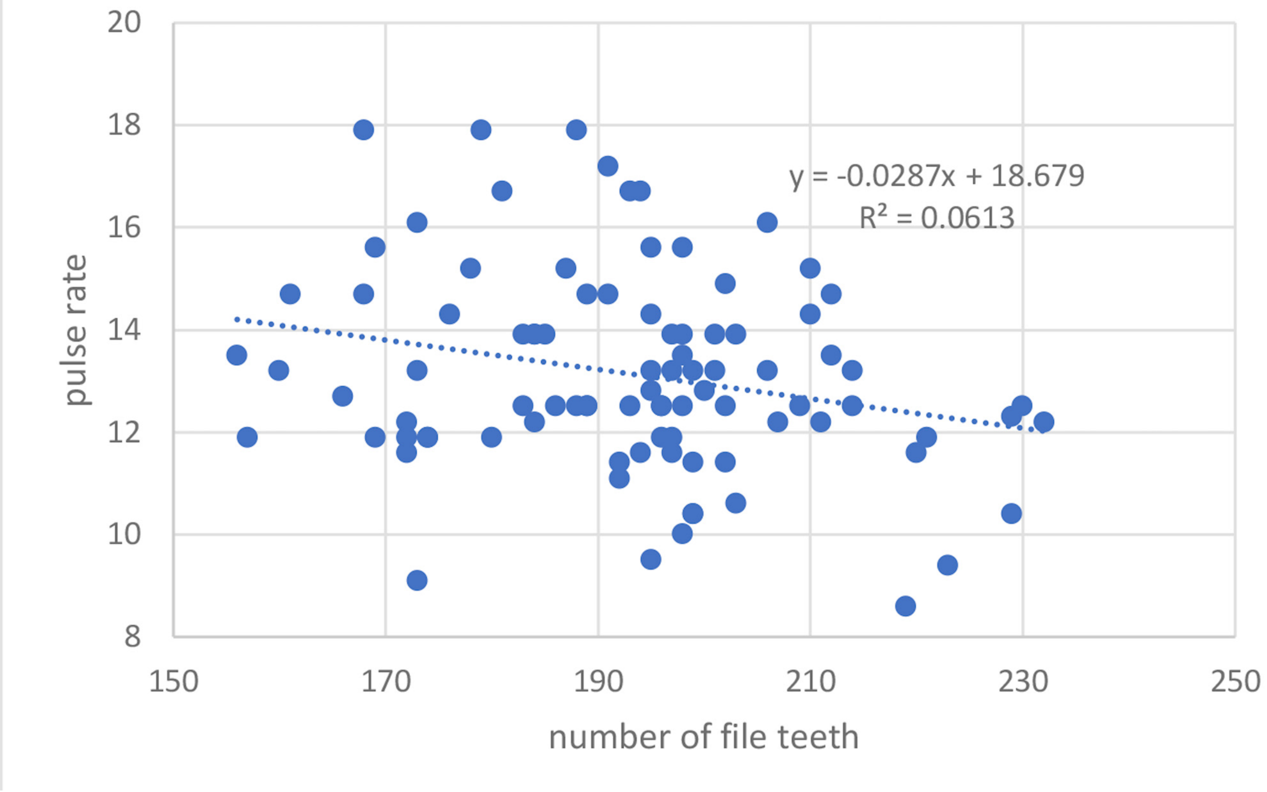

FIGURE 51. Regression number of file teeth vs. pulse rate in *G. firmus*.

2. File tooth number and pulse rate: Harrison & Arnold (1982) state that *G. firmus* has more file teeth than *G. pennsylvanicus* and that the pulse rates differ between the species but with overlap. We find file tooth numbers to be useful in coastal Texas, as they are in Florida (Nickle & Walker 1975), because they separate TX *G. firmus* from all other sympatric congenerics, including microsympatric *G. thinos.* Nickle & Walker (1975) give a range of 166-210 teeth for Florida *G. firmus.* For *G. firmus* west of the Mississippi River, along coastal Texas and somewhat inland, we find a range of 156-233 teeth, in the 91 males examined, with pulse rates ranging from 8.6-20 between 23-27°C. Regressing number of file teeth against pulse rate yields an R^2=0.06131 (Fig. 51). In other words, more teeth in the file does not necessarily result in a slower pulse rate and indicates that in the limited geographic distribution of TX *G. firmus* examined, female crickets would have a difficult time distinguishing between males with different tooth numbers strictly based on pulse rate.

In contrast, we find a complex, and very different situation for *G. pennsylvanicus* west of the Mississippi River (Fig. 52). File tooth numbers ranged from 124-223 in the 114 males collected by us, without any obvious geographical pattern or cline seen (see map, Fig. 34, p. 50). Pulse rates range from 10.9-22.7 between 23-27°C.

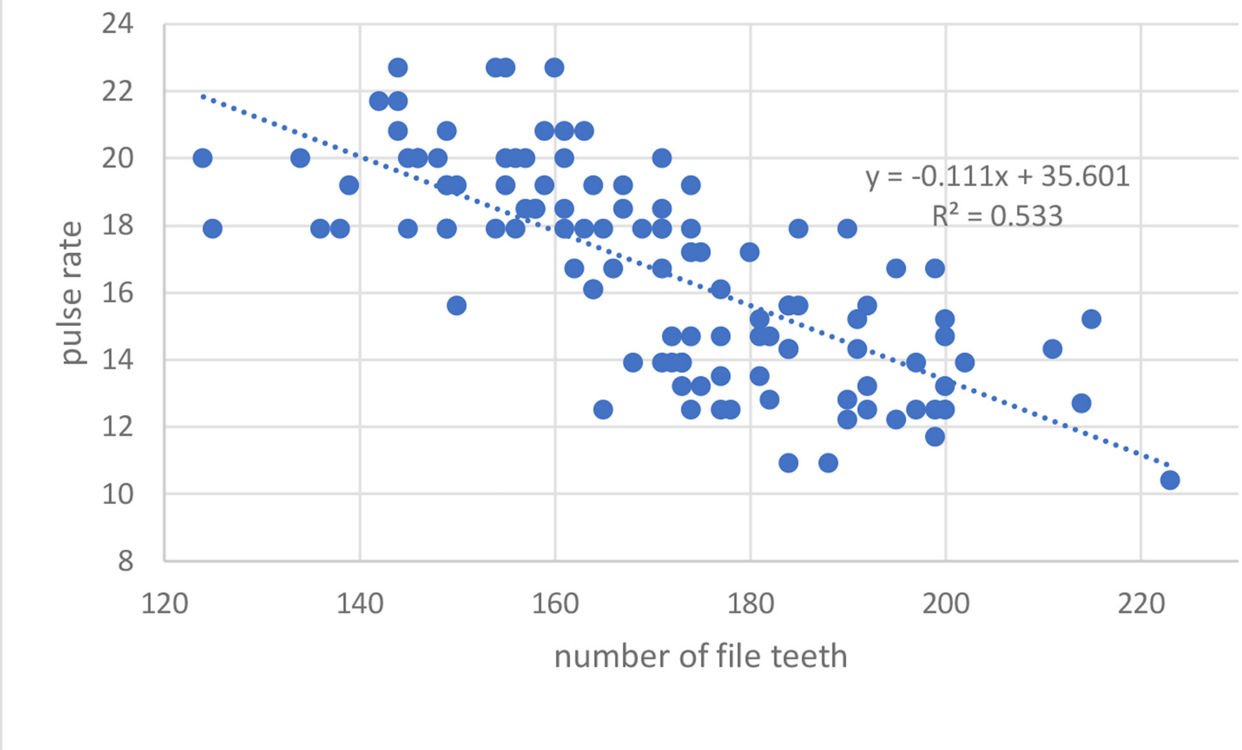

FIGURE. 52. Regression number of file teeth vs. pulse rate in *G. pennsylvanicus* showing males with higher numbers of file teeth have lower pulse rates.

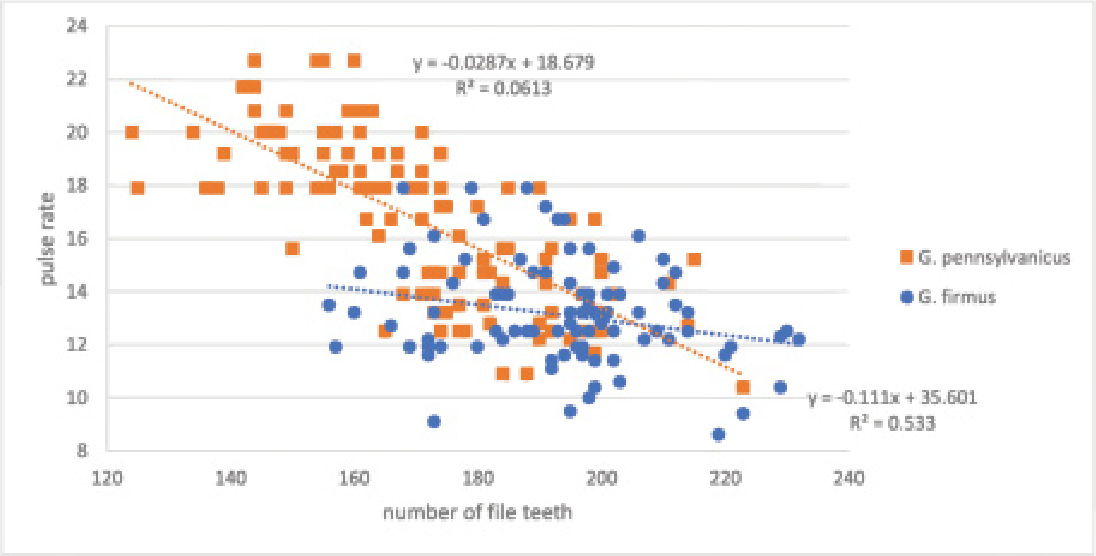

FIGURE 53. Regression number of file teeth vs. pulse rate for combined comparison between *G. firmus* and *G. pennsylvanicus*.

Modeling pulse rate as a function of tooth number shows that, if we combine both samples (Fig. 53), *G. firmus* and *G. pennsylvanicus* differ in tooth number ($F_{1,202} = 164.06$, $P < 2e\text{-}16$), pulse rate ($F_{1,202} = 61.90$, $P < 2.15e\text{-}13$), and their interaction (teeth*species, $F_{1,202} = 64.92$, $P < 6.7e\text{-}14$). Male *G. pennsylvanicus* with many file teeth have lower pulse rates than those with fewer teeth. Nevertheless, file teeth and pulse rates are not reliable ways to separate these two taxa because of the extensive overlap.

These combined data could explain Fig. 15 in Alexander (1957) where, at the same temperature, *G. firmus* has a lower pulse rate than *G. pennsylvanicus* because the number of file teeth were not determined and compared with pulse rate, as we have done.

3. Color of adult tegmina: Many authors (Fulton 1952; Alexander 1957, 1968; Lutz 1908; Harrison & Arnold 1982; Broughton & Harrison 2003; Larson *et al*. 2013) have commented how *G. firmus* adults can best be distinguished from *G. pennsylvanicus* because of lighter tegminal color associated with living in coastal sandy habitats. In our coastal Texas study area, we find a mixed pattern (Fig. 41, p. 58) of tegminal colors in TX *G. firmus* that vary from black to red/beige. The lighter colored ones are limited to sandy coastal areas while more inland populations, such as Schulenburg and Brackettville, are almost uniformly black. As discussed above, we call these inland populations TX *G. firmus* because they lack an egg diapause. Additionally, some 40% of these adults from coastal sand dune areas have longitudinal head stripes, a condition never seen in *G. pennsylvanicus* because all western adult *G. pennsylvanicus* have dark heads. The light color adults of *G. pennsylvanicus* noted by Alexander (1957) in sandy habitats along the Great Lakes are an apparent edaphic adaptation.

4. Presence or absence of egg diapause: Inherently included in calling a population *G. pennsylvanicus* is the presence of an obligate egg diapause resulting in one generation/year. While *G. firmus* is also generally classified as being univoltine with an egg diapause, females from populations in Gainesville, Florida, and Carolina Beach, North Carolina, produce both fast-developing and diapause eggs (Walker 1980; Masaki & Walker 1987). We document (p. 56) this same egg diapause polymorphism from one field-collected adult female from Schulenburg (29° 41'), Texas. We also document (p. 56) that other Texas coastal and lowland populations of TX *G. firmus,* from between 25 and 30 degrees north latitude (coastal Boca Chica, Alice, Sabine Pass) and more inland (Brenham and Brackettville), with only black individuals, lay eggs with no diapause. Relevant to these observations, Masaki & Walker (1987, p. 354) discuss that crickets, worldwide, living north of 30°N are usually univoltine. Schulenburg, Texas (at 29° 41'N) and Gainesville, Florida (at 29° 39'N) thus appear situated at the latitude where a species might start to transition from only having non-diapausing eggs (southern populations) and two generations/year to having all diapausing eggs (northern populations) and one generation/year, apparently in response to cooler temperatures and shorter growing seasons. In support of this contention, The Climate Source web site (http://www.climatesource.com/map_gallery.html) shows that Schulenburg and Gainesville are, climatically, very similar for (1) mean July total growing degree days, (2) mean annual extreme minimum temperature, (3) mean date of last spring freeze, and (4) degree days heat sum above 5.55°C during growing season. We failed to find any TX *G. firmus* north of Austin. Continuing farther north, high file tooth count, slow chirping crickets, presumably fall *G. pennsylvanicus,* were first found at Oklahoma City, and probably in the Texas Panhandle (Lubbock, 1 female only) with the latter two localities collected in September.

G. firmus in southern Florida occur year around (Capinera *et al*. 2004) and may have no diapause eggs, as per Alexander (1968) for south of Lake Okeechobee at 26° 56'N. The point is that egg diapause properties in this assemblage could be related to latitude, and thus winter temperature, and that a gradual transition in egg diapause may occur as one proceeds either north or south. We are not convinced if this cline represents one, or more species, but for purposes of this discussion, we call populations with no, or variable, egg diapause *G. firmus* and morphologically similar crickets with an obligate egg diapause, *G. pennsylvanicus.* Which we believe is another example of the circular reasoning applied to this complex.

In conclusion, we do not claim to understand this situation. After all, it has taken the Harrison lab many years of studying a geographically narrow area to uncover some of the peculiarities of this situation. But it is clear to us that the relationship between these two, or more, presumed taxa is still muddled. In fact, one could make the argument that the multilocus tree (Gray *et al.* 2019) supports the separation of Florida *G. firmus* from TX *G. firmus.* If so, then we have no idea where the transition between these two taxa occurs since their distribution along the Gulf of Mexico from coastal Florida to Brownsville, Texas, seems continuous and uninterrupted.

The Veintinueve Group

Gryllus veintinueve Weissman & Gray, n. sp.

Treated here as a single-species Group, *G. veintinueve* nonetheless is most closely related to a number of currently undescribed species in Mexico that will be the subject of future work. Of the species considered in this treatment, most closely related to the Assimilis Group and *G. locorojo* (Fig. 54, Fig. 6, p. 28).

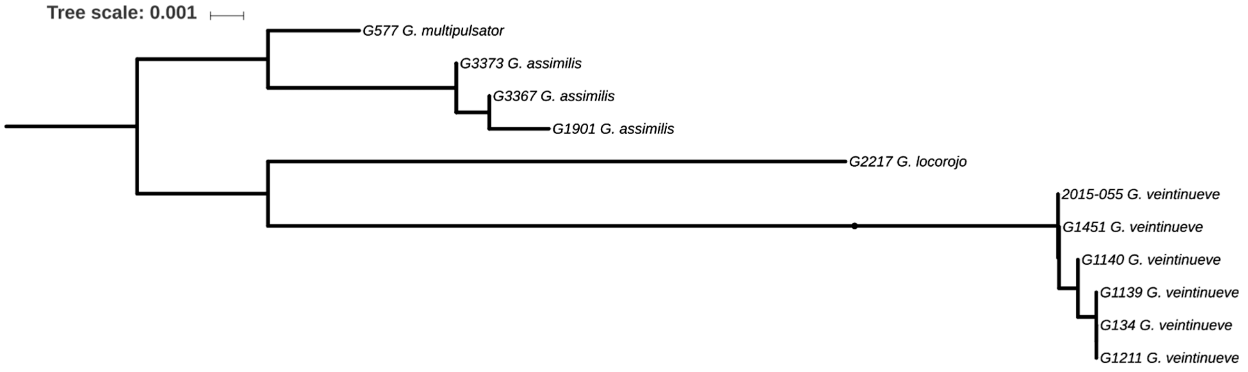

FIGURE 54. ITS2 gene tree. ***G. multipulsator*** sample: S03-41 (G577); ***G. assimilis*** samples: S10-64 (G1901); S16-12 (G3367, G3373); ***G. locorojo*** sample: type locality (Rainbow Mealworms); ***G. veintinueve*** samples: S02-39 (G134); S07-21 (G1139); S07-27 (G1140, G1211); S09-71 (G1451); OK, Love Co., Hwy 32 at Boggy Creek (2015-055).

Gryllus veintinueve **Weissman & Gray, n. sp.**

Number 29 Field Cricket
Figs 54–59, 62, Table 1

'Gryllus #29' in DBW notebooks.

Distribution. Known from Oklahoma and Texas within the study area.

Recognition characters and song. –In an unusually diverse variety of habitats, which is atypical of *Gryllus* species: rocky areas, grasslands and sparse woodlands. Small to medium sized, short cerci, pronotum shiny, always short hind winged. *Song* (Fig. 55, R09–89) a fast chirp, usually 3 (range 2 to 4) p/c, 130–250 c/m, PR 19–28 @25°C. Morphologically resembles allopatric *G. vernalis* in being almost pure black (except for inside of hind femurs) and with female tegmina separated (Fig. 58) although can be separated from the latter by its longer body length, head never narrower than pronotum, no overlap in teeth/mm (Table 1. p. 18), tegmina length and different DNA (Fig. 6, p. 28). Also sounds like *G. vernalis* with which it has an overlapping CR and PR. Distinguished from sympatric *G. fultoni* in eastern Oklahoma and eastern Texas, by *G. veintinueve* never having yellow cerci when alive, head not narrower than pronotum, and no overlap in PR (always faster in *G. fultoni*). Distinguished from sympatric, probably earlier maturing *G. veletis,* which has longer, frequently brown (not black as in *G. veintinueve)* tegmina in both sexes, wider pronotum when compared to hind femur (Fig. 56), and different DNA (Fig. 6, p. 28; Fig. 57).

From always allopatric, more western *G. vocalis,* the latter has a faster chirp rate and almost non-overlapping and faster pulse rate (Table 1, p. 18), in addition to different DNA.

Holotype. Male (Fig. 58). USA: Texas, Howard Co., Big Springs State Park, 2880', 30-vi-2009, 32° 13' 26.5" -101° 28' 26.2". DB Weissman & DC Lightfoot. S09-71, R09-145, DNA sample G1453. 16S GenBank accession # MK446645. BL 19.61, HF 10.96, right cercus 8.04. Right tegmen removed, 146 teeth, file 3.3, tegmen width 4.65, tegmen length 10.9. Type deposited in CAS, Entomology Type #19263.

Paratypes. (Total 64♂ 49♀) **Oklahoma:** *Atoka Co.,* Hwy 43 2.5 m NE Stringtown, 600', 16-vi-1988 (S88-47) 3♂ 1♀. *Comanche Co.,* Hwy 49 E entrance Wichita Mts. Wildlife Refuge, 1300', 6-viii-2002 (S02-46) 5♂ 4♀. *Love Co.* Hwy 32 at Boggy Creek, road cut, 33.98385 -96.97518, 650', 5-xi-2015 (2015-055) RW & JE Cohen, 1♀, as nymph. *Osage Co.,* 9 m NW of Hwy 64 on S209 W Ave. 600', 15-vi-1988 (S88-44) 2♂ 1♀. *Tulsa Co.,* Keystone State Park, 600', 15-vi-1988 (S88-42) 4♂ 4♀. Lake Keystone Dam Area, 740', 22-v-2001 (S01-47) 7♂ 2♀; 9-vi-2007 (S07-21) 5♀. Tulsa, near 5828 W. Skelly Dr., 36° 04' 56.7" -96° 02' 58.0", 775' 15-vii-2013 (S13-67) 6♂ 1♀. 2 m E Tulsa city limits off I44, 36° 09' 38.1" -95° 47' 04.7", 756' 15-vii-2013 (S13-68) 5♂ 2♀. **Texas:** *Hidalgo Co.,* Bentsen Rio Grande Valley State Park, 110', 3-viii-2002 (S02-34) 4♂ 1♀; 10-vi-2007 (S07-27) 4♂ 4♀. *Howard Co.,* Big Springs, Big Springs State Park, 2880' 30-vi-2009 (S09-71) 8♂ 3♀. *Tarrant Co.,* Fort Worth Nature Center and Refuge 2 m NE Lakeside 600', 5-viii-2002 (S02-39) 8♂ 17♀. Grapevine Lake Dam, 23-v-2001 (S01-48) 1♂. *Taylor Co.*, 17 m S Abilene on Hwy 277, 2250', 11-vi-1988 (S88-34) 3♂ 1♀. *Val Verde Co.,* 7.5 m E Del Rio on Hwy 90. 27-vi-1986 (S86-50) 4♂ 2♀.

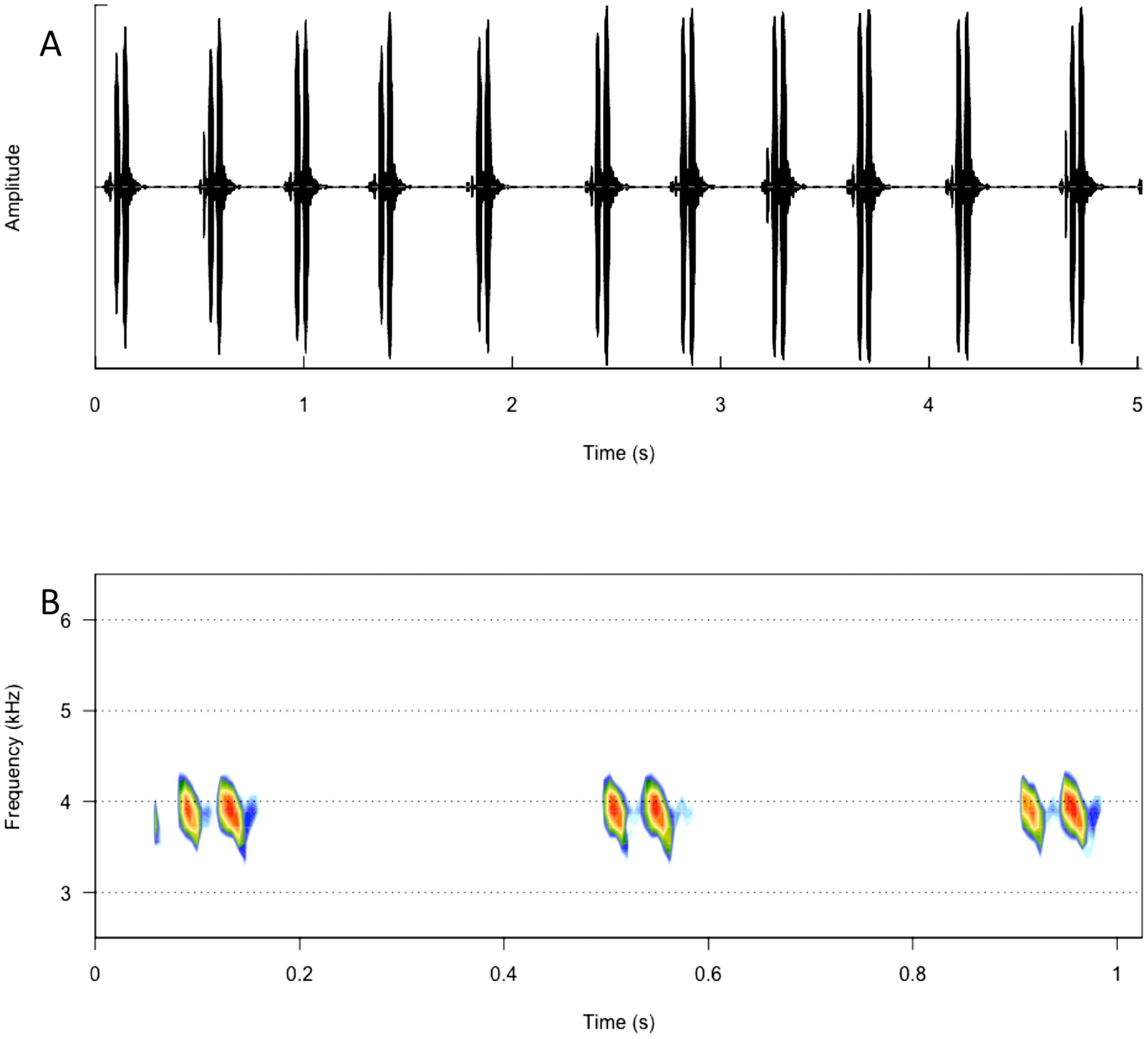

FIGURE 55. Five second waveform (A) and one second spectrogram (B) of calling song (R09-89) of *G. veintinueve* from type locality (S09-71), recorded at 25°C.

Derivation of name. In homage to the notebook number that this species was designated by for some 30+ years. Also, we couldn't think of a good name, although Variable Habitat Field Cricket, 'G. habitolatus', was entertained, but discarded, since it might engender confusion with the (Color) Variable Field Cricket *G. lineaticeps.*

Geographic distribution. Fig. 59. Also into adjacent northern Mexico.

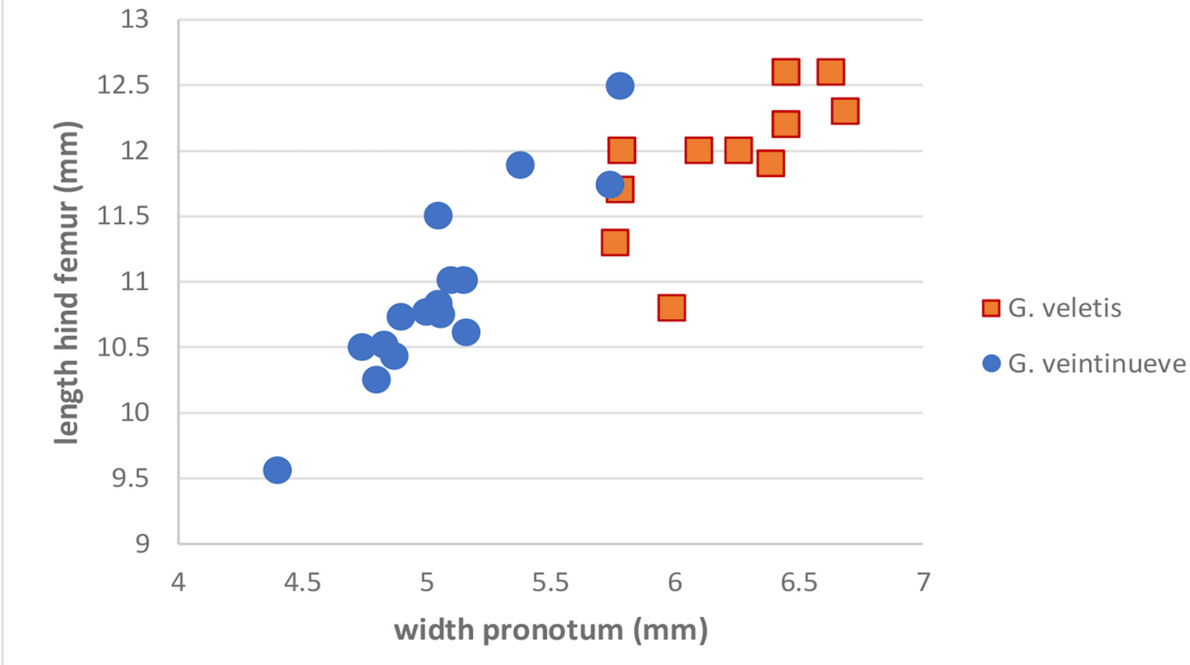

FIGURE 56. Regression width pronotum vs. length hind femur in *G. veintinueve* vs. sympatric *G. veletis*, showing near morphological separation.

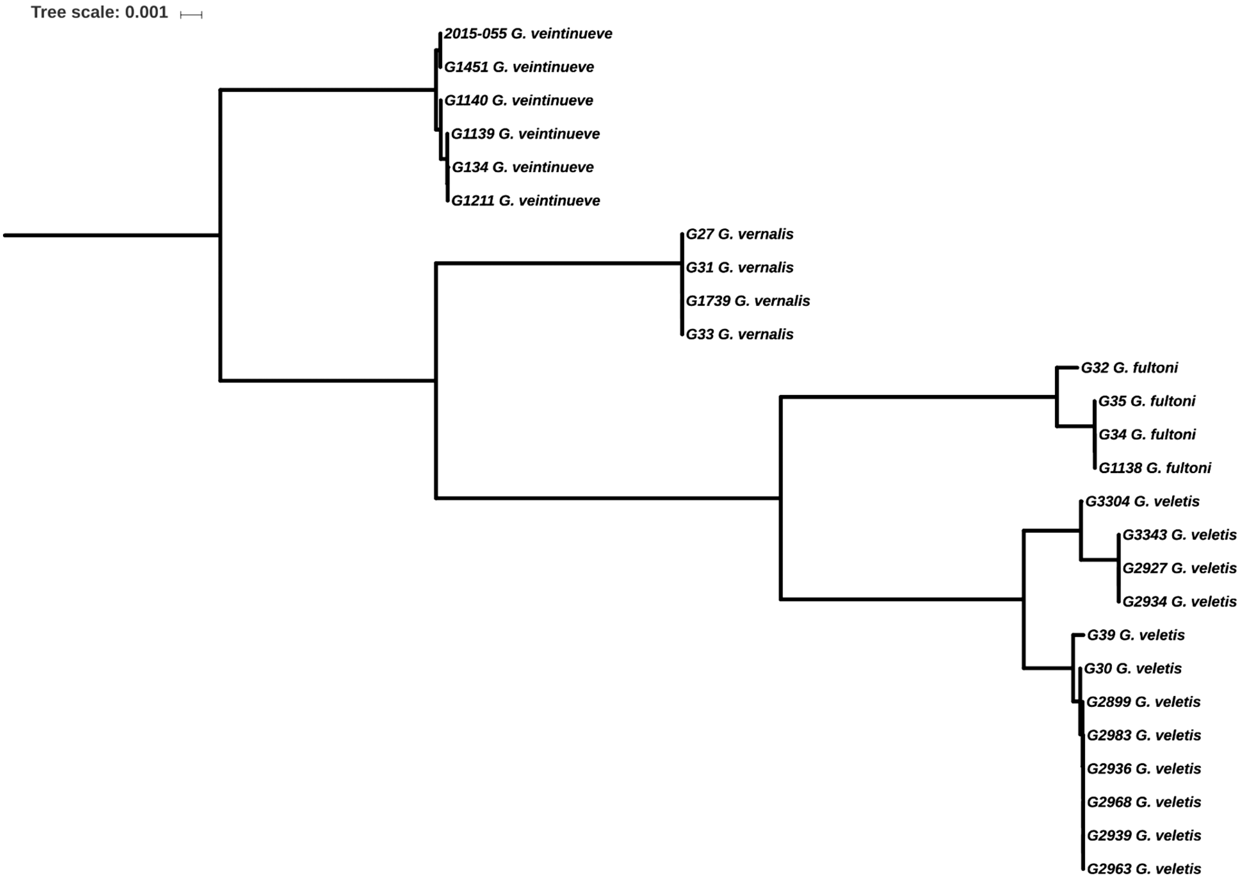

FIGURE 57. ITS2 gene tree. ***G. veintinueve*** samples: S02-39 (G134); S07-21 (G1139); S07-27 (G1140, G1211); S09-71 (G1451); OK, Love Co., Hwy 32 at Boggy Creek (2015-055). ***G. vernalis*** samples: S03-56 (G27, G1739); S03-62 (G31, G33). ***G. fultoni*** samples: S03-62 (G32, G34); S03-64 (G35), S07-22 (G1138). ***G. veletis*** samples: S03-58 (G39); S03-60 (G30); S15-9 (G2939); S15-16 (G2927, G2934); S15-21 (G2899); S15-24 (G2936); S15-25 (G2963, G2968, G2983); S15-53 (G3304, G3343).

FIGURE 58. Holotype male (left), *G. veintinueve*, paratype (middle) female (S09-71), and color variant (right) male (S02-46).

Habitat. Variable: rocky areas, such as road cuts south of Abilene (S88-34), Osage Co. (S88-44), and Stringtown (S88-47); rocky dam areas at Keystone State Park (S88-42, S01-47 and S07-21) and Grapevine Lake Dam (S01-48); grassy areas E Del Rio (S86-50) and Wichita Mts. Wildlife Refuge (S02-46); and sparse woodland usually with grass at Bentsen Rio Grande Valley State Park (S02-34 and S07-27), Fort Worth Nature Center (S02-39), and Big Springs State Park (S09-71). These crickets climb trees: (1) At Big Springs State Park (S09-71), two males singing from 1–2 m above ground, with a female approaching the singing, higher male. (2) At 3.2 km E Tulsa (S13-68), two males singing from tree trunks 1–2.5 m above ground and a third male 0.3 m above ground on tree truck but not singing. The 2 singing males moved around the tree truck before dropping to the ground where they were collected.

Life cycle and seasonal occurrence. No egg diapause: Osage Co. (S88-34) and Big Springs State Park (S09-71). Probably 2 generations/yr. Field collected nymphs matured as followed: late July and 12-viii (Big Springs State Park, S09-71); 18 & 30-viii (Bentsen Rio Grande Valley State Park, S02-34); 5-viii & 10-viii (Tulsa, S13-67), and several in early August (E Tulsa, S13-68) and probably all represent second generation, although variable maturing rates in first generation individuals can't be ruled out without more extensive field work.

Variation. **Body length:** Largest adults collected at Lake Keystone Dam (S01-47). **Inside hind femur:** Varies from bright orange (Fig. 58) to almost absent (Fig. 58).

DNA. Multilocus G1330 (type locality) and 2015-055 (OK, Love Co.) most closely related to several undescribed Mexican species (Gray *et al.* in prep). In our abbreviated US tree (Fig. 6, p. 28), maps closest to Assimilis Group and *G. locorojo.* DNA helped confirm that one habitat-diverse species is involved here. Does not map close to the three US *Gryllus* species that it, physically, most closely resembles: *G. vernalis, G. veletis,* and *G. fultoni.*

Discussion. Occurs with *G. fultoni* at Keystone State Park (S88-42 and S01-47), and around Tulsa (S13-68). Occurs with *G. veletis* around Tulsa (S13-67 and S13-68). In these situations, populations of *G. veintinueve* seem to be peaking when most spring singing *G. fultoni* and *G. veletis* have died out.

The Assimilis Group

G. assimilis (Fabricius) and *G. multipulsator* Weissman.

Sister species with a slow chirp rate typically consisting of 6–9 (*G. assimilis*) or 11–17 (*G. multipulsator*) pulses per chirp (Figs. 60, 61). Separated by geography (Fig. 66 vs Fig. 72), DNA (Fig. 62), and song differences.

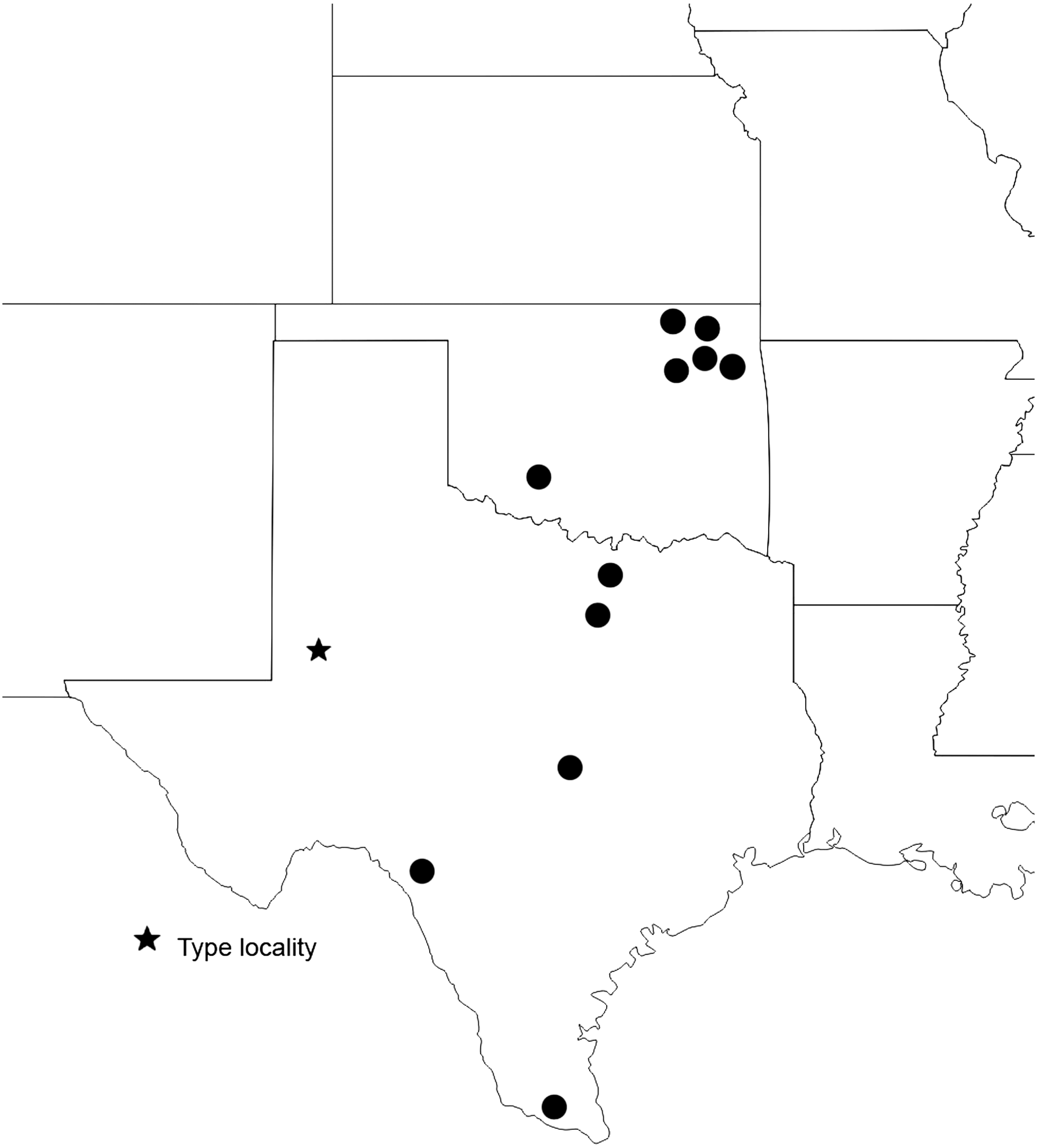

FIGURE 59.. Known US distribution of *G. veintinueve*.

***Gryllus assimilis* (Fabricius)**
Jamaican Field Cricket
Figs 54, 60–66, Table 1

1775 *Acheta assimilis*. Systema Entomologiae, p. 280. Type from Jamaica lost, according to Alexander (1957). Neotype male (Fig. 63) selected by Weissman *et al*. 2009: Jamaica, St. Catherine Parish, Worthy Park, 27-xi-1968. T.J. Walker. Type deposited in CAS, Entomology Type #18172.

‘Gryllus #1’, in part, of DBW notebooks.
2009 *Gryllus assimilis* Weissman *et al*. 2009.
See Cigliano *et al.* (2019) for complete list of synonymies.

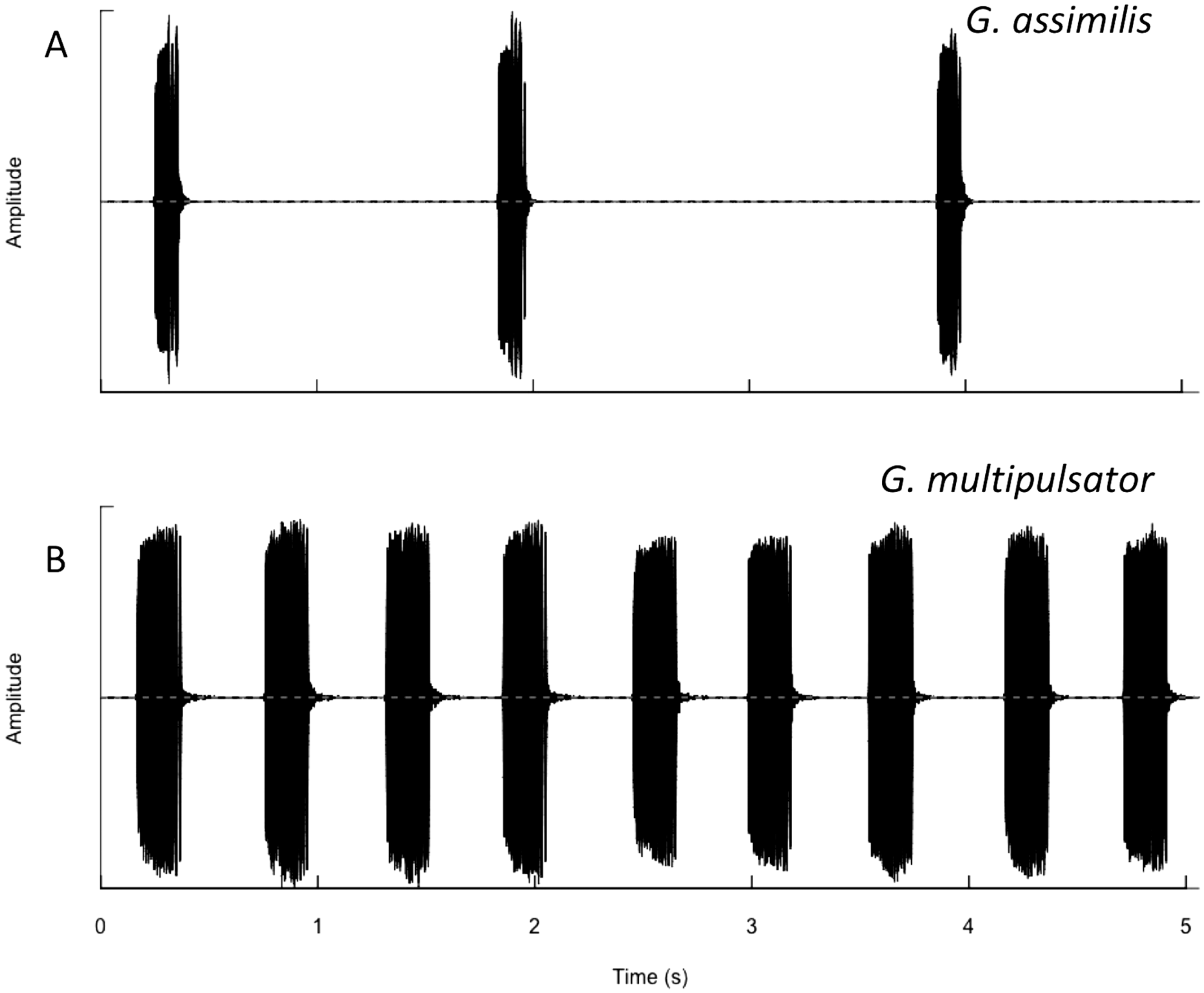

FIGURE 60. Five second waveforms of calling songs of (A) *G. assimilis* and (B) *G. multipulsator*. (A) *G. assimilis*: (R13-231) Rio Hondo, TX (S13-44), at 25°C; (B) *G. multipulsator*: (R15-325) Pima Co., AZ (S15-108), at 25.4°C.

Distribution. Texas and Florida only within the US.

Recognition characters and song. Always macropterous, although rare individuals apterous after shedding hind wings. Medium to large size (Table 1, p. 18), head frequently narrower than pronotum (Fig. 64), dorsal pronotal surface covered with short, fine hairs usually resulting in dull appearance. *Song* (Fig. 65, R13-231, S13-44) loud, 6–9 (rarely 10) p/c, PR for first pulse pair ranges from 50 to 111, PR of last pair ranges from 40 to 83 (Weissman *et al.* 2009). Chirps/second variable, but distinctive and usually <2.5 at 25°C. In the US, only native in southern Texas but introduced in southern Florida (Alexander & Walker 1962). Probably continuous generations. Only sympatric Texas species (and then only in Brackettville (S10-63) and Big Bend (S16-12), TX) with a similar, but distinctive song is *G. personatus*, the latter having a faster chirp rate, a shiny pronotum, different microhabitat requirements, and different head and pronotum color patterns.

Derivation of name. “as” = a copper coin; “similis’ = like, resembling, perhaps with reference to an orange/reddish specimen that reminded Fabricius of the color of a copper coin.

Geographic range. (Fig. 66). Native in southern Texas, introduced in Florida (Alexander & Walker 1962). Fieldwork in 2013 in southern coastal Texas uncovered a much wider distribution than seen in previous years (Weissman *et al*. 2009). Ranges through Mexico and Central America, usually east of the Continental Divide. On many Caribbean Islands (Otte & Perez-Gelabert 2009, Weissman *et al.* 2019), and possibly into South America

(Weissman *et al*. 2009). Widespread sale of this cricket species by US pet-feeder suppliers raises the possibility that feral populations could be established outside its normal US-North American distribution (Weissman *et al.* 2012). Barranco (2012) claims feral populations of *G. assimilis* in Spain but doesn't supply an oscillogram to confirm identification. We believe those crickets could be *G. locorojo* (Weissman *et al*. 2012).

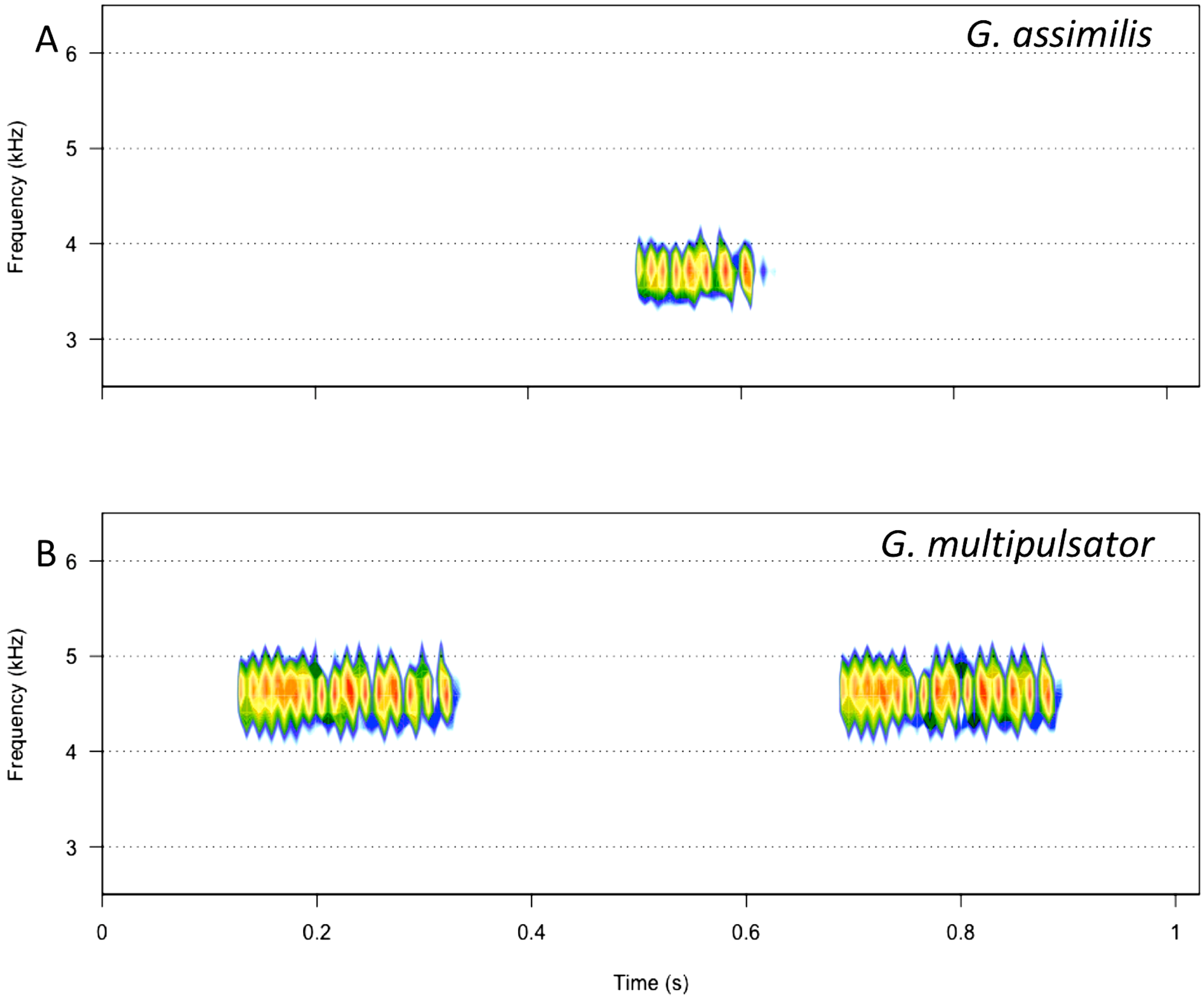

FIGURE 61. One second spectrograms of *G. assimilis* (A) and *G. multipulsator* (B), same males as in Fig. 60.

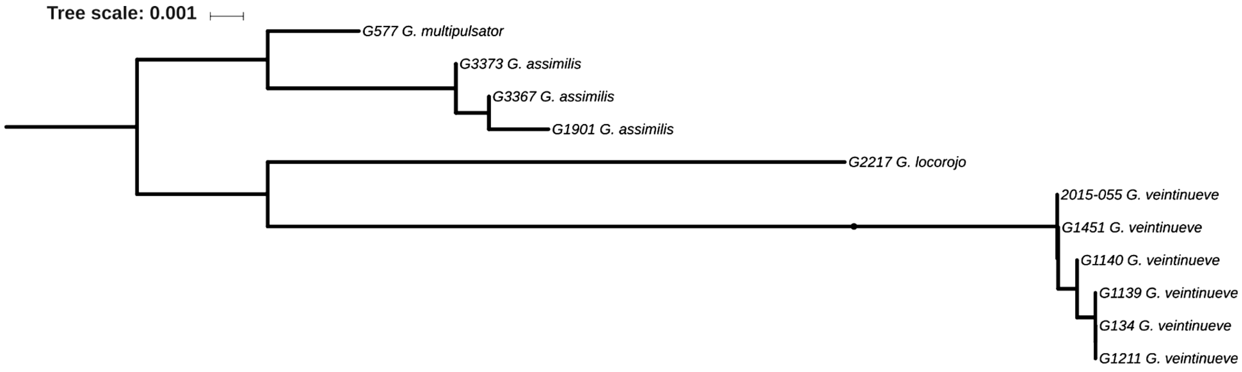

FIGURE 62. ITS2 gene tree. ***G. assimilis*** samples: S10-64 (G1901); S16-12 (G3367, G3373); ***G. multipulsator*** sample: S03-41 (G577); ***G. locorojo*** sample: type locality (Rainbow Mealworms); ***G. veintinueve*** samples: S02-39 (G134); S07-21 (G1139); S07-27 (G1140, G1211); S09-71 (G1451); OK, Love Co., Hwy 32 at Boggy Creek (2015-055).

FIGURE 63. Neotype male, *Gryllus assimilis,* photographs and labels.

FIGURE 64. Color variation in *G. assimilis* from reddish female (left, Brackettville, TX, S10-63) to dark male (right, Quintana Roo, Mexico, S02-12). Note head narrower than pronotum and hirsute and dull pronotum surface.

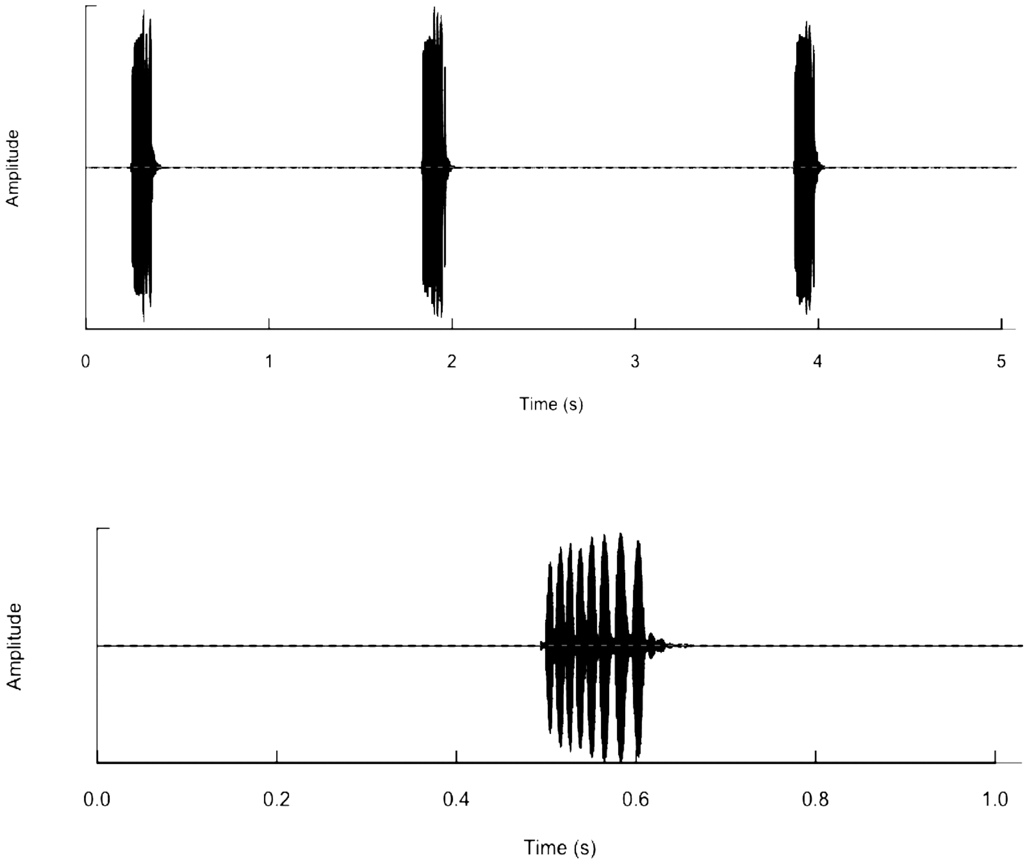

FIGURE 65. Top: Five second waveform of calling song of *G. assimilis* (R13-231) Rio Hondo, TX (S13-44), at 25°C; Bottom: One second waveform of same song showing individual pulses.

Habitat. Almost always associated with people and their watered environs such as lawns, golf courses, school grounds, and in towns. Usually in mowed grassy areas and sometimes in holes.

Life cycle and seasonal occurrence. Diapause unknown for any stage of development. Probably 2 or 3 generations/year with overlap of the continuous generations. Collected early June to mid-September, but obviously present at other times of the year.

Variation. **Color:** Head, pronotum, body, tegmina, and legs from black to tan (Fig. 64). As we have not seen winter/spring individuals, we may be missing darker colored individuals.

Specimens examined. **Texas:** *Bastrop Co.,* Smithville, 325', late September. S.M. Bertram. *Brazoria Co.,* Farm Road 521 5.5 m SE Brazoria, 38', 13-vii-2013 (S13-61). *Brewster Co.,* Big Bend National Park, Rio Grande Village, 1860', 28-v-2016, (S16-12). *Calhoun Co.,* Port Lavaca, 18', 12-vii-2013 (S13-57). *Cameron Co.,* Brownsville, sea level, 3-vi-1991 (S91-38). 3.1 m W Boca Chica State Park on Hwy 4, 10-vi-2007 (S07-26). Rio Hondo, 8m, 10-vii-2013 (S13-44). Intersection Farm Roads 510 and 2480. 2m, 10-vii-2013 (S13-43). *Fayette Co*., 2 m S Schulenburg, 440', 9-ix-2010 (S10-65). Schulenburg, 460', 9-ix-2010 (S10-66); 14-vii-2013 (S13-66). *Hidalgo Co.,* Benson Rio Grande State Park, sea level, 3-viii-2002 (S02-34); 10-vi-2007 (S07-27). *Jim Wells Co*., Alice, 171', 11-vii-2013 (S13-48, 49, 50). *Kinney Co.,* Brackettville, 1160', 7-ix, 2010 (S10-63). *Nueces Co.,* Corpus Christi, sea level, 11-vi-2011 (S11-36); 12-vii-2013 (S13-53). *Refugio Co.,* Tivoli, 12', 12-vii-2013 (S13-56). *Val Verde Co*., Del Rio, 1140', 7-ix-2012 (S10-64). *Victoria Co.,* Victoria, 20', 4-viii-2007 (S02-37). *Willacy Co.,* Raymondville, 10-vii-2013 (S13-47). Farm Road 1420 near intersection FR 498, 15', 10-vii-2013 (S13-46).

DNA. G3373 (Big Bend, TX [S16-12]) in multilocus species tree (Gray *et al.* 2019); *G. multipulsator* is closest DNA relative, at least within our study area. DNA data from a more extensive series is presented in Weissman *et al*. 2009.

Discussion. In Texas, before 2013, we found this species generally uncommon and dispersed, which contrasts with the situation along the east coast of Mexico where *G. assimilis* is more common. For unknown reasons, collecting in coastal Texas in 2013 uncovered several dense populations and much wider distributions than in previous years. This cricket is loud and singing males are not easily overlooked. Perhaps because of its adaptation to lowland, cool coastal habitats, *G. assimilis* males still sing well at 04:00 when most other *Gryllus* species have long ceased singing.

Bertram & Rook (2011a, b) have studied calling songs and biological aspects in this species from the Austin, Texas area, while Pollack & Kim (2013) and Vedenina & Pollack (2012) studied female phonotaxis and variable courtship song in long-term laboratory cultures. Sturm (2014) and Villarreal *et al.* (2018) examined aspects of mating strategies. Weissman *et al.* (2012) documented efforts by US and European cricket farms to utilize another *Gryllus* species, *G. locorojo,* misidentified as *G. assimilis,* to replace virus-infected *Acheta domesticus* as the preferred pet-feeder cricket.

S.M. Bertram notes (pers. comm. to T.J. Walker, March, 2015) that she and her group have encountered thousands of flying individuals at lights in the fall around Smithville, Bastrop Co., TX, in 2007, 2008 or 2009, and 2014. This situation seems similar to those outbreaks described by Alexander & Walker (1962) in Florida.

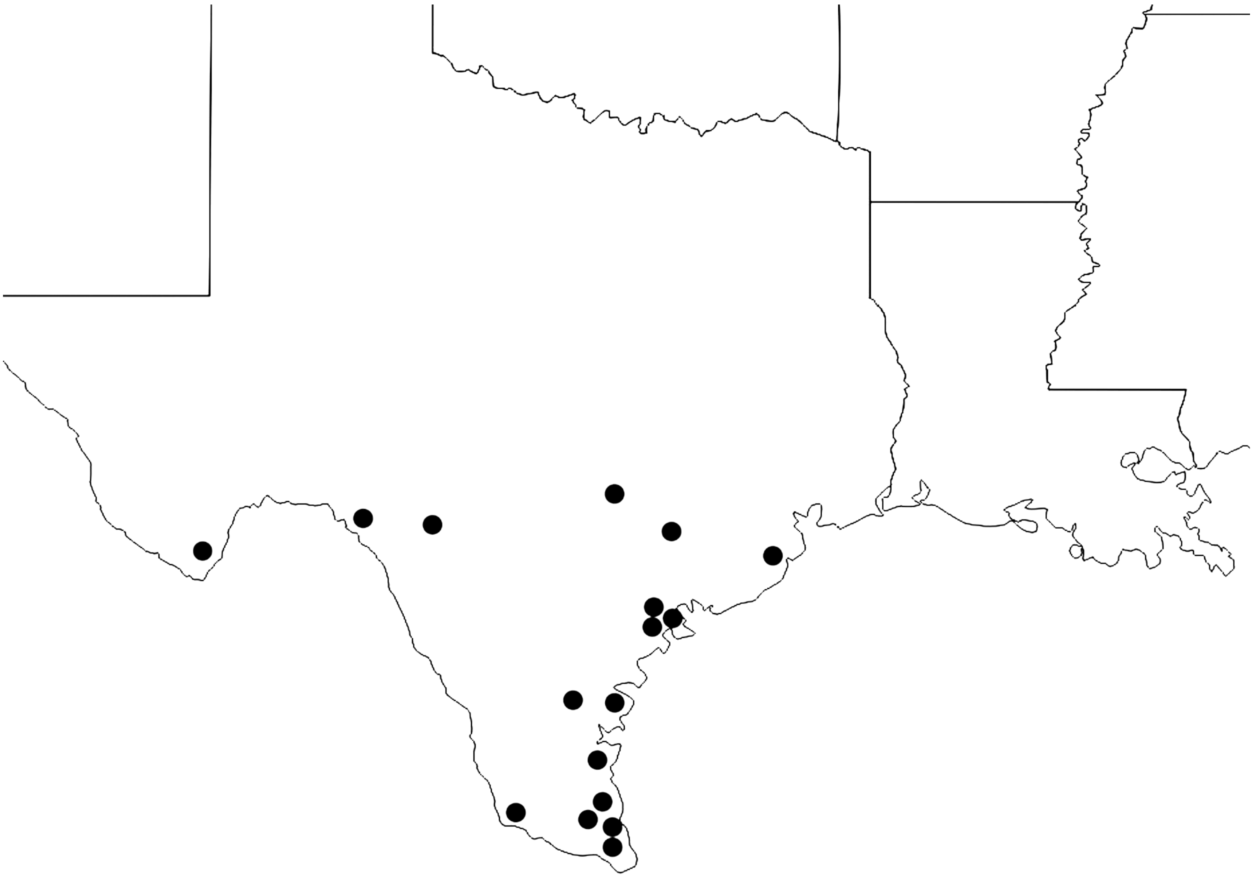

FIGURE 66. Known US distribution, *G. assimilis* within native range (also found introduced in south Florida, see SINA: https://sina.orthsoc.org/).

Gryllus multipulsator Weissman

Long-Chirp Field Cricket
Figs 54, 60–62, 67–70, Table 1

2009 *Gryllus multipulsator* Weissman *et al*. 2009, p. 375. Holotype male (Fig. 67): Alpine, San Diego Co., California. Deposited in CAS, Entomology type #18174.
1980 *Gryllus assimilis* Weissman *et al*. 1980.
1981 'Gryllus I' Rentz & Weissman 1981.
'Gryllus #1' in DBW notebooks.

Distribution. Known from southern California, southern Nevada, and southwestern-central Arizona.

Recognition characters and song. Always macropterous (Figs 67, 68), medium to large crickets, head usually narrower than pronotum, pronotum covered with fine hairs resulting in dull appearance. *Song* (Fig. 69; R15-325) loud, unique in US with 11–17 p/c and usually <2 c/s. Individual chirps demonstrate how pulse duration increases during a chirp while pulse rate simultaneously decreases (Fig. 71, and Weissman *et al.* 2009). Body measurements as in Table 1, p. 18. Most similar US song is *G. assimilis* but latter with fewer p/c and found considerably east in Texas.

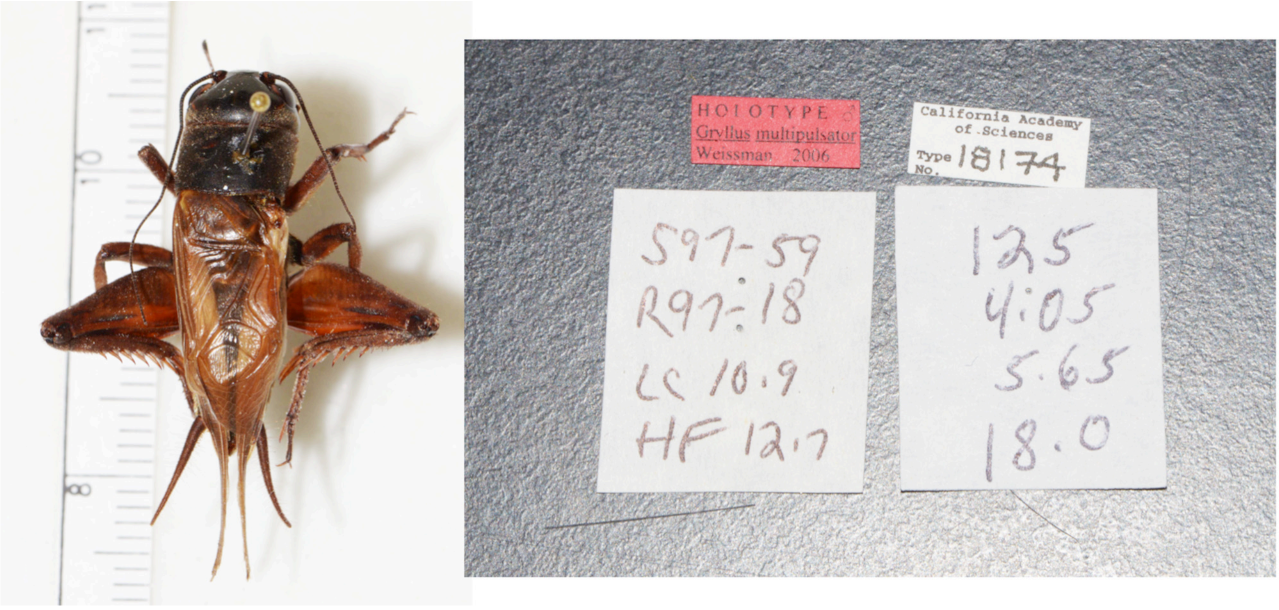

FIGURE 67. Holotype male, *Gryllus multipulsator,* specimen and labels.

FIGURE 68. Color variation in *G. multipulsator,* from reddish male (left, Riverside Co., CA, S03-41); brown female (middle, Santa Cruz Island, CA, S04-65); black male (right, Riverside Co., CA, S03-41).

Derivation of name. Reflecting the high number of pulses in each chirp.

Geographic range. Southern California, far southern Nevada, and southwestern Arizona (Fig. 70), including on the Channel Islands of Santa Cruz and Santa Catalina. Also extends into Mexico west of the Continental Divide (Weissman *et al.* 2009) and throughout much of Baja California, Mexico (Weissman *et al.* 1980).

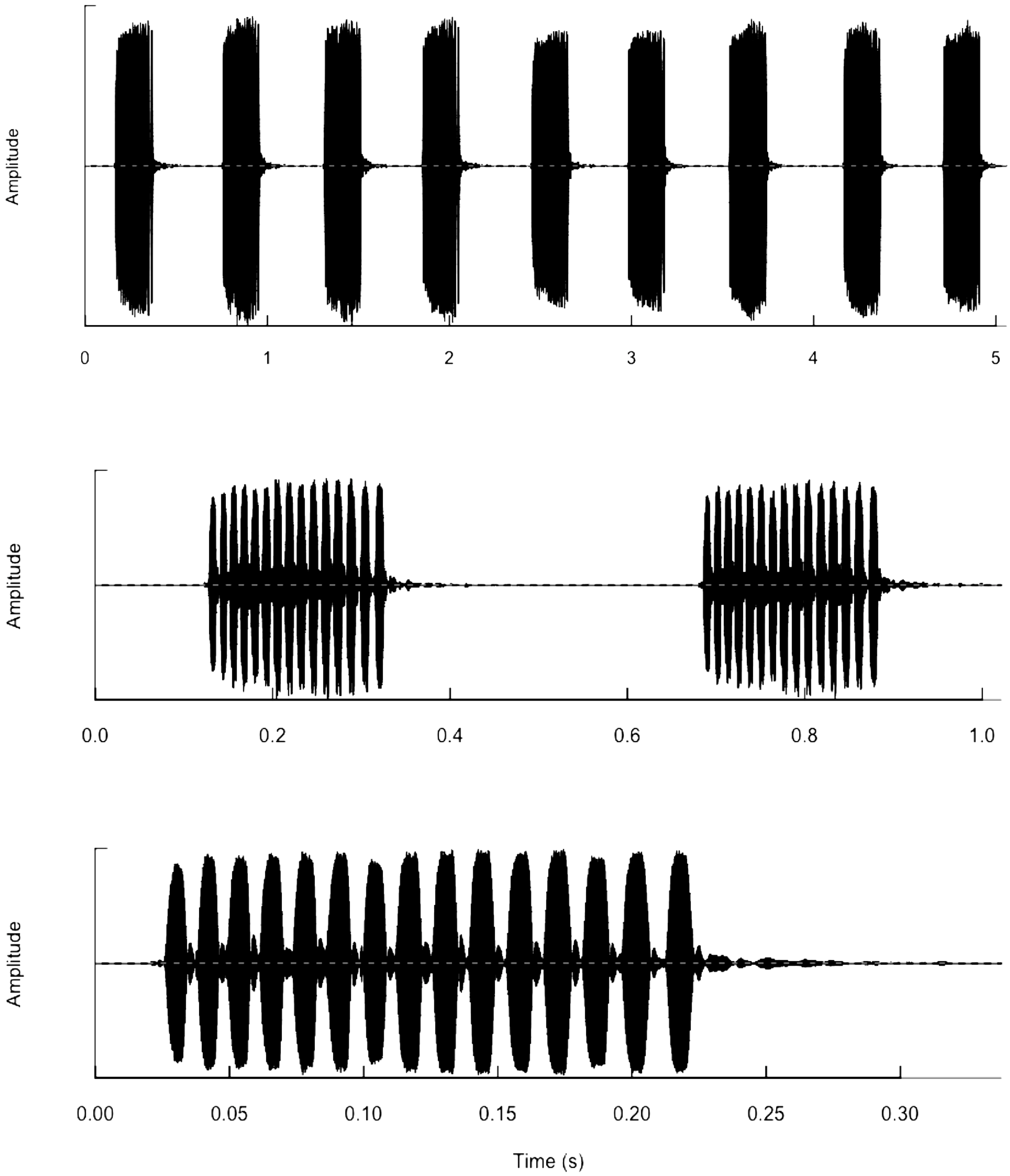

FIGURE 69. Top: Five second waveform of calling song of *G. multipulsator* (R15-325) Pima Co., AZ (S15-108), at 25.4°C; Middle: One second waveform of same song showing individual pulses; Bottom: Expansion of an individual chirp showing decreasing pulse rate towards end of chirp.

Habitat. Almost always associated with people and their watered environs such as lawns, golf courses, schools, around towns but also from salt and fresh water marsh areas. Usually singing from under dense vegetation. Most common in low elevation areas under coastal weather influences but also up to 1700 m at Sky Forest, San Bernardino Co., California.

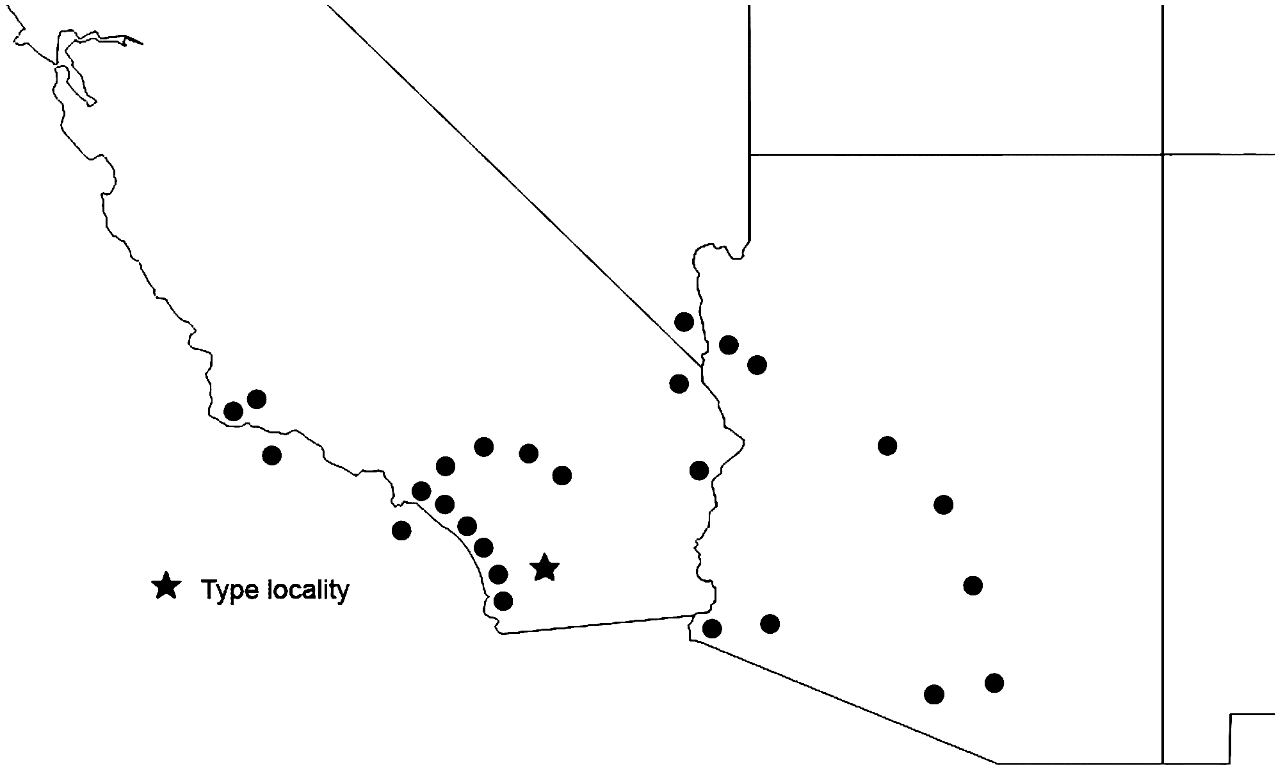

FIGURE 70. Known US distribution, *G. multipulsator.*

Life cycle and seasonal occurrence. No diapause at any stage. Continuous generations with two or three generations/year with adult males heard singing in coastal southern California even in the middle of winter.

Variation. **Color:** Individuals vary from almost entire body solid black (Fig. 68) 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 (tegminal bar) along the forewing angle. It is unknown if colors change with generation and/or time of year maturing.

Specimens examined. **ARIZONA**. *Gila Co.*, Globe, 3544' 25-viii-1982 (S82-103). *Maricopa Co.*, Buckeye, 840' 18-ix-2011 (S11-102). Hwy 85 just E Goodyear, 980' 31-vii-1981 (S81-46). Phoenix, 1140' 16-v-1999 (S99-25). Scottsdale, 22-iv-1985 (S85-41). *Mohave Co.*, Davis Dam, 900' 14-vi-1990 (S90-46). Kingman, 3600' 19-vi-1990 (S90-58). *Pima Co.,* Ajo, 1720' 20-viii-1998 (S98-72). Gila Bend, 1700' 1-viii-2009 (S09-103). Saguaro Rd near Tucson, 2400' 28-vii-1981 (S81-35). Hwy 86 just W Sells, 2276', 29-vii-2015, 31° 57' 25.4" -111° 56' 46.4" (S15-108) 2♂. *Yuma Co.*, Telegraph Pass, 676' 15-ix-2011 (S11-92). Yuma, Western College, 300' 10-viii-1988 (S88-89). Yuma, 156', 1-xi-2003, 32.63011 -114.59740 (2003-333 and 2003-334) A. Izzo. **CALIFORNIA**. *Los Angeles Co.*, Santa Catalina Island, Middle Ranch, 28-iv-1970, 15-vi-1971; 2-vii-1972. Santa Catalina Island, Isthmus, 4-Vvii-1973. Santa Monica Mts., Trancas Reservoir, 18-viii-1973. *Orange Co.*, Newport Beach, Backbay Dr., 7-vii-1976. Irvine, on UC Irvine Campus, 7-vii-1976. *Riverside Co.*, Banning, 2400' 22-viii-2006 (S06-88). Blythe, 400' 26-vi-1980 (S80-47). Indio, 6-viii-1988 (S88-74). Palm Springs, 2-iv-1989 (S89-8); 6-iv-1991 (S91-14,). Rancho Mirage, 850' 30-ix-2006 (S06-114). Riverside near UC Riverside Campus, 6-vi-2003 (S03-41). *San Diego Co.*, Alpine, 1900' 5-vi-1997 (S97-59). Borrego Springs, 8-viii-1988 (S88-83.) Camp Pendleton, 10 & 11-vii-1976. Cardiff by the Sea, sea level, 12 and 13-vii-1976; 27-vi-1980 (S80-48). La Jolla, near Prospect and Beach Blvd., sea level, 11-vii-1976. San Diego, Mission Bay, sea level, 18-vi-1994 (S94-34). *San Bernardino Co.*, Essex, 2000' 22-vii-1990 (S90-69). 3 m N Essex, 1680' 21-viii-1998 (S98-75). Mentone, 2000' 25-vii-1981 (S81-28). San Bernardino Mts., Sky Forest, 5600' 17-viii-1982 (S82-64). *Santa Barbara Co.*, Gaviota State Park 14-vii-1976. Santa Cruz Island, Prisoner's Harbor, sea level 11-vii-2004 (S04-65). Santa Ynez Mts., Lake Cachuma, 600' 24-vii-1981 (S81-20). **NEVADA**. *Clark Co.*, Cottonwood Cove, 800' 14-vi-1990 (S90-44).

DNA. Multilocus species tree G1414 (S09-103, Gila Bend) *G. multipulsator* is a sister species of *G. assimilis*—see DNA comparisons in Weissman *et al*. (2009) and in Gray *et al.* (2019). Also, closely related to *G. locorojo* and *G. veintinueve* (Fig. 6, p. 28).

Discussion. When we described this taxon in 2009, it was thought to have the highest number of p/c of any *Gryllus*. Otte (1987) described *G. mzimba* from Malawi with 17p/c and Martins (2009) discussed an undescribed *Gryllus* from southern Brazil (his *G*. n. sp. 2) that has from 13-21 p/c. Because *G. multipulsator's* distribution ends in central Mexico (Weissman *et a*l. 2009), Martins' undescribed cricket will be the new record holder for p/c once published.

Tachinid *Ormia ochracea* emerged from 2 males collected in Yuma, AZ (2003-333 and 334).

The Rubens Group

G. rubens Scudder; *G. texensis* Cade & Otte; *G. regularis* Weissman & Gray, n. sp.

Sister species of trilling field crickets distributed from south-central Arizona into far western Texas (*G. regularis*), from western Texas and the southern Great Plains eastwards to western Florida (*G. texensis*), and from eastern Texas eastwards to Florida and the southeastern Atlantic states (*G. rubens*). The only regular trilling species of *Gryllus* in the US (*G. cohni* is more of an irregular triller), differing from each other most notably in pulse rate (Figs 71 & 72) with *G. regularis* 30-50; *G. rubens* 45-65; and *G. texensis* 62-91. Geography, female morphology, and genetics also useful (Fig. 73, and Gray *et al.* 2019).

***Gryllus rubens* Scudder**

Southeastern Field Cricket

Figs 71–82, 85, 86, 90, Table 1

1902 *Gryllus rubens* Scudder. Psyche 9: p. 295. Holotype female, Auburn, Alabama. Type in ANSP, photos (Fig. 74) courtesy of J.D. Weintraub, ANSP. Plotting Scudder's female holotype measurements of pronotal width of 6 mm and ovipositor length of 16 mm (Scudder 1902) falls within *G. rubens* measurement cluster (Fig. 75).
1957 *Acheta rubens* (Scudder). Alexander, 1957. p. 586.
1964 *Gryllus rubens* Scudder. Randell 1964.

Distribution. One (Fig. 71, R13-220) of only two trilling US *Gryllus* found between 99° longitude (central Texas) and the Atlantic coast. See Walker (2019) and Gray (2011) for additional eastern localities.

Recognition characters and song. Medium sized, short or long hind winged crickets with an average PR of ~55 at 25°. Distinguished from morphologically similar and trilling, sometimes sympatric, *G. texensis* in that the latter has an average PR of ~80 at 25° (Figs 71, 84), more teeth in the file (Figs 78, 79), a shorter ovipositor (Gray *et al*. 2001), and frequently, but not always, shorter bursts of pulses. Pulse rate at a given temperature faster, but with greater separation from *G. texensis*, in the late summer/fall generation than in the spring generation (Walker 1998).

Along coastal Texas, in 2013, we found no overlap in dominant frequency, in many males, which was <5000 Hz in *G. rubens* but >5000 HZ in *G. texensis*. Yet around Tulsa, Oklahoma (S13-68), there is overlap and we wonder if this might reflect hybridization, environmental effects during development, or both. Additionally, Blankers (pers. comm.) stated that dominant frequency values that he used in Blankers *et al.* (2015) had a range of 4.18–5.88 KHz in *G. rubens* and 4.66–5.56 KHz in *G. texensis.* Unfortunately, these measured males were all from laboratory generations with unknown effects on the song.

Derivation of name. "rubens" apparently for the general reddish and rufo-testaceous markings on Scudder's unique, long tegmina female specimen.

Geographic range. (Fig. 76.) Most of our collection localities are near the western and northwestern boundaries of *G. rubens'* distribution. See Gray (2011) and Walker (2019) for more complete eastern US distribution maps. Our most western locality is Bastrop State Park (S91-23), Texas, where *G. rubens* occurred with *G. texensis*. There we collected one male *G. rubens* (R91-39) with a PR of 53 at 25°C and with 100 file teeth and three *G. texensis*

(R91-5, 6, 7) with PRs from 80–100 at 25°C and with 110–121 file teeth. We could not distinguish these two songs in the field.

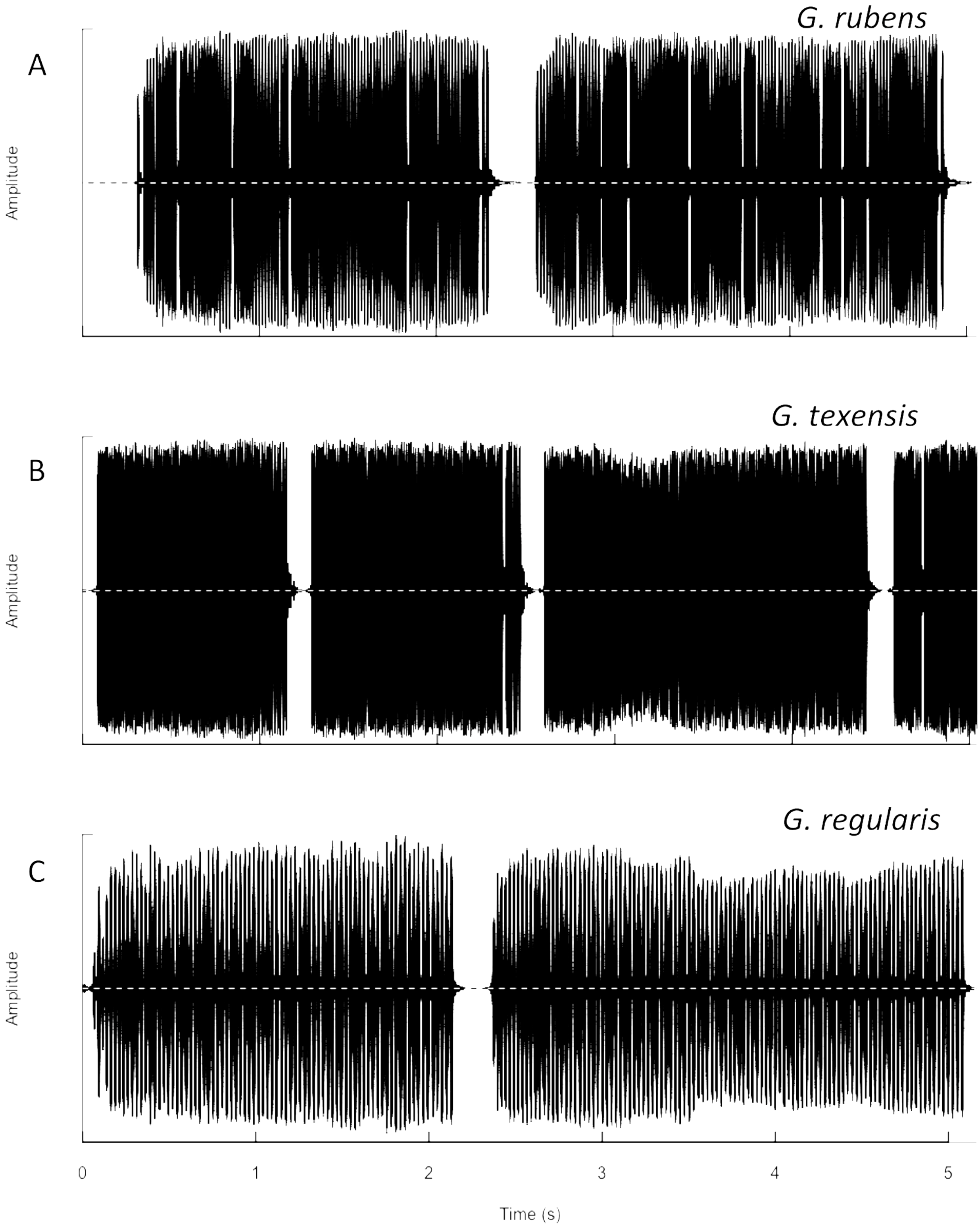

FIGURE 71. Five second waveforms of calling songs of (A) *G. rubens,* (B) *G. texensis*, and (C) *G. regularis*. (A) *G. rubens*: (R13-220) Tulsa, OK (S13-68), at 25°C; (B) *G. texensis*: (R13-224) Rio Hondo, TX (S13-44), at 26°C; (C) *G. regularis* (R99-211) Sinaloa, MX (S99-86), at 25.5°C.

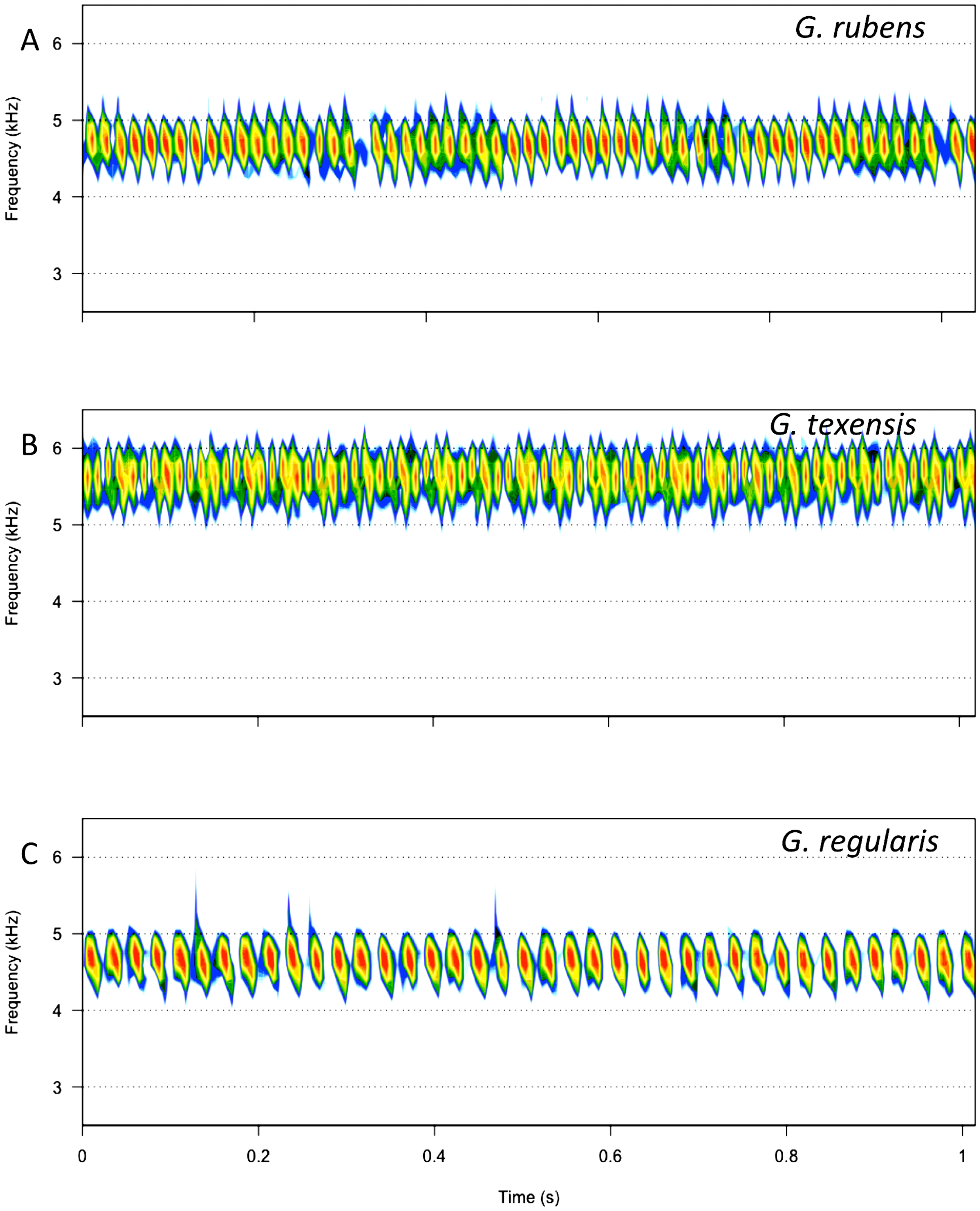

FIGURE 72. One second spectrograms of (A) *G. rubens,* (B) *G. texensis*, and (C) *G. regularis*, same males as in Fig. 71.

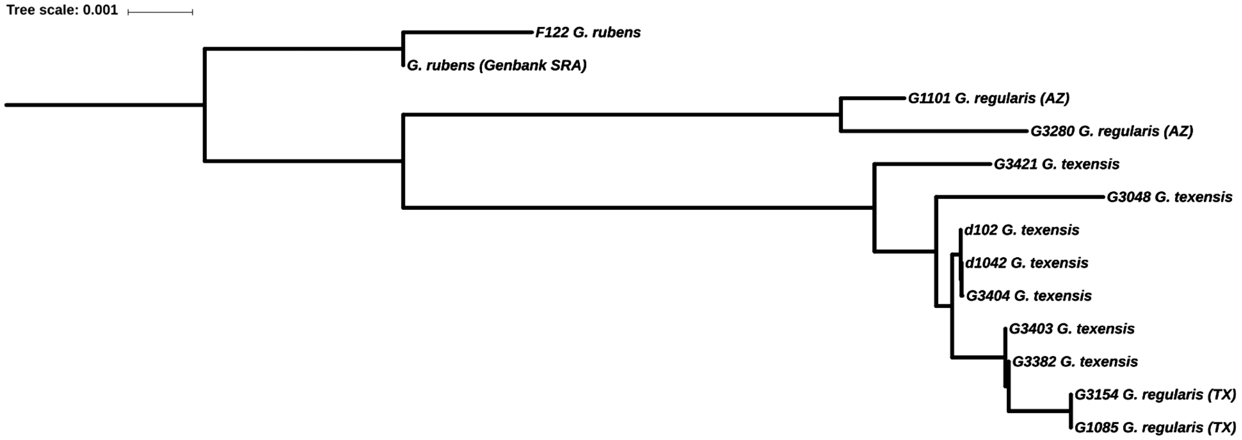

FIGURE 73. ITS2 gene tree. ***G. rubens*** samples: Orlando, FL (F122); Lake City & Ocala, FL (Genbank SRA, Berdan *et al.* 2016); ***G. regularis*** samples: S07-2 (G1101); S07-41 (G1085); S15-67 (G3154); S15-102 (G3280); ***G. texensis*** samples: S15-43 (G3048); S16-12 (G3382, G3403, G3404, G3421); Uvalde, TX (d102); Bastrop, TX (d1042).

FIGURE 74. Holotype female *G. rubens, with labels.*

Habitat. Lawns, pastures, and grassy roadsides.

Life cycle and seasonal occurrence. No egg diapause. Two generations/year even at the northern extremes of its range (Capinera *et al.* 2004). Adult peak abundances in spring and fall, representing the separate generations. Continuous generations in Florida (Vélez & Brockmann 2006). Can be locally common.

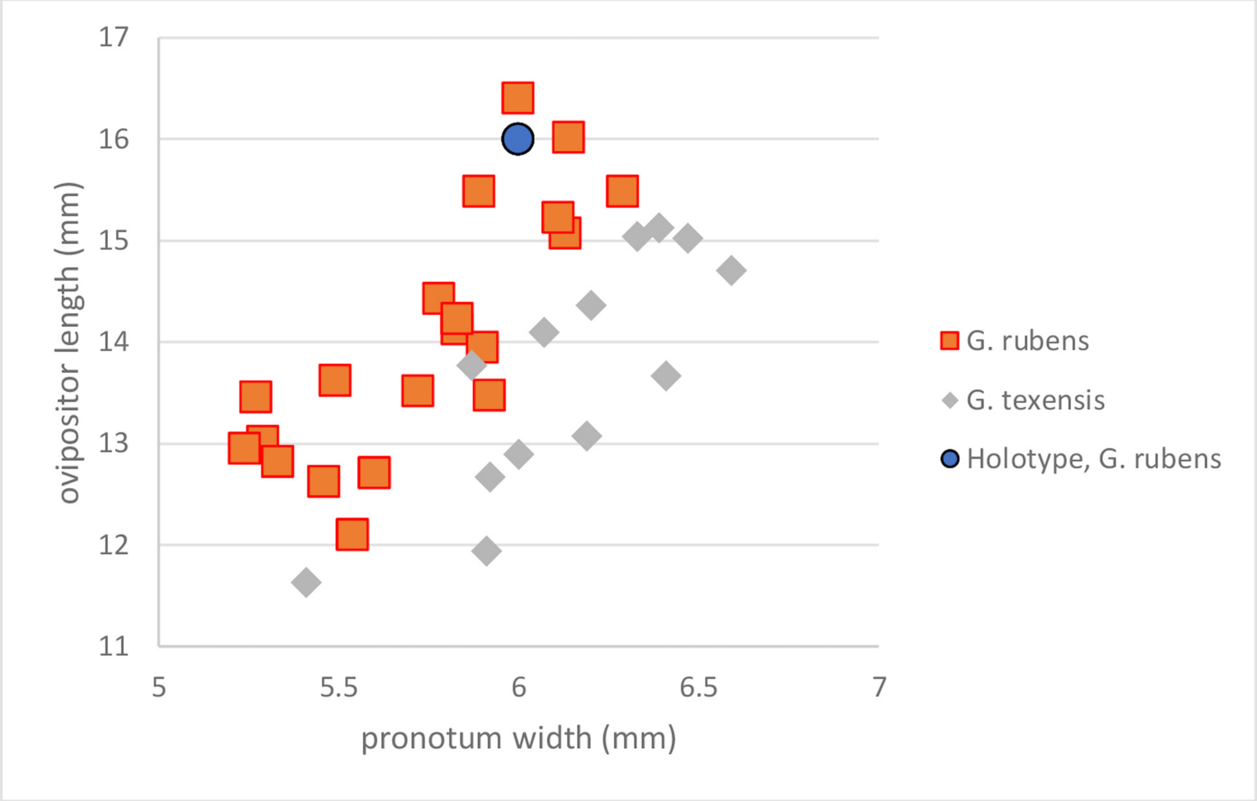

FIGURE 75. Regression of pronotum width vs. ovipositor length in the only two trilling eastern US taxa shows that holotype most consistent with *G. rubens.*

Variation. **Hind wing length:** Populations variable for short and long hind winged individuals of both sexes (Veazey *et al.* 1976, Walker 1987). **Color:** Within a population (e.g. S02-58, Missouri), individuals (Fig. 80) may have black hind femurs and tegmina compared to more typical brown/reddish ones. **Pronotum:** Usually very shiny in males, possibly less so in females. **Song:** Usually an evenly spaced trill but one male from Missouri, with 95 file teeth, (Fig. 81, R02-74, S02-58) with variable grouping of pulses.

Specimens examined. (Total: 54♂ 27♀). **Arkansas:** *Garland Co.,* Jessieville, 19-vi-1993, 750' (S93-46) 1♂. *Yell Co.,* Dardonelle, 19-vi-1993, 400' (S93-48) 2♂. **Florida:** *Alachua Co.,* Gainesville, 2-x-1986 (S86-128), TJ Walker, 20♂ 7♀. **Indiana:** *Warrick Co.,* 4 m S Dale 4-vi-2003, 650', 38° 7.228' -87° 1.591' (S03-61) 1♂. **Maryland:** *Prince George Co.,* College Park, 30-v-2004, 500' (S04-35) 2♂. **Missouri:** *Cape Girardeau Co.,* Millersville, 9-viii-2002, 320' (S02-58) 6♂ 9♀; *Iron Co.,* Pilot Knob, 9-viii-2002, 840' (S02-57) 2♂ 1♀. **Oklahoma:** *Texas Co.,* Guymon, 1-vii-2009, 3380' (S09-77) 1♂. *Tulsa Co.,* Lake Keystone Dam area, 22-v-2001, 650', 36° 9.092' -96° 15.043' (S01-47) 1♂; Tulsa, 15-vii-2013, 775' (S13-67, 68) 9♂. **Texas:** *Bastrop Co.,* Bastrop State Park, 31-v-1991, 700' (S91-23) 1♂. *Galveston Co.,* High Island, 10-vi-2011, 5' (S11-28) 4♀. *Harris Co.,* Cypress, 148', 13-vii-2013 (S13-64) 3♂. *Jefferson Co.,* Sabine Pass, 10-vi-2011, 20' (S11-31) 3♂ 5♀; Sea Rim State Park, 10-vi-2011, 5' (S11-29) 1♀; *Marion Co.,* Caddo Lake State Park, 18-vi-1993, 300' (S93-42) 1♂. *Orange Co.,* Beaumont, 1-vi-1991, 50' (S91-32) 1♂.

DNA. Multilocus d437 from Florida, Jackson Co., Marianna, 28-ix-1999, 117', 30.774°, -85.227°, pulse rate in this male 53 at 25°C. Closest relatives (Gray *et al.* 2019): *G. texensis* (see Gray 2006; Gray *et al.* 2006) and *G. regularis*. See also Blankers *et al.* (2018), which compared transcriptomic genetic variation in *G. rubens* and *G. texensis*. In that study, several loci were fixed for genetic differences between *G. rubens* and *G. texensis*, so in principle there are diagnostic genetic differences between these taxa, but they are not applicable in any practical sense.

Discussion. When standing near simultaneously trilling males of *G. rubens* and *G. texensis*, one can sometimes hear subtle differences between the two songs, probably reflective of the different pulse rates and dominant frequencies. Currently, there is no single, definitive morphological character that separates male *G. rubens* from male *G. texensis* (Walker 1998, Gray *et al.* 2006), although we do present new data (Fig. 79) showing promise when comparing number of file teeth vs. teeth/mm. In the past, positive male identification has been exclusively linked to differences in song PR. Unfortunately, the ability of this one song parameter to separate the two species gets murky in some populations. Gray & Cade (2000a) demonstrated an increase in PR in *G. rubens* of ~3 for each 1°C rise in temperature and an increase in PR in *G. texensis* of ~5 for each 1°C rise. Martin *et al.* (2000) demonstrated an increase in PR of 3.5 for every 1°C increase in recording temperature in *G. texensis* (called "*G.* integer" by Martin *et al.* 2000). We applied a modification of this temperature correction (+4 pulses for each 1°C difference from 25°C because we did not want to prejudge which species that we decided that we were recording) to 16 males from Tulsa, OK (S13-68) recorded in the laboratory between 22–28°C and whose PR we normalized to 25°C: we find no unambiguous separation at this locality and get only a modestly bimodal PR (Fig. 82).

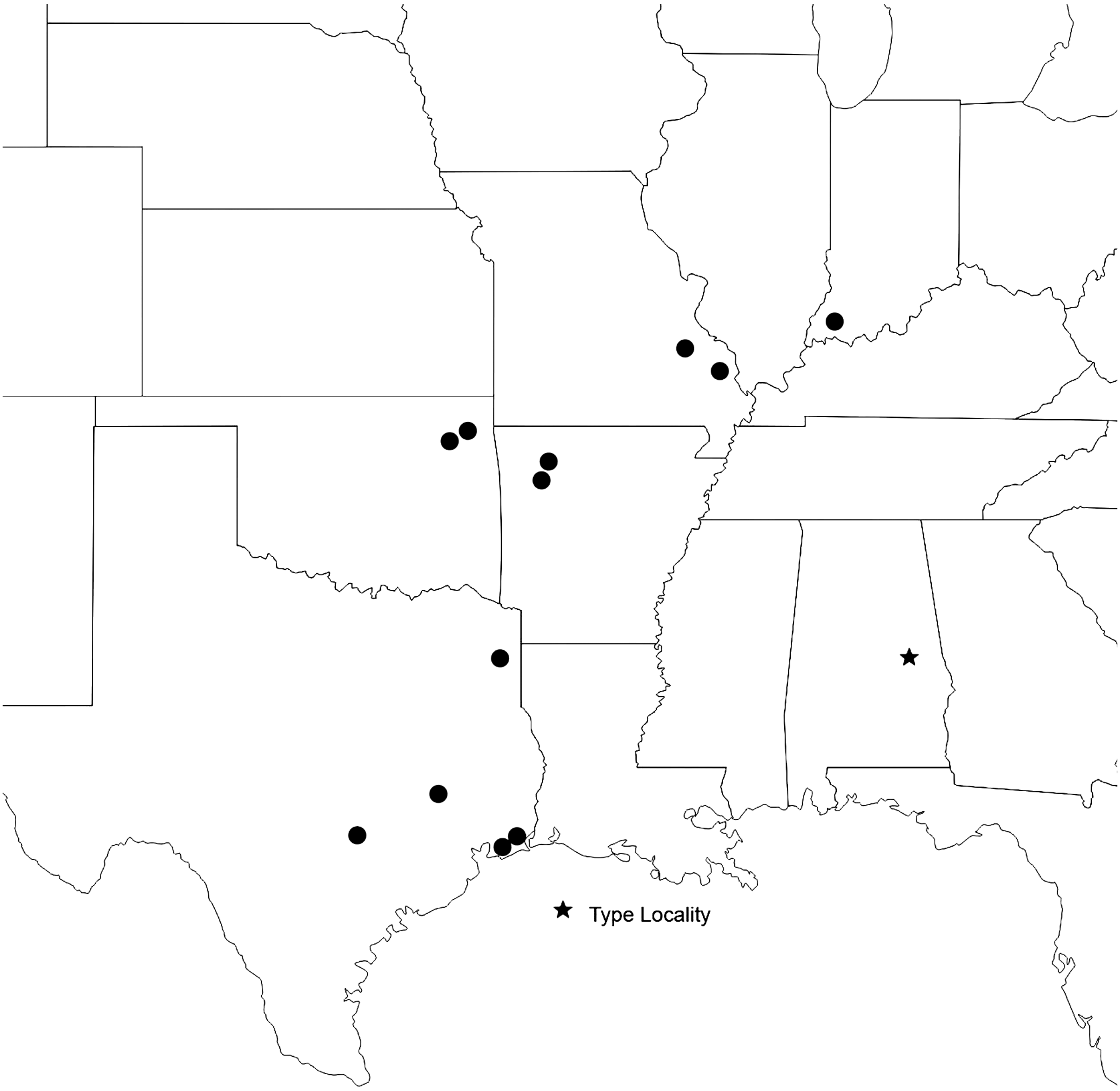

FIGURE 76. Populations of *G. rubens* that we studied.

While we did not find this ambiguity, in pulse rate, to be geographically widespread, it is also not unique: For instance, Walker (1998, p. 175) notes:

"…songs I attributed to *G. rubens* had a slightly higher average pulse rate in the zone of overlap [with *G. texensis* between western Florida and eastern Texas] than farther east and both species varied more in pulse rate between individuals from the same site and for the same individual from time to time than in the many other cricket species

I had studied. *G. rubens* and *texensis* [called *'G. integer'* by Walker in 1998] were not as clearly separated by their songs as other sympatric pairs of sibling species of crickets."

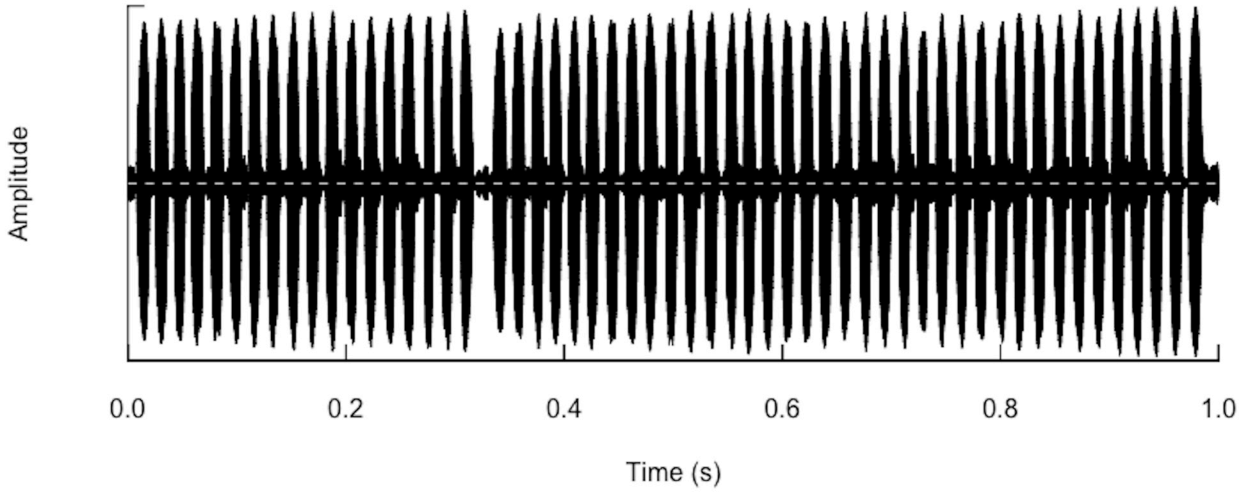

FIGURE 77. One second waveform, pulse rate of 56, of calling song of *G. rubens*: (R13-220) Tulsa, OK (S13-68), at 25°C.

FIGURE 78. Regression of number file teeth vs. hind femur length showing separation of sympatric *G. rubens* from *G. texensis.*

Instead of finding character displacement where they overlap, Walker (1998) found the opposite and concluded that the two species may hybridize in areas of overlap in western Florida. Such hybridization is achievable in the laboratory (Smith & Cade 1987), but, based on song phenotype, appears to be rare in sympatry (Izzo & Gray 2004). Nonetheless, we wonder if they may be hybridizing at our Tulsa, OK, site (S13-68), as discussed above. Using transcriptomic data, Blankers *et al.* (2018) found no evidence of interspecific gene flow more recently than ca. ~18K years, but, it must be noted, the source populations for that study were from allopatry. Additionally, Walker (1998) documented that different generations have different pulse rates, now further investigated by Beckers *et al.* (2019), so variable environmental effects are certainly possible.

G. rubens has been used in hybridization studies (Smith & Cade 1987; Cade & Tyshenko 1990), tachinid fly parasitism (Vélez & Brockmann 2006), effect of temperature on pulse rates (Doherty & Callos 1991; Walker 2000), female phonotaxis (Doherty & Callos 1991), song character displacement (Walker 1998; Izzo & Gray 2004), courtship song divergence (Fitzpatrick & Gray 2001) and impact on potential for hybridization (Gray 2004), peripatric speciation (Gray *et al.* 2008, Blankers *et al.* 2018), genetics of speciation (Blankers *et al.* 2019), aggressiveness related to habitat (Jang *et al.* 2008), and male response to conspecific song (Jang 2011). Past research is summarized in Gray (2011).

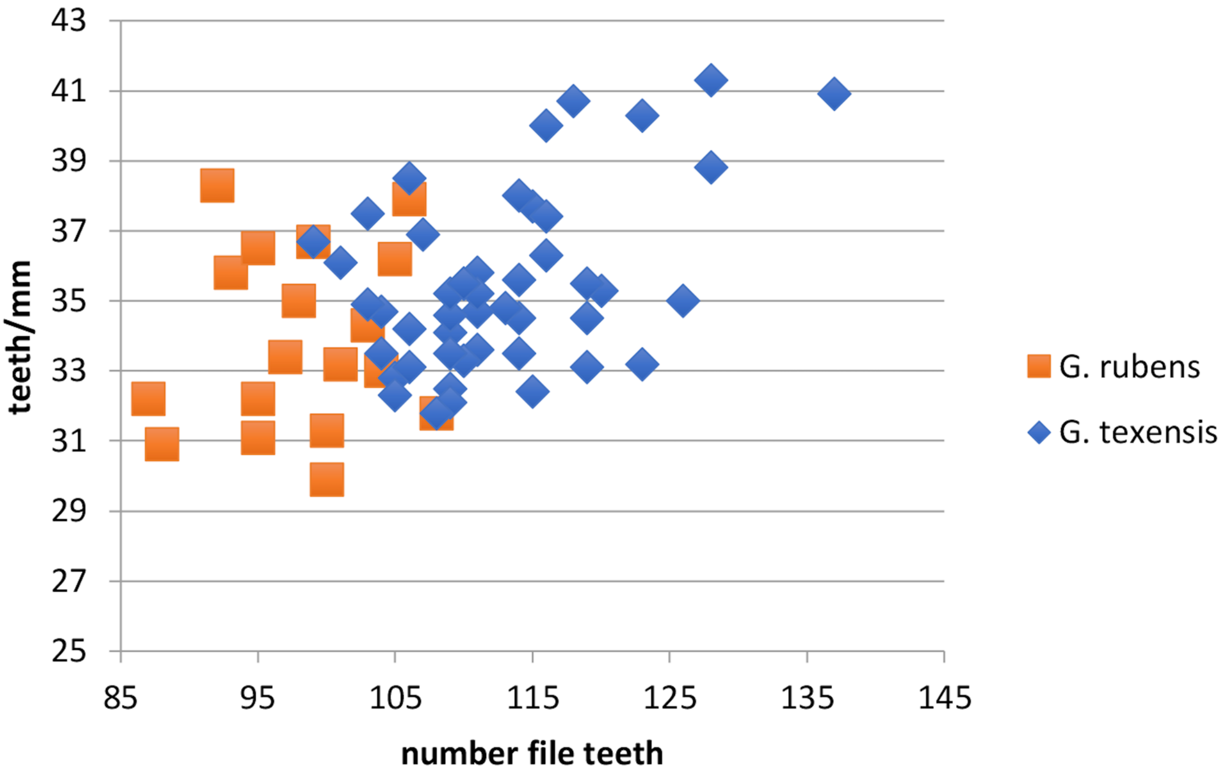

FIGURE 79. Regression of number file teeth vs. teeth/mm showing separation of sympatric *G. rubens* from *G. texensis*.

Gryllus texensis Cade and Otte

Southeast Fast Trilling Field Cricket

Figs 71–73, 78, 79, 82–90, Table 1

2000 *Gryllus texensis* Cade & Otte. Transactions of the American Entomological Society 126: p. 117. Holotype male, Austin, Texas. Holotype male noted as deposited in ANSP, but never done. Neotype male (in alcohol), since no paratypes listed in 2000, designated in 2016 by W. Cade (Fig. 83): Texas, San Antonio, 26-ix-2015, W. Cade. Deposited in ANSP (photos courtesy of J. Weintraub, ANSP).

'G. bivoltinus' or *G. integer* of pre-2000 DBW notebooks. 'G. bivoltinus' was an early manuscript name used by W. Cade for this taxon.

G. integer or '*G. integer'* in various published studies prior to 2000.

Distribution. One of three trilling US *Gryllus* found between western Texas and the Atlantic coast.

Recognition characters and song. Medium to large sized, short or long hind winged trilling crickets with an average PR between 70–80 at 25° (Fig. 84) (but see discussion below for exceptions). Distinguished from morphologically similar and trilling, sometimes sympatric, sister species *G. rubens* which has an average PR of 55 at 25° and fewer teeth in the file (Fig. 85) and a longer ovipositor (Fig. 86; Gray *et al.* 2001).

FIGURE 80. Color variation in *G. rubens,* all three individuals from Cape Girardeau Co., MO (S02-58).

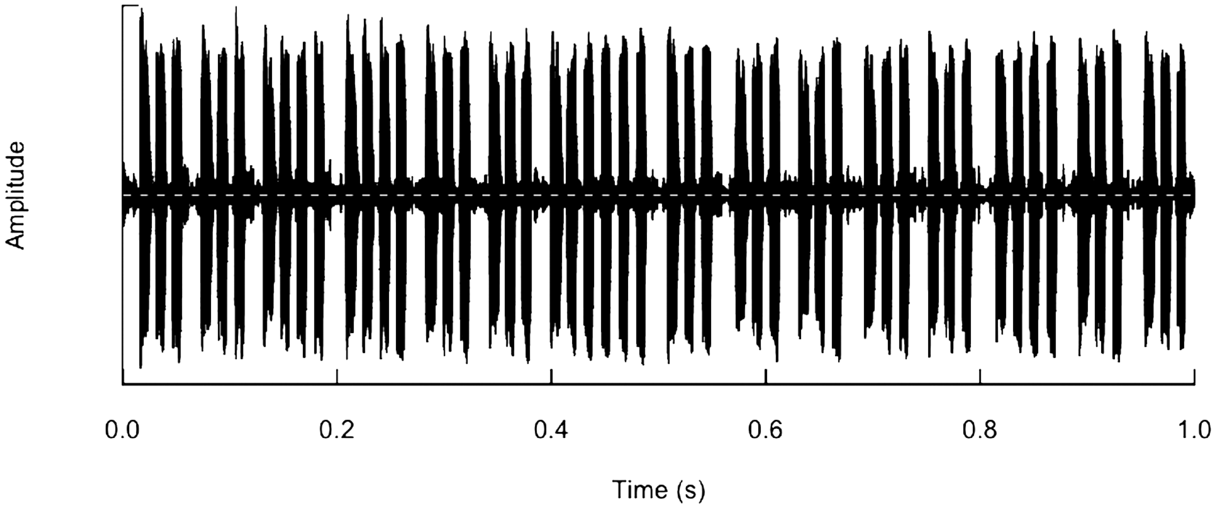

FIGURE 81. Atypical *G. rubens* calling song: (R02-74) Cape Girardeau Co., MO (S02-58), at 26°C.

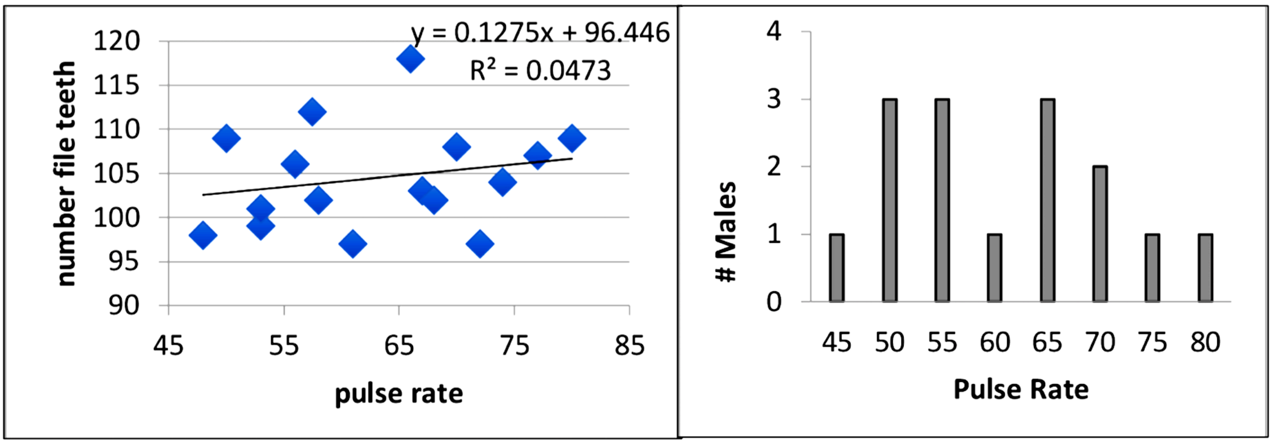

FIGURE 82. Left: Regression of sympatric *G. rubens* and *G. texensis* from Tulsa, OK (S13-68) showing lack of separation in individuals for pulse rate vs. file teeth number. Right: Histogram of pulse rates of these same males.

FIGURE 83. Neotype male, *G. texensis*, specimen and labels.

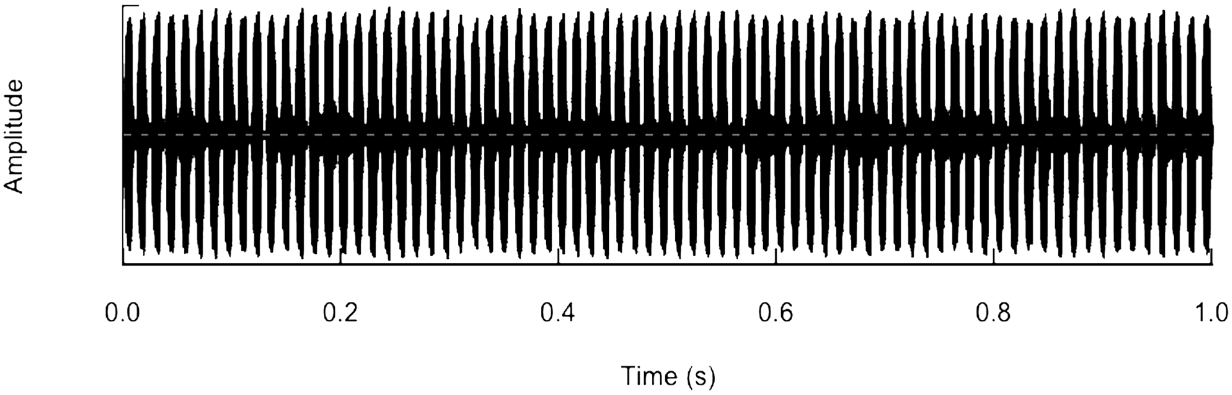

FIGURE 84. One second waveform, pulse rate of 75, of calling song of *G. texensis*: (R13-224) Rio Hondo, TX (S13-44), at 26°C

There is no one morphological or song character that always separates *G. texensis* from *G. rubens*. Interestingly, along coastal Texas, in 2013, we found no overlap in dominant frequency, in many males, which was <5000 Hz in *G. rubens* but >5000 Hz in *G. texensis*. Yet around Tulsa, Oklahoma (S13-68), there is overlap; see under *G. rubens* (p. 88) for further discussion.

Distinguished from sympatric (western Texas only at Alpine [S07-41]), sister species *G. regularis* which has non-overlapping PR of 29–50 at 25°. In its most western distribution, *G. texensis* can be sympatric with *G. armatus* and while their songs are difficult to separate in the field, unless males are singing near each other when a difference in "evenness" and pitch may be appreciated, the two can be separated by song analysis (2 or 3 p/c in *G. armatus* vs. a trill in *G. texensis*), and by number of file teeth vs. hind femur length (Fig. 87).

Derivation of name. Originally named after the type locality of Texas because much of the early biological research on this taxon was performed in that state.

Geographical range. (Fig. 88.) Eastern limits in Gray *et al*. (2008). Also into adjacent Mexico.

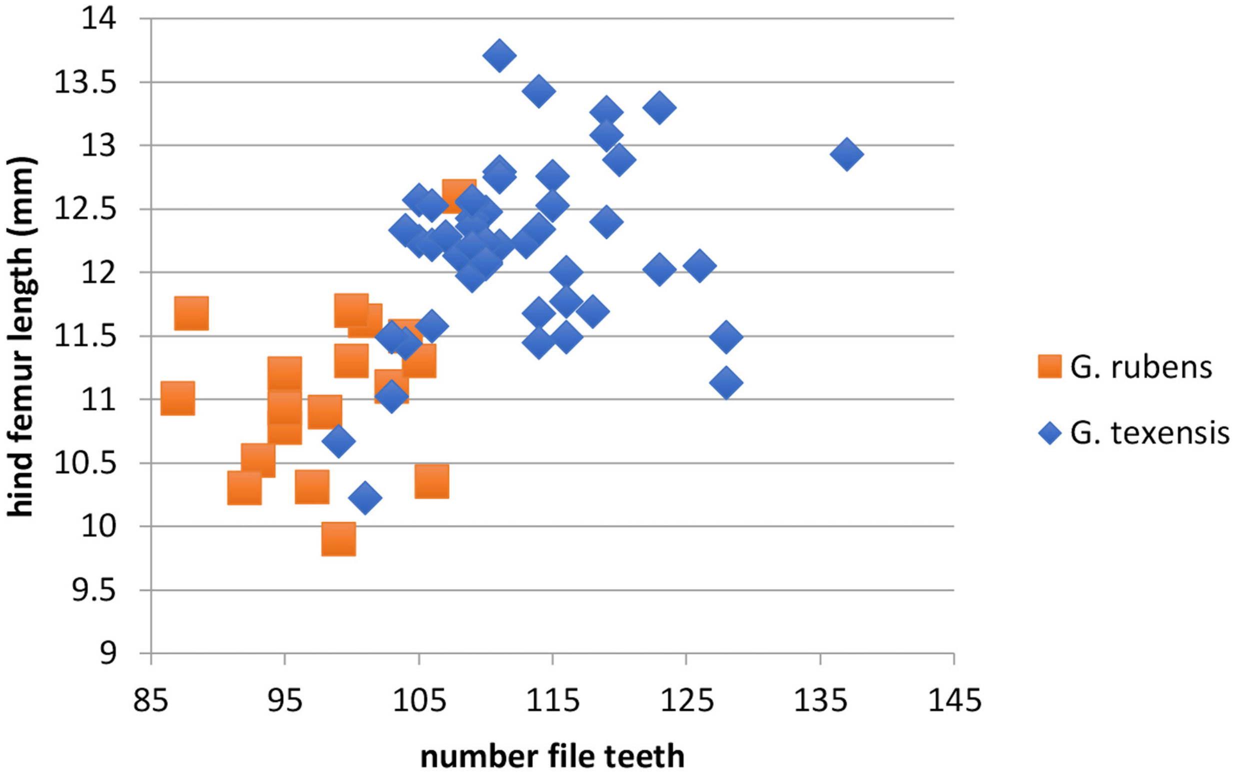

FIGURE 85. Regression of file teeth number vs. hind femur in *G. texensis* vs. *G. rubens* showing overlap but lower number of teeth in latter.

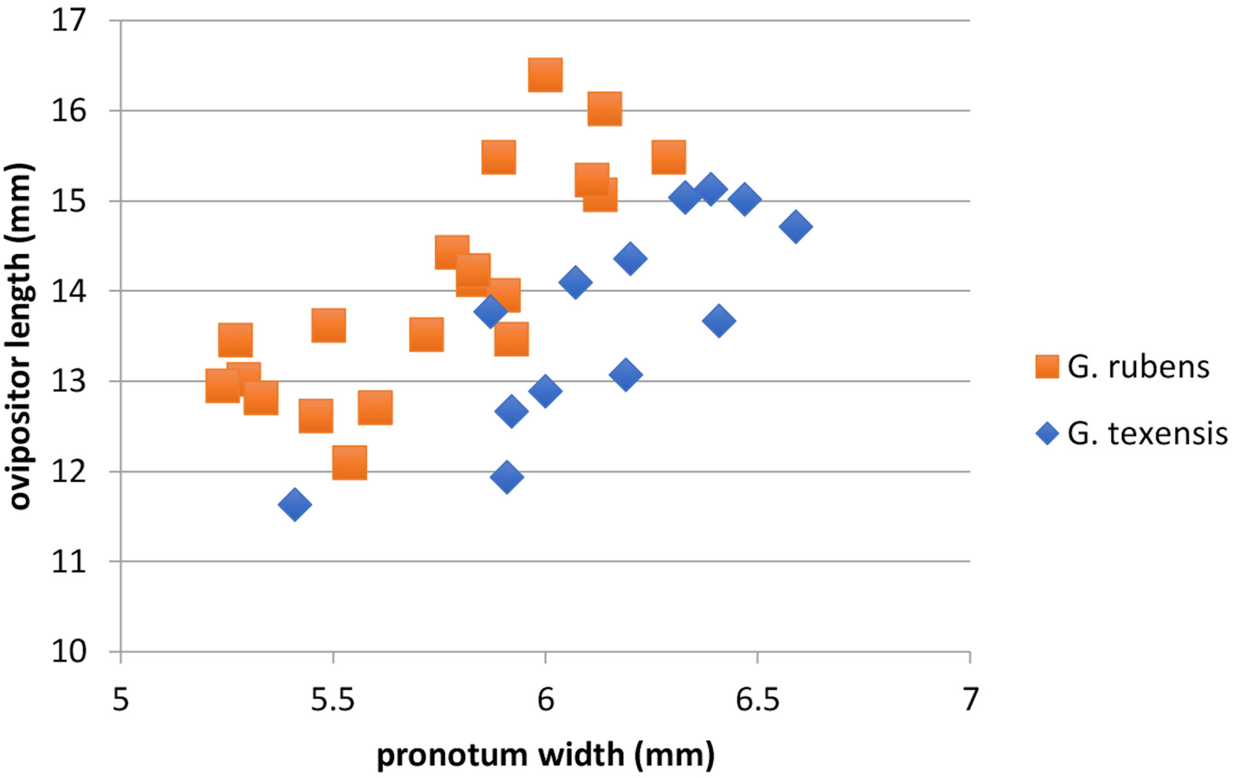

FIGURE 86. Regression of pronotum width vs. ovipositor length in *G. texensis* vs. *G. rubens* showing generally shorter ovipositor length in former.

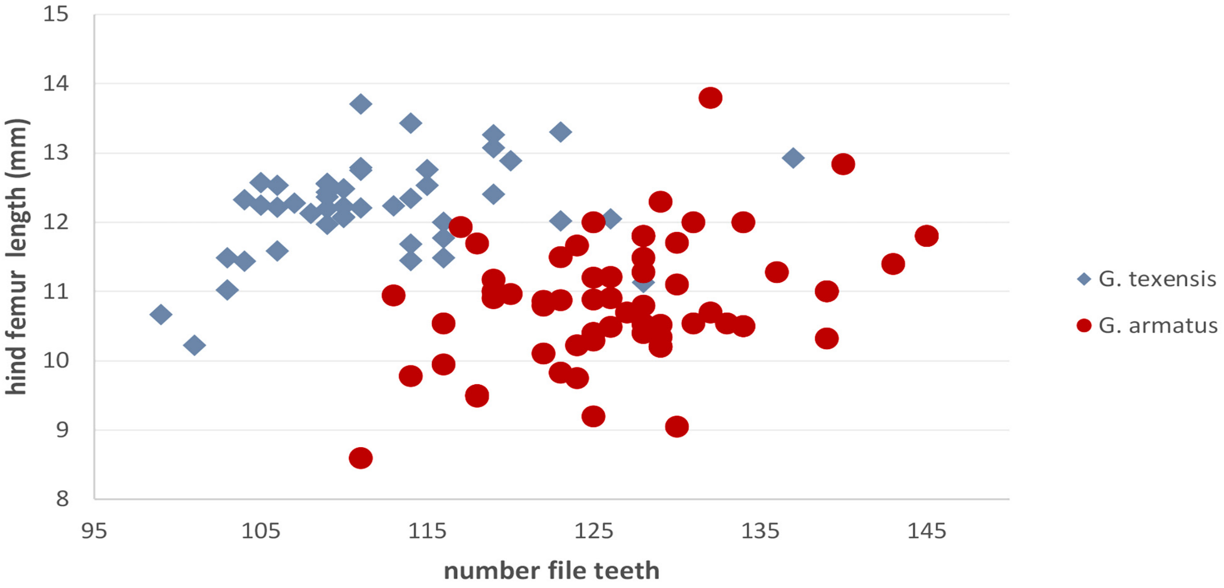

FIGURE 87. Regression of file teeth number vs. hind femur length in *G. texensis* vs. *G. armatus* showing overlap but generally more teeth in latter.

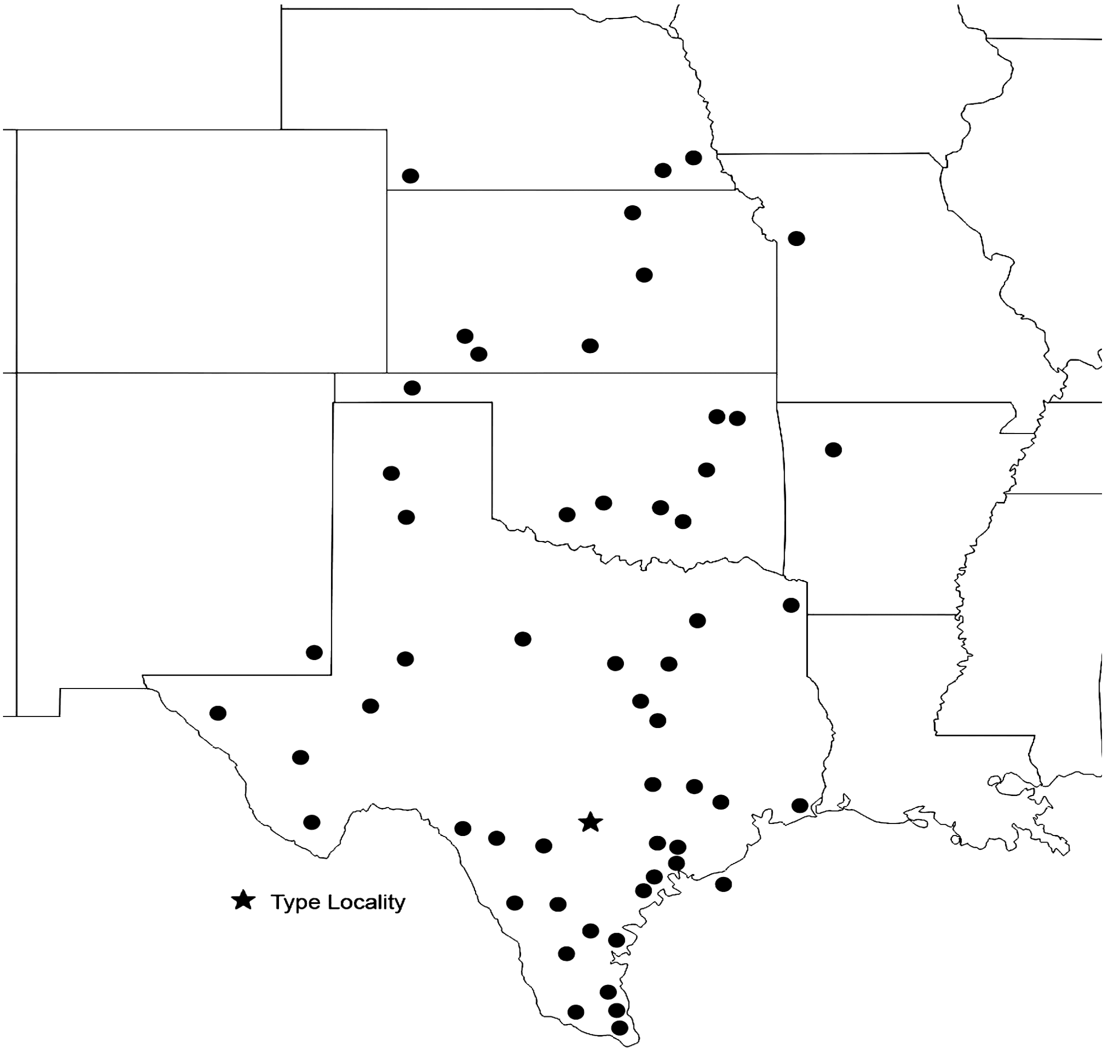

FIGURE 88. Populations of US *G. texensis* that we studied.

Habitat. Characteristic of pastures, lawns, and other open, grassy areas from sea level to 1300m.

Life cycle and seasonal occurrence. No egg diapause. Two generations/year, second generation more numerous than first and can be locally very common: responsible for cricket outbreaks in Waco, Texas, in early October, 2012 (S12-119, G2432, live specimens courtesy of S. Halvorson, Drug Emporium, Waco)): http://www.npr.org/2012/10/01/162110687/plague-of-crickets-bring-nuisance-stink-to-waco; Norman, Oklahoma, in early September, 2013: https://www.huffingtonpost.com/2013/09/04/oklahoma-cricket-invasion_n_3866683.html; and central Texas in 2015: http://www.cnn.com/2015/09/20/us/cricket-swarm-season-invades-central-texas/index.html.

Variation. **Color:** Besides black of neotype, individuals can be lighter in color (Fig. 89). **Hind wing length:** Of 335 adults, 74 (22%) have short hind wings. Females frequently have tegmina bars. **Song:** A male from Arkansas, Yell Co. (S93-47), was recorded on 19-vi-1993, in the field, (R93-14) at 24.5°C singing with a PR of 49 and pulses grouped into 2's and 3's. This same male was re-recorded in the laboratory, while trilling, on 28-vi at 25°C (R93-43) with a PR of 65 and without any grouping of pulses. This male has 121 teeth in his file, 41.7 teeth/mm, and a hind femur length of 11.4 mm, all parameters placing it within *G. texensis* (see Fig. 87 and Fig. 90). We wonder if this male had recently molted to adult and had an "immature" song when first field recorded, even though he did not appear teneral when captured.

FIGURE 89. Color variation in *G. texensis,* both pictured individuals from Brackettville, TX (S10-63).

A male from Texas, Travis Co. (S85-63), singing at 24°C (R85-46), had a small peak before each large peak, and a PR of 80. Walker (1998) documents that first and second-generation males of *G. texensis* have different mean modal pulse rates because of both developmental conditions and parental effects. Duration of trills usually shorter in *G. texensis* than *G. rubens* but some individuals of *G. texensis* had long series in Brackettville (S10-63) and Tulsa (S13-68).

Specimens examined. (Total: 224♂ 109♀) [No paratypes designated, or localities cited in original description]. **Arkansas:** *Yell Co.,* Ola, 19-vi-1993, 500' (S93-47). **Kansas:** *Barber Co.,* Medicine Lodge, 23-vi-1987 (S87-68).

Clark Co., Ashland, 27-viii-1989, 1950' (S89-70); 12.2 m E Ashland, 27-viii-1989 (S89-69). *Cloud Co.,* Concordia, 7-viii-2002, 1100' (S02-50). *Ford Co*., Dodge City, 27-viii-1989, 2400' (S89-71). *Salina Co.,* Salina, 7-viii-2002, 1100' (S02-49). **Missouri:** *Jackson Co*., Kansas City, 8-viii-2002, 860' (S02-54). **Nebraska:** *Fillmore Co.,* Geneva, 7-viii-2002, 1420' (S02-51). *Lancaster Co.,* Lincoln, 7-viii-2002, 940' (S02-52). *Red Willow Co.,* McCook, 28-viii-1989, 2500' (S89-74). **New Mexico:** *Lea Co.,* Eunice, 6-ix-2010, 3420' (S10-62). **Oklahoma:** *Atoka Co.,* 2.5 m NE Stringtown, 16-vi-1988, 600' (S88-47). *Carter Co*., Lake Murray State Park, 24-vi-1993, 900' (S93-58). *Comanche Co.,* Medicine Park, 6-viii-2002, 1200' (S02-47). Wichita Mts. Wildlife Refuge, 6-viii-2002, 1300' (S02-46). *Oklahoma Co*., Oklahoma City, 6-viii-2002, 1000' (S02-48). *Texas Co.,* Guymon, 1-vii-2009, 3380' (S09-77). *Tulsa Co.,* Keystone State Park, 15-vi-1988, 600' (S88-42); 23-vi-1993 (S93-56). Lake Keystone Dam area, 22-v-2001, 650' (S01-47). Tulsa, 23-vi-1993, 500' (S93-57); 9-vi-2007 (S07-22); 15-vii-2013 (S13-68). **Texas:** *Bastrop Co.,* Bastrop State Park, 31-v-1991, 700' (S91-23). *Bosque Co.,* Clifton, 10-vi-1988, 400' (S88-29). *Brewster Co*., Alpine, 4270', 5-vi-1991 (S91-44), 12-vi-2007 (S07-41). Big Bend National Park, Rio Grande Village, 9-vi-1985, 2100' (S85-56); 5-vi-1991 (S91-43); 28-v-2016 (S16-12). *Calhoun Co*., Magnolia Bay, Indian Point Historic Park, 4-viii-2002 (S02-36); Port Lavaca, 12-vii-2013, 18' (S13-57); 26 m S Victoria, 4-viii-2002, 20' (S02-37). *Cameron Co.,* Brownsville, 3-vi-1991, 0' (S91-38); Harlingen, 3-vi-1991 (S91-39); Rio Hondo, 10-vii-2013, 8m (S13-44); FR510 at intersection with FR 2480, 10-vii-2013, 0' (S13-43); FR510 E near intersection FR100W, 10-vii-2013, 0' (S13-42). *Cass Co.,* 3 m S Queen City, 18-vi-1993, 400' (S93-43). *Culberson Co.,* Van Horn, 6-vi-1991, 4100' (S91-48). *Dallas Co.,* DWF Airport, 23-v-2001 (S01-49). Dallas, 23-v-2001 (S01-50). Irving, 10-vi-1988, 400' (S88-25). *Dimmit Co.,* Carrizo Springs, 11-vi-2007, 660' (S07-28). *Duval Co.,* Freer, 25-v-2001, 980' (S01-52). 4.5 m E Freer, 30-vi-1986 (S86-58). *Fayette Co.,* Schulenburg, 380', 4-viii-2002 (S02-38), 13-vii-2013 (S13-65); 2.3 m S Schulenburg, 9-ix-2010, 440' (S10-65). *Gillespie Co.,* Fredericksburg, 1-vii-1986 (S86-65). *Harris Co.,* Cypress, 148', 13-vii-2013 (S13-64). *Hidalgo Co.,* Bentsen-Rio Grande Valley State Park, 3-viii-2002, 120' (S02-34); 10-vi-2007 (S07-27). *Howard Co.,* Big Springs VA Hospital, 30-vi-2009, (S09-72). *Jefferson Co.,* Port Arthur, 1-vi-1991, 0' (S91-31). *Jim Wells Co.,* Alice, 11-vii-2013, 171' (S13-48, 49, 50). *Kinney Co.,* Brackettville, 1100', 10-vi-1985 (S85-61); 27-vi-1986 (S86-47); 4-vi-1991 (S91-40); 12-vi-2007 (S07-35); 7-ix-2010 (S10-63). *Matagorda Co.,* Hog Island, 13-vii-2013, 5' (S13-59). *McLennan Co.,* Waco, 400', 10-vi-1988 (S88-26), 3-x-2012 (S12-119), S. Halvorson. Intersection of Hwy 6 and Hwy 35, 10-vi-1988 (S88-27). *Nueces Co.,* Corpus Christi, 29-vi-1986 (S86-56); 2-vi-1991 (S91-35); 12-vii-2013 (S13-53). *Potter Co*., Amarillo, 12-vi-1988, 3600' (S88-38). *Tarrant Co.,* Fort Worth Nature Center & Refuge, 5-viii-2002, 600' (S02-39). Grapevine Lake Dam, 23-v-2001 (S01-48). *Randall Co.,* Palo Duro Canyon State Park, 12-vi-1988, 3600' (S88-37). *Refugio Co.,* Tivoli, 12-vii-2013, 12' (S13-56). *Taylor Co.,* Abilene, 11-vi-1988 (S88-35). *Tom Green Co.,* San Angelo, 11-vi-1988, 1900' (S88-30). *Travis Co.,* Austin, 11-vi-1985 (S85-63). *Uvalde Co.,* Uvalde, 10-vi-1985 (S85-62). 2.3 m W Uvalde 11-vi-2007, 940' (S07-29). 6.9 m W Uvalde, 11-vi-2007, 940' (S07-30). *Val Verde Co*., Del Rio, 11-vi-2007, 1000' (S07-33); 7-ix-2010 (S10-64). Del Rio on Amistad Lake some 5 m N Del Rio, 10-vi-1985, 1200' (S85-60). 5 m E Del Rio on Hwy 90, 27-vi-1986 (S86-49). *Ward Co.,* Monahans, 2-vii-1986 (S86-69). *Washington Co.,* Brenham, 31-v-1991, 300' (S91-26); 6-ix-1992 (S92-123); 24-v-2001 (S01-51). *Webb Co.,* 20-48 m W Freer on Hwy 44, 30-vi-1986 (S86-61).

DNA. Multilocus G3382, Big Bend (S16-12), PR 79 at 25°C. Sister species are *G. rubens* and *G. regularis* (Gray *et al.* 2019). See Gray *et al.* (2008) for results for many specimens east of our main study area. See also Blankers *et al.* (2018), which compared transcriptomic genetic variation in *G. rubens* and *G. texensis*. In that study, several loci were fixed for genetic differences between *G. rubens* and *G. texensis*, so in principle there are diagnostic genetic differences between these taxa, but they are not applicable in any practical sense.

Discussion. Probably the most common and widespread *Gryllus* species in Texas. Sympatric with *G. rubens* at Bastrop State Park, Texas (S91-23), and Lake Keystone State Park (S01-47) and Tulsa (S13-68) in Oklahoma. Sympatric with *G. armatus* at Texas localities of: Big Springs (S09-72); Big Bend (S91-43); Brackettville (S85-61 & S91-40); Monahans (S86-69); Alpine (S91-44); Van Horn (S91-48) and Kansas, Dodge City (S89-71). Microsympatric with both *G. armatus* and *G. regularis* at Alpine, Texas (S07-41).

We found males parasitized by tachinid *Ormia ochracea* from these Texas localities: 5 8 km E Del Rio on Hwy 90 (S86-49), Brownsville (S91-38), Bentsen-Rio Grande Valley State Park (S02-34), Schulenburg (S02-38), and Cameron Co. (S13-43). The Cade lab (Cade *et al.* 1996, Gray & Cade 2000b) has done much work on *Ormia* parasitism of *G. texensis* in Texas.

Other published studies on *G. texensis* include those on sexual selection (Gray & Cade 1999b, Gray & Cade 2000a, Bertram 2002a, b); aggression (Sandford 1987), fine-scale temperature effects on calling song (Martin *et al.*

2000) which demonstrated an increase in PR of 3.5 for every 1°C increase in recording temperature; influence of photoperiod on signaling (Bertram & Bellani 2002); female cricket mating preferences (Wagner *et al*. 1995, Blankers *et al.* 2015); life history trade-offs (Guerra & Pollack 2007); hybridization studies (Cade & Tyshenko 1990); predator-induced stress responses (Adamo *et al.* 2013), courtship songs (Fitzpatrick & Gray 2001); peripatric speciation (Gray *et al*. 2008, Blankers *et al.* 2018); and interactions between temperature, reproduction and immune function (Adamo & Lovett 2011).

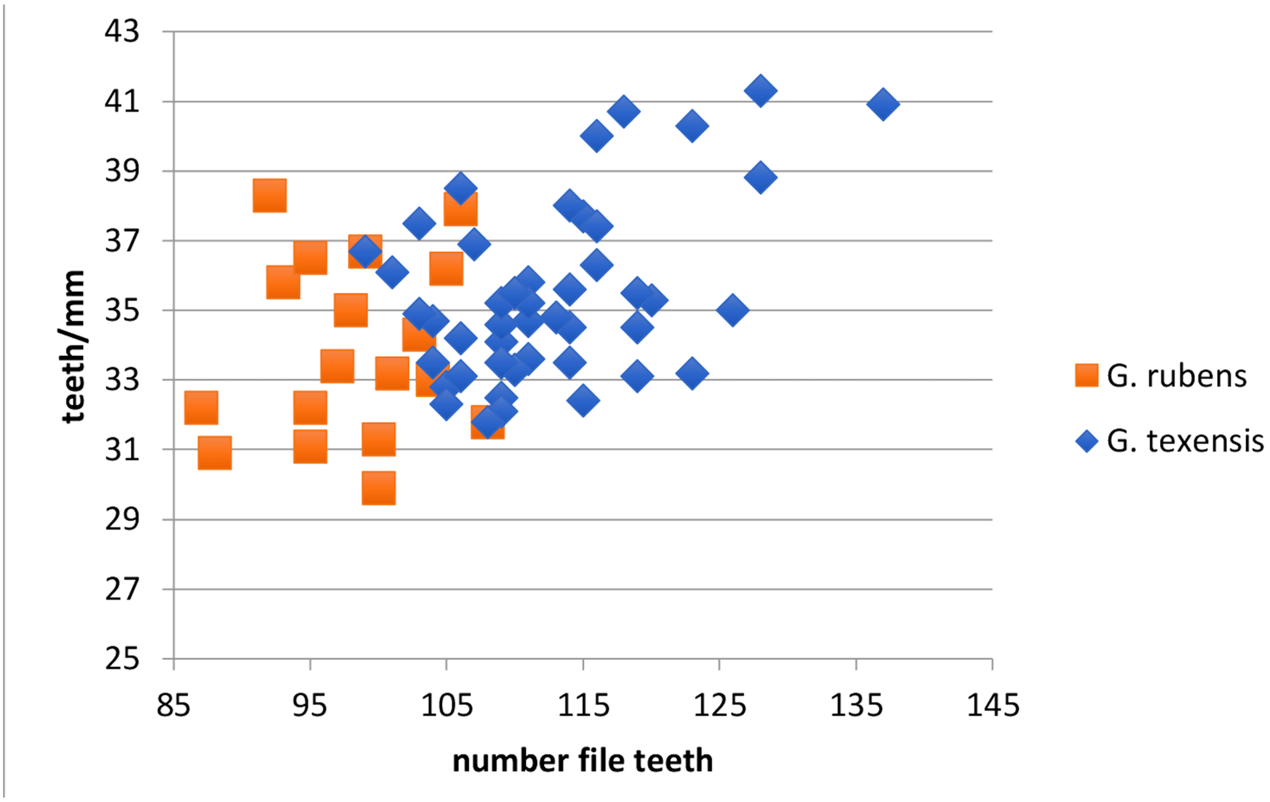

FIGURE 90. Regression of file teeth vs. teeth/mm showing separation of sympatric *G. rubens* from *G. texensis.*

Gryllus regularis **Weissman & Gray, n. sp.**
Southwest Regular-Trilling Field Cricket
Figs 71–73, 91–95, 168, Table 1

'Gryllus #14' in DBW notebooks.
'Arizona triller' of Sakaguchi & Gray (2011).
'G. #14' of Blankers *et al.* 2015.

Distribution. Known from central-southeastern Arizona, southwestern New Mexico, and western Texas.

Recognition characters and song. Medium to large, usually short hind winged crickets with a broad and usually shiny pronotum. *Song* (Fig. 91, R99-211) a long trill with pulses evenly spaced, PR 30–45 at 25°C. Distinguished from the two other sympatric, trilling *Gryllus*, as follows: from *G. cohni,* the latter is smaller and has an irregular trill with groupings of 2 to 11 pulses that results in a slower CR, usually has long hind wings, and a narrower (Fig. 92), hirsute and slightly dull pronotum.

Trilling *G. texensis* is sympatric with sister species *G. regularis* only at Alpine, TX (S07-41), but the former has a PR above 70 at 25°C. The only other western US trilling *Gryllus* is the always allopatric, sister species *G. rubens* from central Texas to Florida and which, while also medium to large in body size, has a higher PR (45–65), non-overlapping file teeth number, and narrower pronotum. Rarely, Arizona males of *G. armatus* trill (see Fig. 109, p. 115), but can be separated from *G. regularis* by their higher pulse rate (60–100), narrower pronotum and file characters.

Holotype. Male (Fig. 93). USA, Arizona, Yavapai Co., Sedona, Sky Ranch Lodge Motel grounds by Sedona

Airport. 15-vi-2007. 5120’. 34° 51.146’, -111° 47.415’. D.B. Weissman, D.C. Lightfoot. S07-61, R07-11, DNA sample G1098. 16S GenBank accession # MK446613. BL 20.48, HF 11.43, RC 10.21. Right tegmen removed: 120 teeth, file length 3.35, TL 12.1, TW 4.55. Type deposited in CAS, Entomology Type #19270.

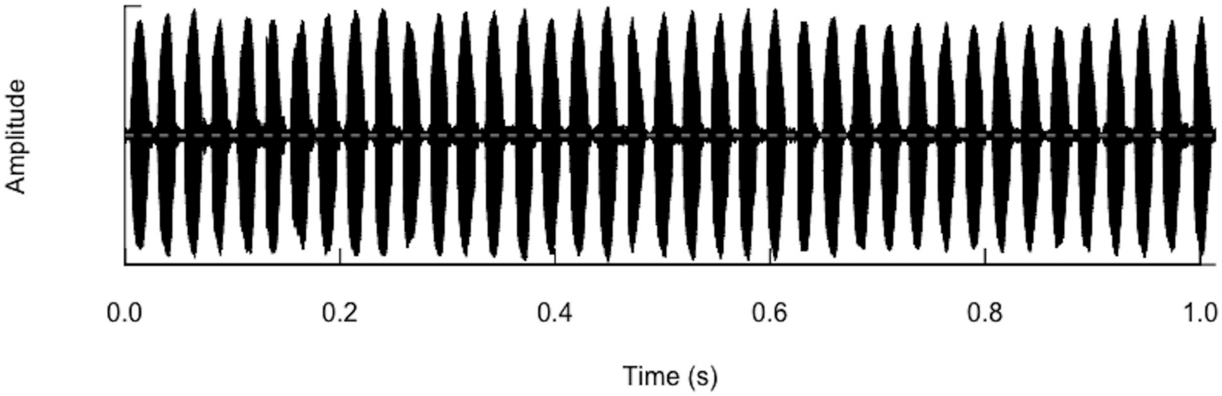

FIGURE 91. One second waveform, pulse rate of 39, of calling song of *G. regularis* (R99-211) from Sinaloa, MX (S99-86), recorded at 25.5°C

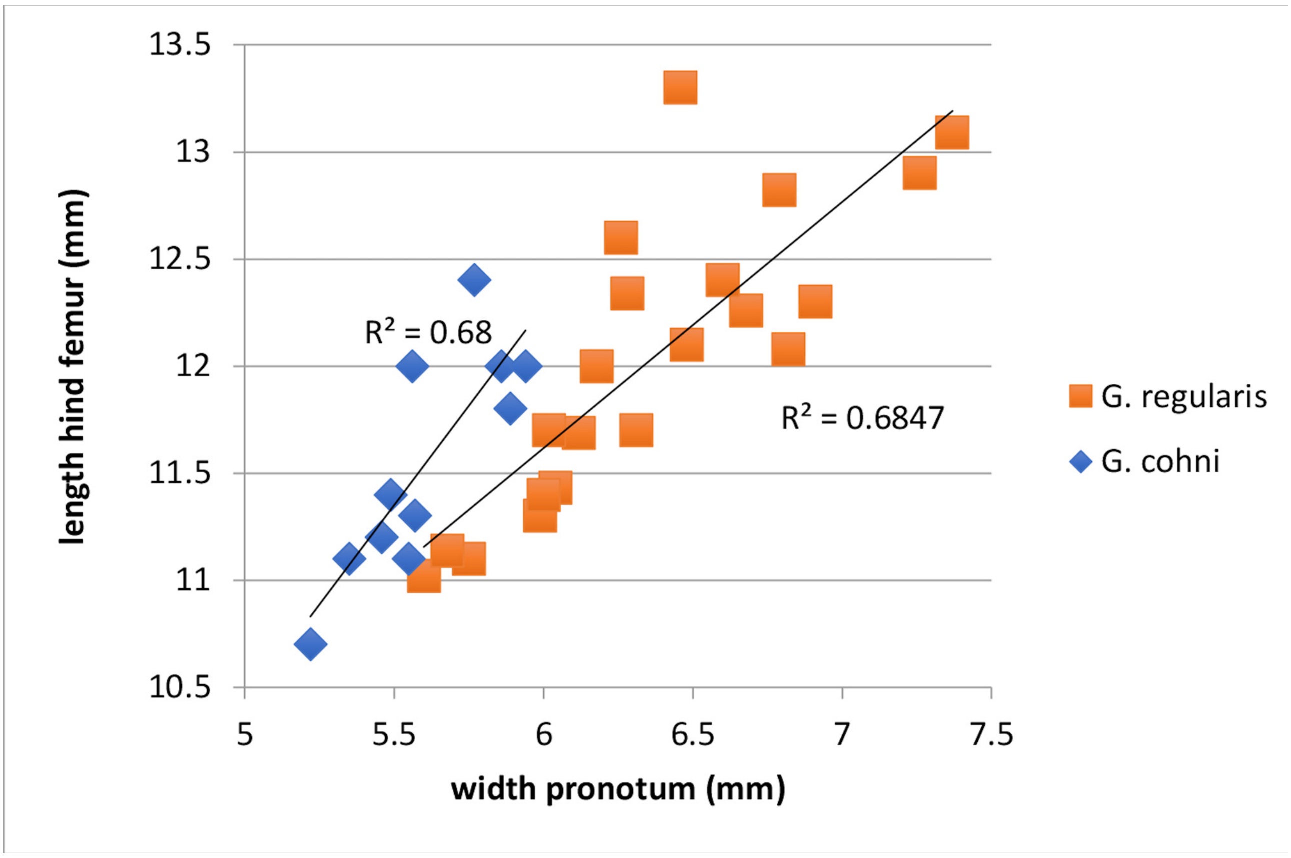

FIGURE 92. Regression of width pronotum vs. hind femur length in *G. regularis* vs. *G. cohni* showing narrower pronotum in the latter.

Paratypes. (Total: 25♂ 11♀). **Arizona.** *Coconino Co.,* Sedona, north end of town, 4400’, 25-vi-1980 (S80-45) 3♂ 2♀; 15-vi-1990 (S90-49) 1♂; 5-viii-1991 (S91-78) 2♂; 30-vi-1994 (S94-35) 1♂. *Gila Co.,* Globe, 3544’, 25-viii-1982 (S82-103) 1♂. *Graham Co.,* Hwy 366 near intersection Hwy 191, 3333’, 32° 43’ 04.6” -109° 43’ 34.9” 28-vii-2015 (S15-102) 1♂. *Yavapai Co.,* Agua Fria National Monument 3705’, 34° 14’ 25.0” -112° 01’ 33.4”, 19-ix-2011 (S11-105) 1♂; 12-vi-2012 (S12-24) 1♂. Agua Fria National Monument 3200’, 34° 14’ 50.2” -112° 03’ 28.5”, 12-vi-2012 (S12-25) 1♀. Camp Verde, 3151', 21-viii-2012 (S12-107) 1♂. Cordes Junction, gas station, 3802', 18-viii-2004, 2004-115, 1♀. Sedona, Sky Ranch Lodge Motel grounds by Sedona Airport, 5120', 12-vi-1996 (S96-61) 5♂ 4♀; 15-vi-2007 (S07-61) 5♂ 2♀. Forest Road 525 near Sedona, 4507', 16-viii-2004, 34.91855° -111.91090°, 2004-111, 1♀. 2.5 m W Clear Creek "Bull Pen", 3502', 11-viii-2011, 34.54646° -111.74417°, 2011-097, 1♂. **Texas.** *Brewster Co.,* Alpine, 12-vi-2007, 4270' 30° 35' 49.86" -103° 53' 11.81" (S07-41) 1♂. *Jeff Davis Co.,* Fort Davis, Fort Davis National Historic Site, 4852', 30° 35' 49.86" -103° 53' 11.81", 1-vii-2015 (S15-67) 1♂.

Song records only. **Arizona.** *Cochise Co.,* Apache Pass, 5106', 10-vii-2002, Recording DAG2002-044. 1♂. Subsequent collecting here 2-vi-2013 yielded only nymphs of *G. lightfooti.* **New Mexico.** *Hidalgo Co.,* Coronado National Forest Road 63 (Geronimo Trail), 5330', 31.529° -108.897°, 12-iv-2013. No recording. 1♂ heard.

Derivation of name. "regularis" in reference to the regular spacing of pulses in the trilling song.

Geographic range. Fig. 94. Also into adjacent Mexico.

FIGURE 93. Holotype male (left) and paratype female (right), both from the type locality (S07-61).

Habitat. Mostly known from areas of human disturbance (including rangeland disturbed by cattle grazing), usually in cracks in the soil or in shelter associated with structures, from 960-1560m. Population at type locality fairly dense with deep cracks providing good refuge for singing males.

Life cycle and seasonal occurrence. Adults known from June through October. The Double Tank area (34° 14' 23.64" -112° 01' 37.49") of Agua Fria National Monument, AZ, has two large, man-made cisterns for cattle water in an area of open Sonoran Desert scrub. The 3 common species (*staccato, cohni,* and *regularis*) of *Gryllus* there have been part of a multiyear study on parasitoid tachinid *Ormia* flies (Sakaguchi & Gray 2011). As such, we have multiple collection dates for this area which indicate that there are apparently two field generations/year based on the following collections: (1) adults and late instar nymphs collected in mid-June, 2012, and molting to adult late June and early July and (2) 9 male and 11 female late instars collected 9-x-2010 molting to adult mid-November through early December, 2010. Agreeing with this pattern, from the type locality (S96-61) on 12-vi-1996, adults and many late instars attracted to oatmeal with the nymphs molting to adult in late June/early July that same year.

We also suspect that rainfall patterns can significantly affect these schedules. In the laboratory, no diapause at any developmental stage (Agua Fria, AZ) where they can have 3 or 4 generations/year.

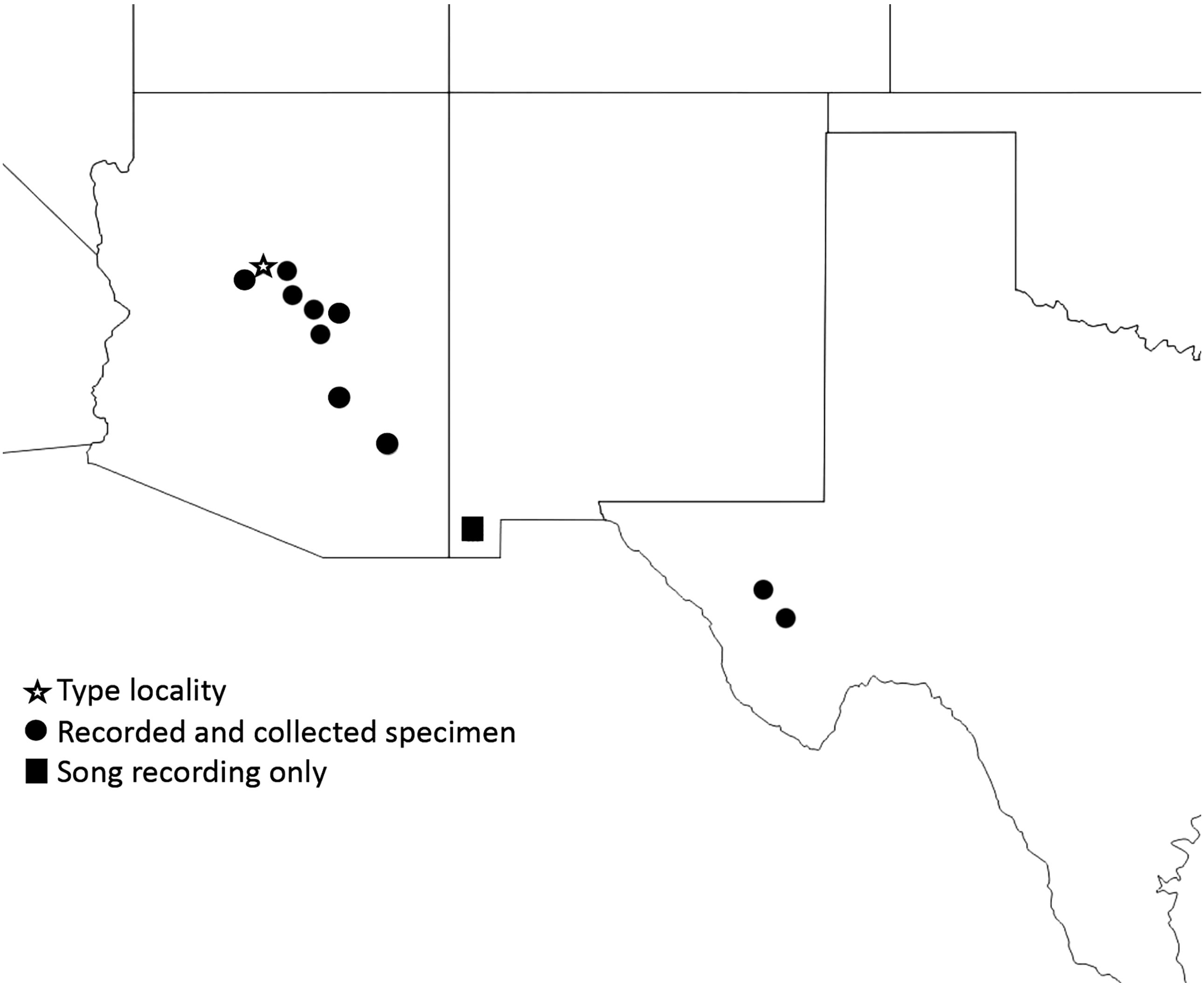

FIGURE 94. Known US distribution of *G. regularis*.

Variation. **Color:** Generally black head and pronotum with dark brown tegmina. **Hind wing length:** Of 37 total field collected adults, only 1 male each from the Arizona localities of Globe (S82-103), Camp Verde (S12-107) Clear Creek (2011-097), and Graham Co. (S15-102) long winged. Late instars brought into the laboratory, usually molt to adult with short hind wings. In contrast, adults reared from eggs, in the laboratory, are all, or almost all, long hind winged. **Song:** Of 27 recorded males, all with 1 p/c except for a male (Fig. 95, R11-167) from Agua Fria (S11-105). This male had short bursts of a "pure" trill of 1 p/c and then switched to 2 p/c. His 16S gene (G2443) mapped with *G. regularis* from other Arizona localities.

DNA. Multilocus 2016-037 from Agua Fria National Monument, 9-viii-2016. Nearest multilocus relatives (Gray *et al.* 2019) are *G. rubens* and *G. texensis.* In the ITS2 gene tree (Fig. 73), the two samples from west Texas (G3154, S15-67, Jeff Davis Co.; and G1085, S07-41, Brewster Co.) appear closer to *G. texensis*. Without further data, we are not sure how to interpret this result.

Discussion. Singing males frequently located deep in extensive soil cracks at Agua Fria and Sedona Airport localities and almost impossible to flush with water. Oatmeal trails through the habitat of singing males can help pull in wandering adult females, nymphs, and occasionally adult males. At the north end of Sedona, Arizona, *G. regularis* occurs with 5 other species of *Gryllus*.

In Alpine, TX (S07-41), *G. regularis* occurred with both faster trilling *G. texensis* and 2p/c *G. armatus*. We have only collected *G. regularis* there once and its distinctive long trilling song and short hind wings were recognized when collected and documented in field notes.

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

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

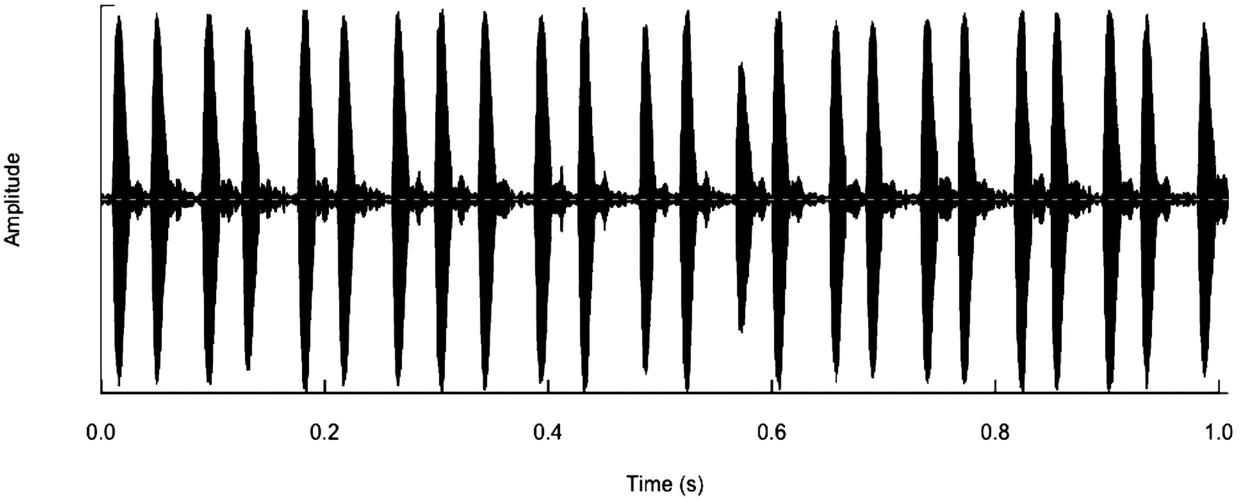

FIGURE 95. *G. regularis* with subtle pairing of pulses (R11-167), from Yavapai Co., AZ (S11-105), at 21°C.

The Integer Group

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

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

Gryllus integer Scudder

Mud Crack Field Cricket
Figs 96–104, 106, Table 1

1901 *Gryllus integer* Scudder. Psyche 9: p. 268. Lectotype male (Fig. 99) designated by Weissman *et al*. 1980: "W. Berkeley, Calif., Aug 20, 1897. S.H. Scudder coll. *Gr. integer,* Scudder's type 1901. Red label, type 14065." Specimen labeled Weissman and Rentz cotype #1). Type in ANSP.
'Gryllus VI' of Weissman & Rentz (1977a) and Rentz & Weissman (1981).
G. integer (in part) of Weissman *et al.* (1980).
'Gryllus #6' of DBW notebooks.

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

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

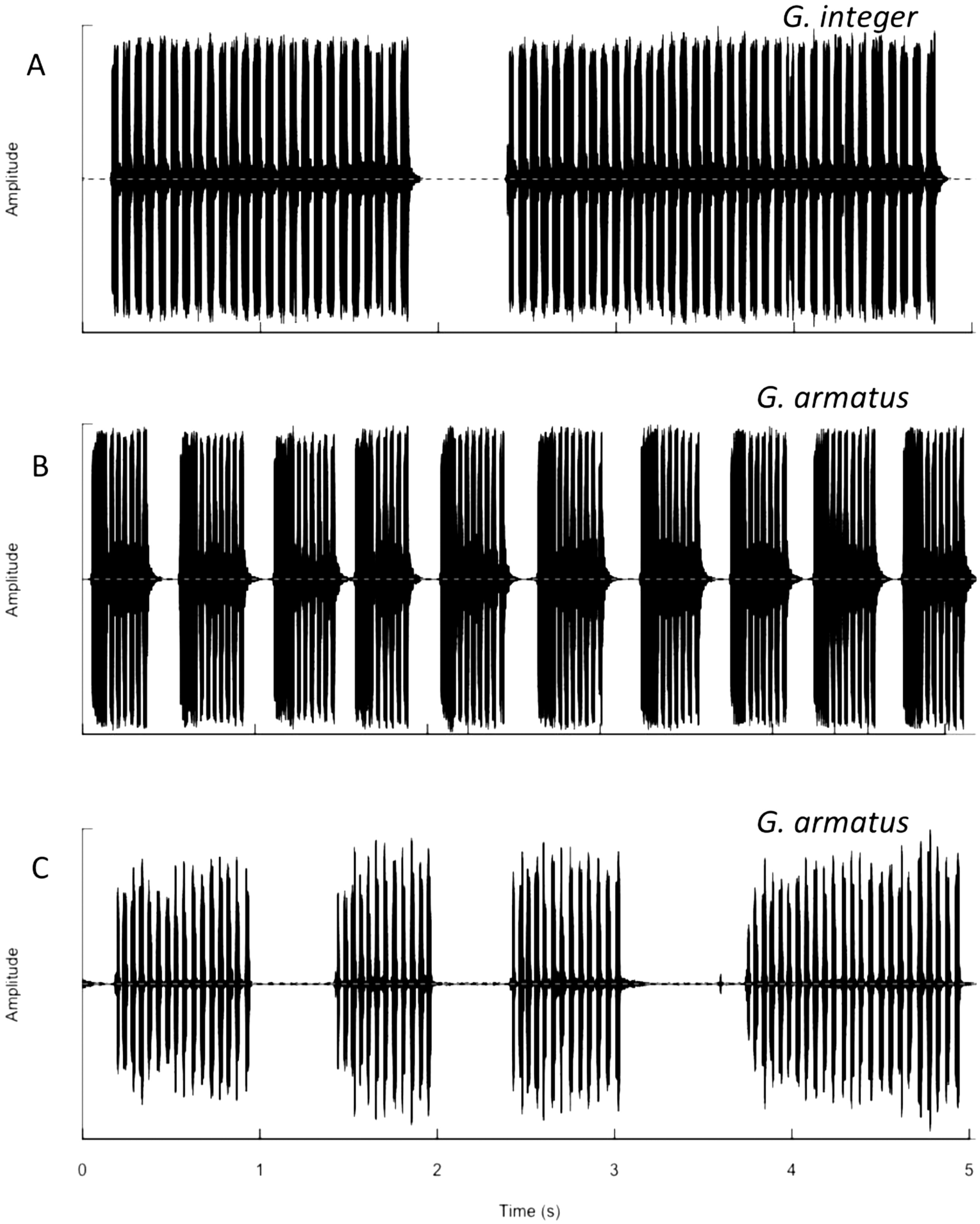

FIGURE 96. Five second waveforms of typical calling songs of (A) *G. integer*, (B) *G. armatus* with introductory trill, and (C) *G. armatus* without introductory trill. (A) *G. integer*: (R16-60) Tulare Co., CA (S16-21), at 24.2°C; (B) *G. armatus*: (R15-177) Artesia, NM (S15-58), at 25.1°C; (C) *G.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

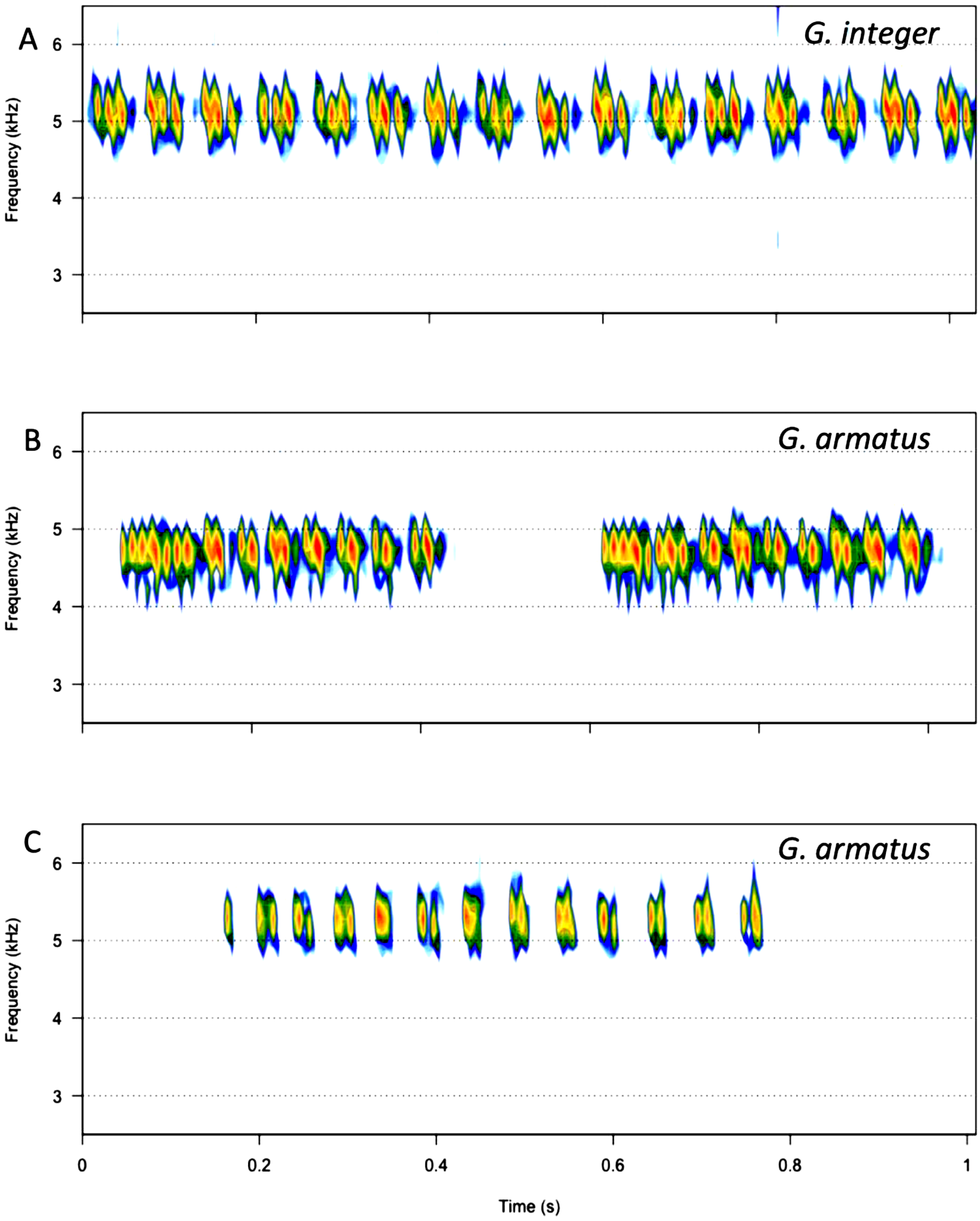

FIGURE 97. One second spectrograms of (A) *G. integer*, (B) *G. armatus*, and (C) *G. armatus*; same male recordings as in Fig. 96.

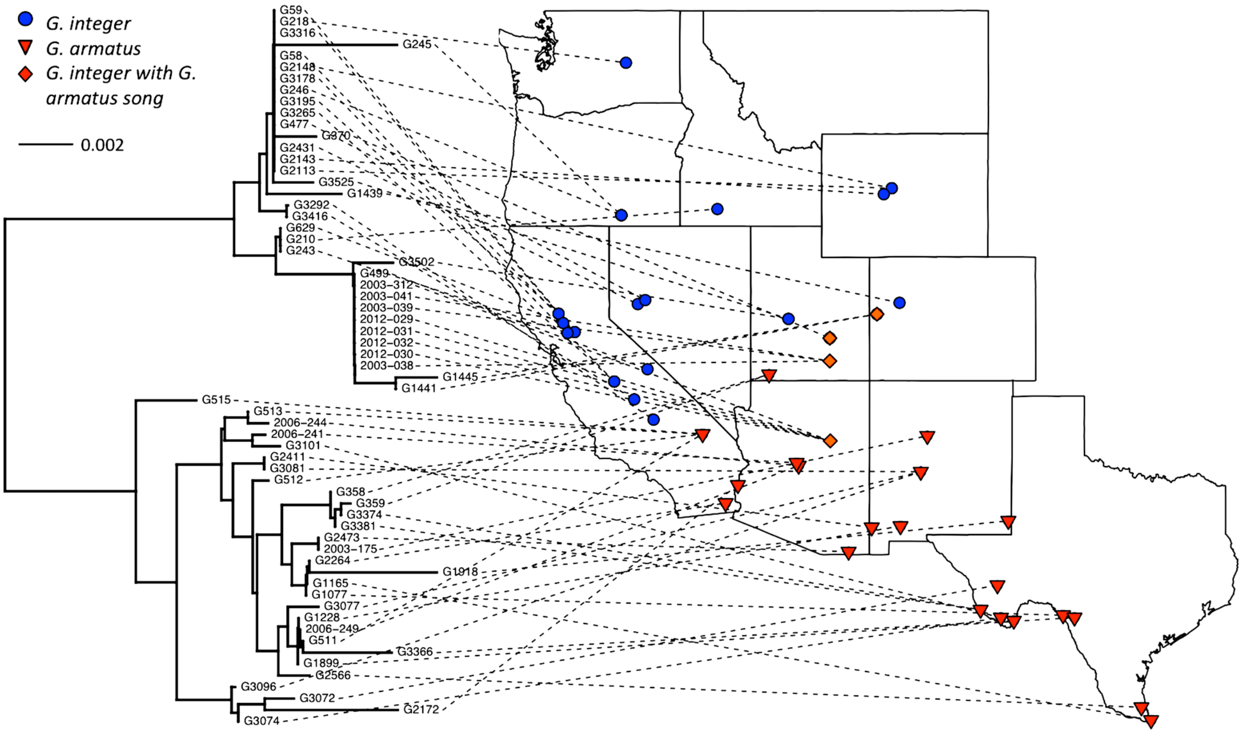

FIGURE 98. ITS2 gene tree and distribution map for both *G. armatus* and *G. integer* showing both geographic separation and zone of possible hybridization. Collection stop numbers for ***G. armatus***: S04-121 (G358, G359); S05-110 (G511, G512, G513, G515); S07-26 (G1165); S07-33 (G1077); S07-79 (G1228);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

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

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

Geographic range. (Fig. 100). Usually sporadically distributed but can be locally common. Not known from the hot Southwestern Sonoran and Chihuahuan Deserts where it is replaced by *G. armatus*, but does occupy the Great Basin Desert and the western part of the Mohave Desert. DC Lightfoot has kindly allowed us to examine some 25 specimens he collected in the Oregon Counties of Harney, Malheur, and Wasco during the early 1980s. While these are morphologically highly suggestive of *G. integer*, none have associated recordings. We believe his specimens indicate a more widespread distribution of this taxon east of the Cascades in Oregon.

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

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

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

Variation. **Color:** Individual crickets, especially second-generation ones from hot climates like the California Central Valley, can have a distinctive two-tone contrasting appearance: black head and pronotum coupled with beige/straw colored tegmina (Fig. 99) and legs. In certain individuals, even the pronotum can be beige/straw colored. **Hind wing length:** Always with long hind wings although these have been occasionally shed in field-collected adult males (Weissman *et al*. 1980). Of 133 studied *G. integer* males, all but 9 had intact long hind wings. All those without long hind wings were, in fact, dealate, a condition discussed elsewhere for *Acheta domesticus* (Weissman & Rentz 1977b, Walker 1977) where both hind wings are shed. This condition is easily diagnosed in those males whose right tegmen has been removed for file analysis. Interestingly, in two populations found away from humans (Mono Lake, CA, S78-123 & S78-125, & Lake Lenore, WA, S04-60), where individuals were living in cracks in dry mud flats with short grass, 4 of 6 males (S78-123 & S78-125) and 1 of 5 males (S04-60) had lost their hind wings. In contrast 6 males from a similar habitat (Washoe Co., NV, S83-49) all had unshed, long hind wings. At some localities, female *G. integer* may be difficult to assign to species. In those situations where we can make such assignments, no female, of 83 collected, was dealate. **Ovipositor length:** The 3 females from Wyoming (S11-72) have the longest ovipositors (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 2–4p/c and, rarely, a pure trill (Fallon, NV, S98-95, R98-123, Fig. 103). A male from Riverton, WY (S11-73) sang with 4 pulses in all chirps. In the face of such variation, multiple male analysis from the same population will usually give a definitive answer.

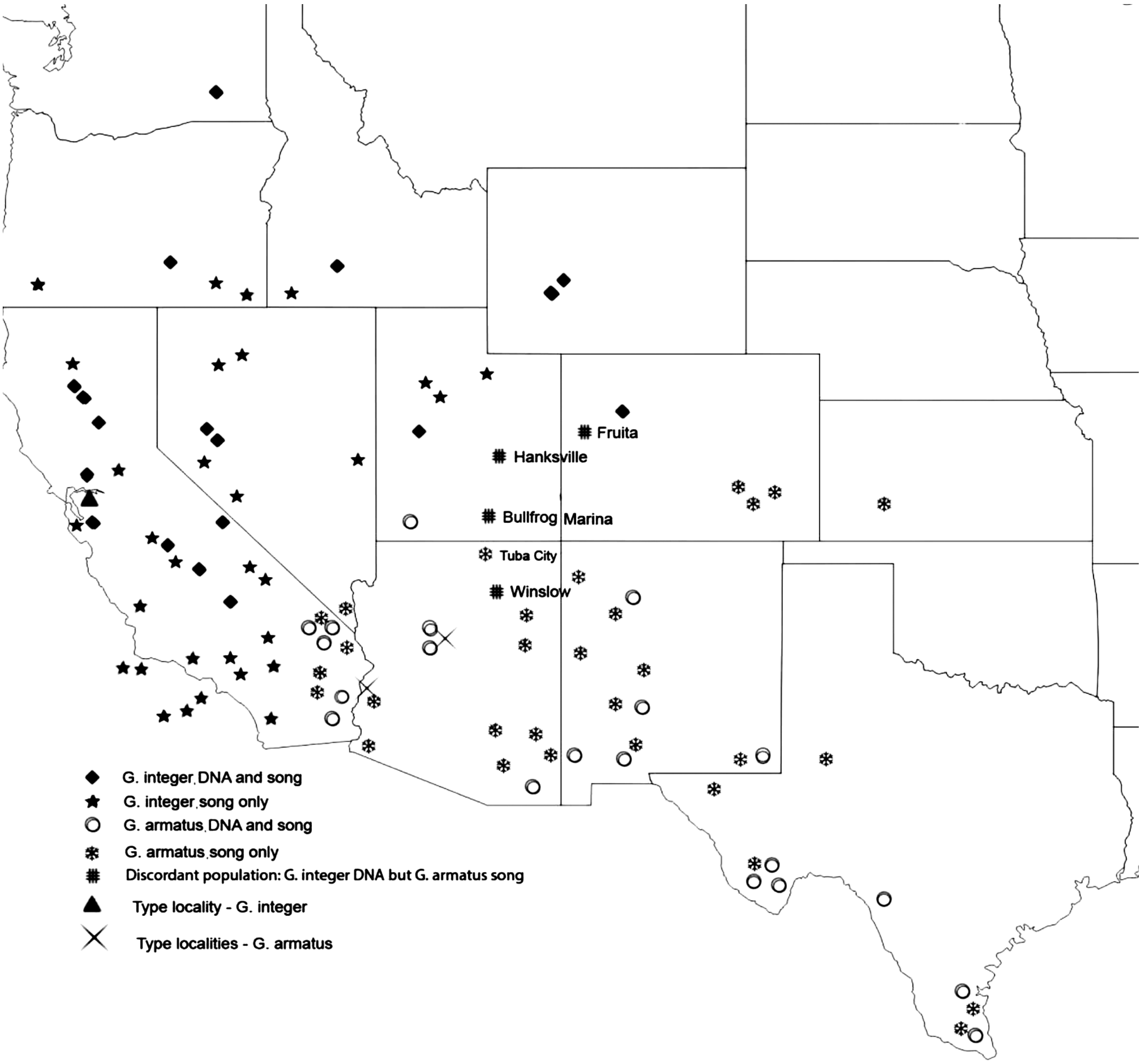

FIGURE 100. Known US distribution, *G. integer*, along with sister species *G. armatus*, showing zone of possible hybridization in the Four Corners area.

Specimens examined. **California:** *Colusa Co.,* Sacramento River SRA, 96', 18-vii-2015 (S15-81). 13m S 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 178 19.4 m W Hwy 14, 3064', 21-vii-2015 (S15-95). *Lake Co.,* Clearlake Oaks, 5-viii-2014, 1428' (S14-63). *Los Angeles Co.,* Santa Catalina Island, Toyon Canyon, 9-x-1983, S. Bennett. *Madera Co.,* Hwy 41 6.2 m E Fresno Co. line, 457', 20-vii-2015 (S15-91). *Mendocino Co.,* Willets, 1300', 2-viii-1980 (S80-58). *Monterey Co.,* King City, 23-viii-1978. *Sacramento Co.,* Folsom, 174', 19-vii-2015 (S15-87). *San Luis Obispo Co.,* Montana de Oro State Park, 24-viii-2006 (S06-97). *Santa Barbara Co.,* San Miguel Island, Cuyler Harbor, 31-viii-1978, S.E. Miller; Santa Barbara Island, widespread, iv-1979, SBMNH; Santa Cruz Island, Stanton Ranch. *Santa Clara Co.,* Los Gatos, 12-viii-2006 (S06-72). Stanford University, Lake Lagunita, 2-v-1992 (S92-45). *Shasta Co.* Lake Shasta

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

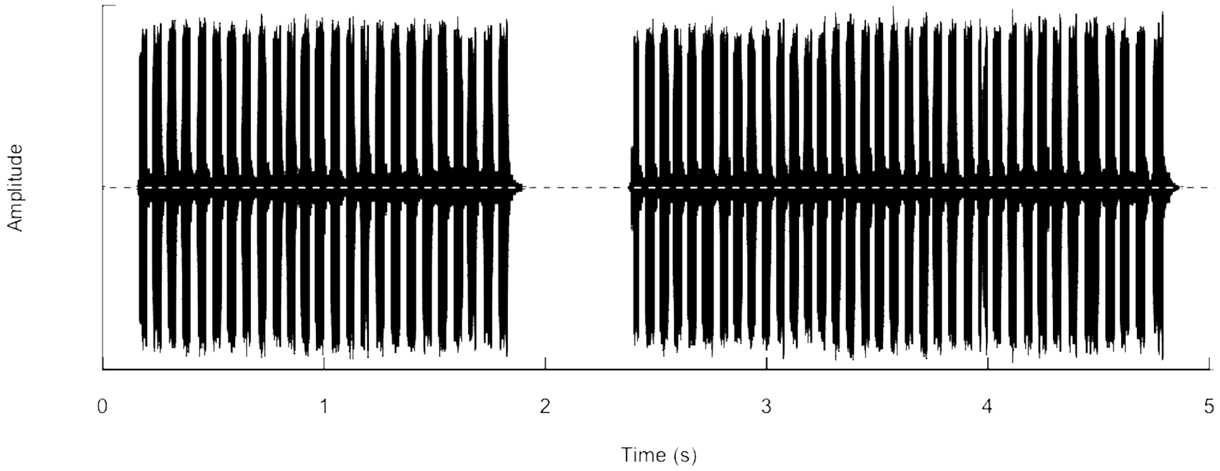

FIGURE 101. Five second waveform of typical calling song of *G. integer* (R16-60) Tulare Co., CA (S16-21), at 24.2°C.

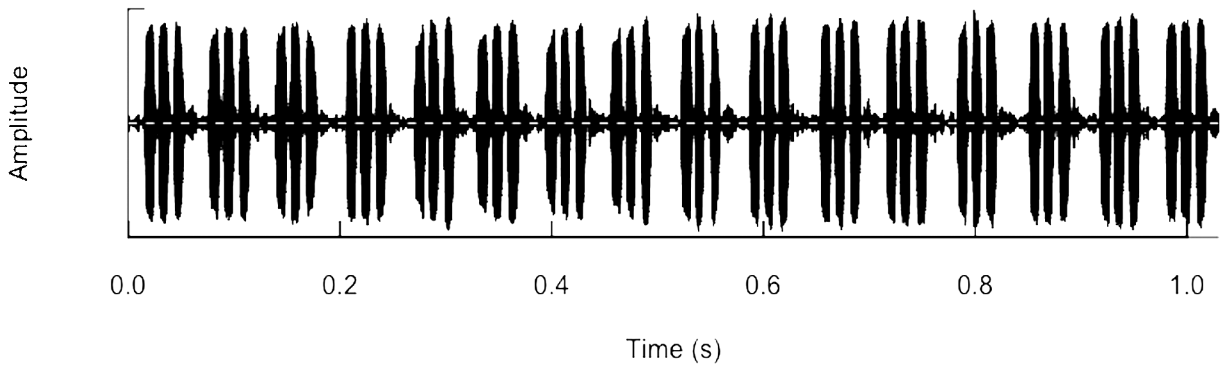

FIGURE 102. One second waveform of typical calling song of *G. integer* (R16-60) Tulare Co., CA (S16-21), at 24.2°C revealing the typical fast 3 pulse/chirp structure.

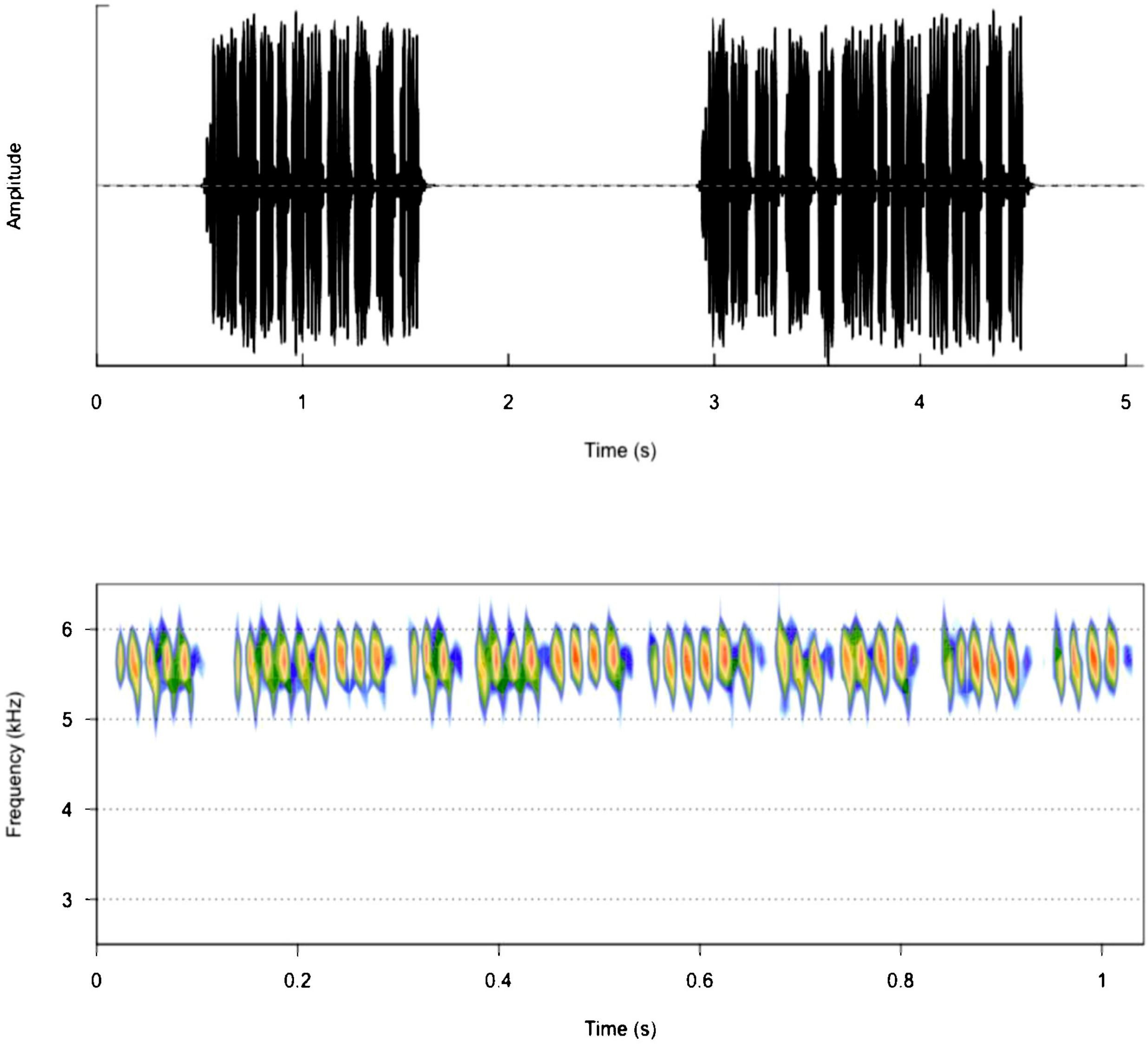

FIGURE 103. Anomalous song (top) of *G. integer* (R98-123) Churchill Co., NV (S98-95), at 25°C, without distinctive 3 pulse chirp structure. Spectrogram (bottom) of same male, but note different time scale.

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

Discussion. Our initial 16S genetic data showed clear separation between *G. integer* and *G. armatus,* but given our previous documentation of 16S clades in other species, such as *G. vernalis, G. veletis,* and *G. lightfooti,* we were unsure of its significance with these two taxa. With the subsequent analysis of the ITS2 gene, such separation was again confirmed (see Fig. 98): that is, individual *G. integer* and *G. armatus* are similarly and consistently different from each other for both 16S and ITS2 sequences. Nevertheless, we found four populations along the song-boundary suture zone between *G. integer* and *G. armatus,* that have both *G.* integer 16S and ITS2 DNA and a mostly *G. armatus* song: (1) Of 2 males recorded from Fruita, CO (S09-114), both had *G. integer* DNA. One male had an introductory trill followed by 3p/c and the second male had an introductory trill usually followed by 3p/c but occasionally by 2 or 4 p/c. A male from nearby Rifle, CO (S09-109) had typical *G. integer* DNA and a *G. integer* song with no introductory trill and 3p/c. (2) At Winslow, Arizona, the ITS2 DNA is definitely *G. integer* but of 11 males recorded from there during 2003 (10-viii-2003), 2010 (10-viii-2010), and 2012 (27-vii-2012), we found the following: 3 males had no introductory trill and 2p/c and 8 males had a short (1-4 pulses) introductory trill followed by 2p/c. Based only on song, we would classify this population as *G. armatus* but per our convention of giving priority to the DNA results, we label this population as *G. integer*. (3) Of 25 males recorded in 2003 (collected 27-vii-2003) from Garfield Co., UT, Hwy 276 some 7.4 m N Bullfrog Marina (= 3.2 m S Ticaboo): 17 males had no introductory trill and 2 (rarely 3) p/c while 7 males had introductory trills followed by 2 (rarely 3) p/c; one male had zero or one introductory pulse and then 2–3 p/c. The ITS2 sequence of 4 males all mapped with *G. integer*. (4) Of 10 1992 males recorded from Hanksville, UT (S92-109), 9 sang with 2–3p/c, without an introductory trill, and the tenth male sang an introductory trill followed by 2–3p/c. In 2004 (S04-128), all 3 recorded Hanksville males had introductory trills usually followed by 3 (range 2–4) p/c. The latter's DNA (G370) mapped with *G. integer* as did a male (EC3035) from 4 km W Hanksville on Hwy 24, who had an introductory trill and then 2p/c.

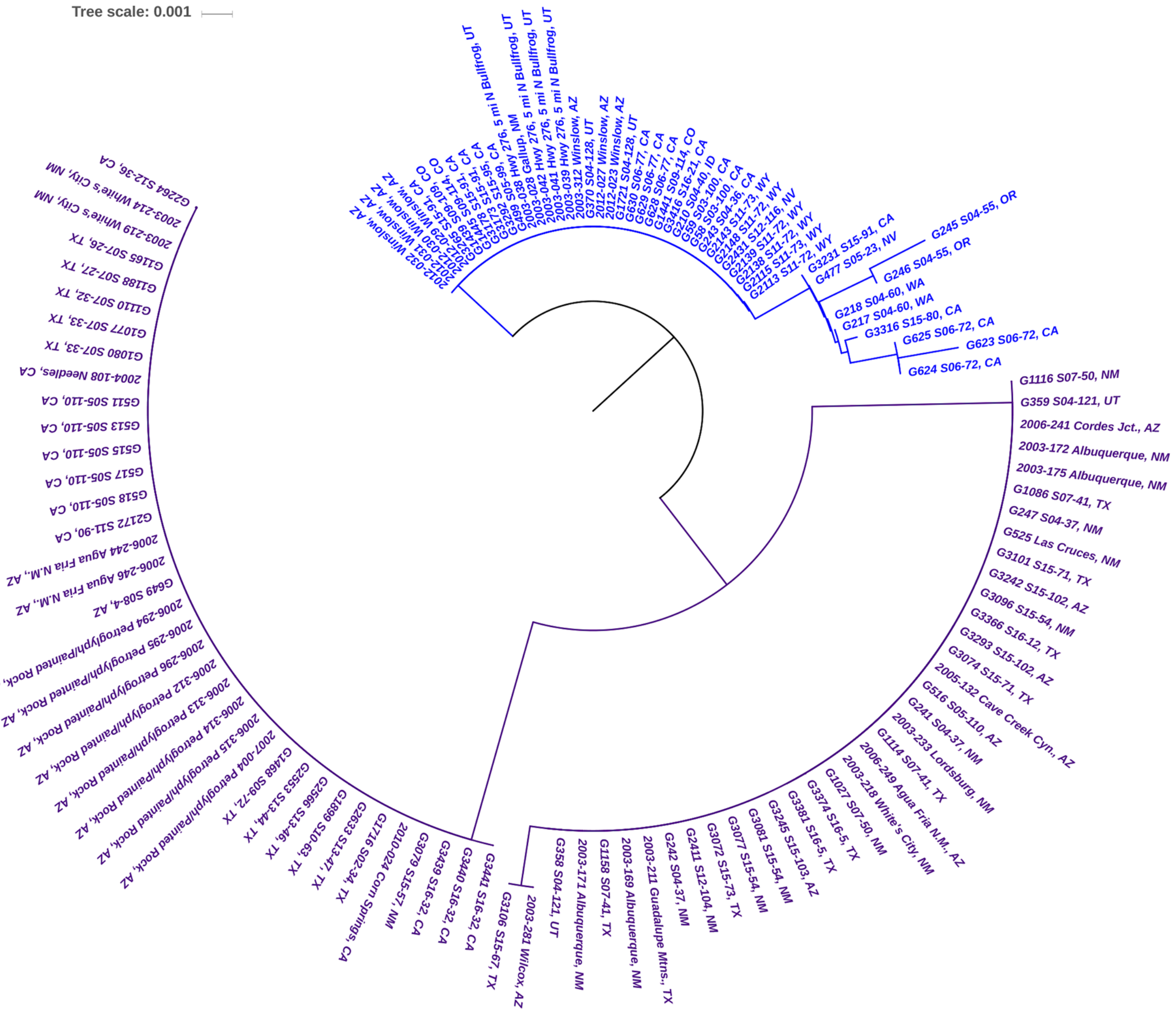

FIGURE 104. 16S gene tree with *G. integer* samples in blue and *G. armatus* samples in purple. Locality information follows all ID numbers. Note the two 16S clades within *G. armatus*.

We have done some preliminary crossing trials between *G. integer* and *G. armatus*: (1) *G. integer* from Santa Clara Co., CA (S92-45, no introductory trill and all 3p/c) x *G. armatus* from Dona Ana Co., NM (S92-127, all with an introductory trill converting to 2p/c). Two of three crosses involving CA males x NM virgin females resulted in good egg hatches. One of four crosses involving CA virgin females x NM males resulted in a good egg hatch. (2) Two virgin *G. integer* females from Yolo Co., CA (S04-36, males with no introductory trill but all 3p/c) x Dona Ana Co., NM (S04-37, all males with an introductory trill converting to 2p/c), produced eggs. Only 2 eggs hatched in one cross and no eggs hatched in the second cross. (3) Four crosses (two reciprocals of each sex) were conducted between F_1 *G. integer,* Lake Co., CA (S14-63) x F_1 *G. armatus,* Dona Ana Co., NM (collected in 2014), and all four crosses yielded good hatches while incubated at 27°C and 12L/12D. The adults were paired from 17-xi-2014 to 19-xi with eggs hatching 16-xii-2014, which is some 10 days longer than typical incubation periods seen in species with no egg diapause, although cooler ambient temperatures probably contributed to the delayed hatch. More controlled crosses could help clarify this situation, but these data certainly suggest compatibility between these two-sister taxa. On the other hand, laboratory hybridization is known in other sister pairs of *Gryllus* (e.g., Alexander 1957, Harrison 1986, Walker 2000).

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

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

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

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

***Gryllus armatus* Scudder**

Armed Field Cricket
Figs 87, 96–98, 100, 104–112, Table 1

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

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

Distribution. Southwest and southcentral US.

Recognition characters and song. A small to medium sized cricket with long, narrow tegmina, always long hind-winged (except in certain dealate individuals), probably 2 generations/year with the second summer generation frequently of contrasting solid black head and usually black pronotum coupled with beige/straw colored tegmina (see Fig. 105) and legs. Morphologically indistinguishable from sister species *G. integer* but separated by habitat and geography, slight song differences, and consistent DNA differences, as follows: (1) *G. armatus* is from hotter, more southern desert US locations (see Fig. 106); (2) Most, but not all *G. armatus*, have an "introductory trill" of 2–8 evenly spaced pulses at the beginning of each burst of chirps (see Figs 107, 108, S15-58, R15-177), usually followed by 2 (range 1–3) p/c until that burst is over. In contrast, *G. integer* usually with no introductory trill and 3 p/c, although some males sing with 2–4p/c); and (3) there is a congruent, and consistent association between those males with 2p/c and parallel differences in the ITS2 gene sequences when compared with *G. integer* (see Fig. 98). In distribution map Fig. 106, note a possible zone of hybridization in the Four Corners area of southeastern Utah, west-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 2–3p/c, 700–1000 c/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 2p/c. (2) In contrast to the "clean and uniform" situation at Deming, of 7 males collected in Baker, CA (S05-110), 5 males had introductory trills and then 2 (occasionally 3) p/c; 1 male had no introductory trill but 2 (rarely 3) p/c; and the 7th 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 2p/c while the other 3 males had no introductory trills and 2p/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.

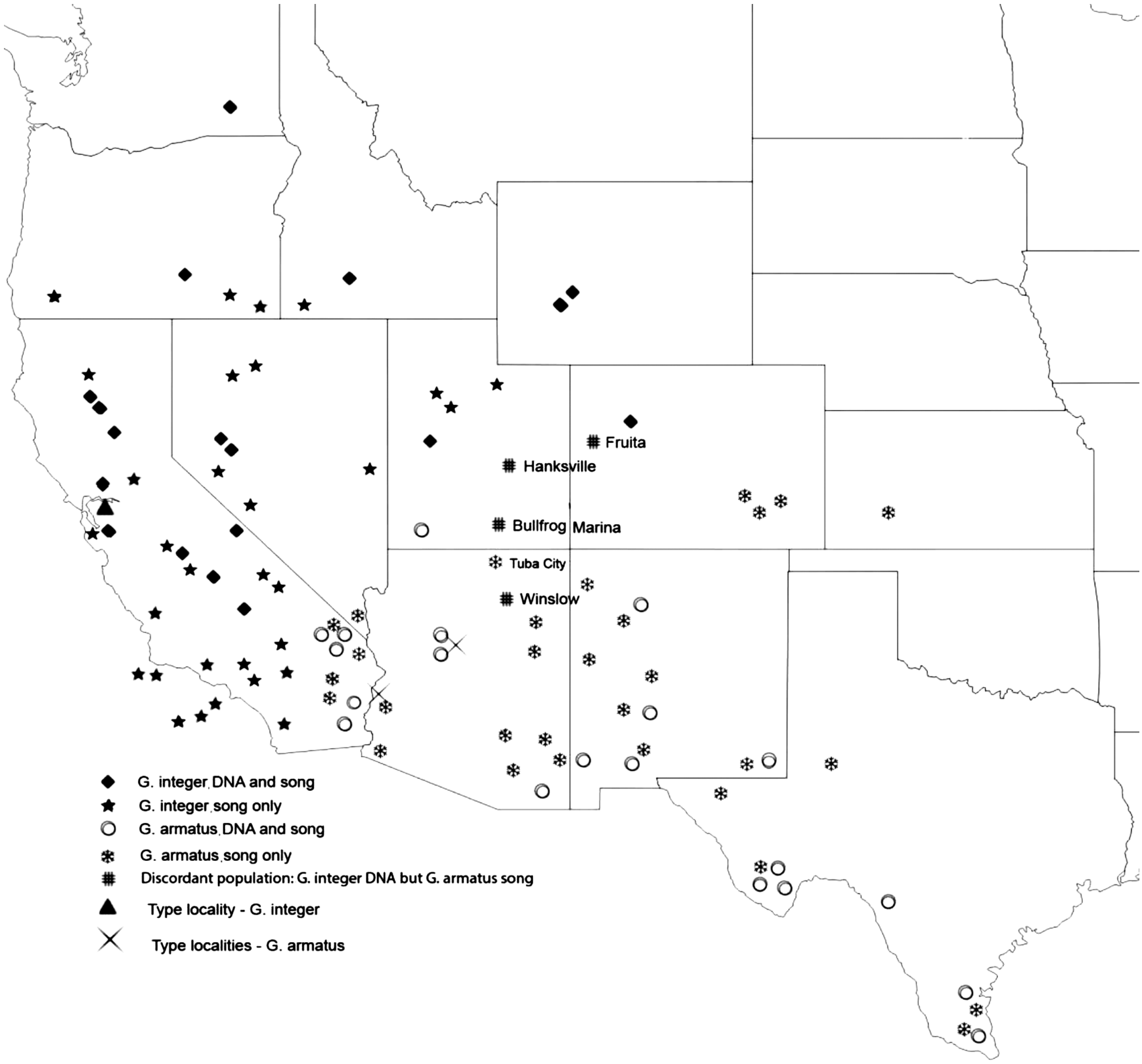

FIGURE 106. Known US distribution, *G. armatus*, along with sister species *G. integer*, showing zone of possible hybridization in the Four Corners area.

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 (>35°C) field-singing individuals of *G. vocalis* can sound like *G. armatus* but are clearly identified when they sing in the laboratory, around 25°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 2190m (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.*

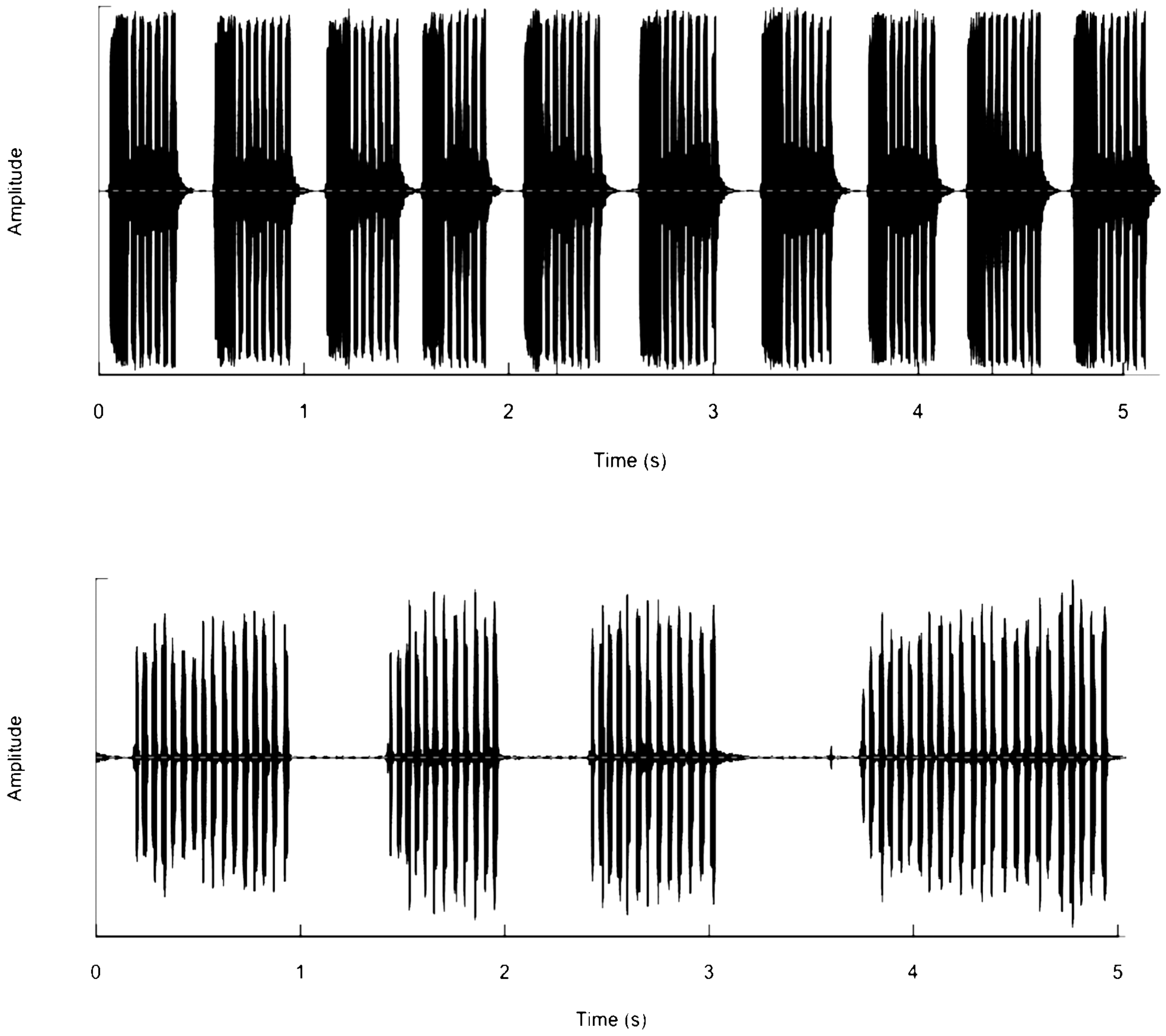

FIGURE 107. Five second waveforms of typical calling songs *G. armatus* with (top) an introductory trill (R15-177) Artesia, NM (S15-58), at 25.1°C, and without (bottom) (2003-170) Bernalillo Co., NM, at 20.6°C.

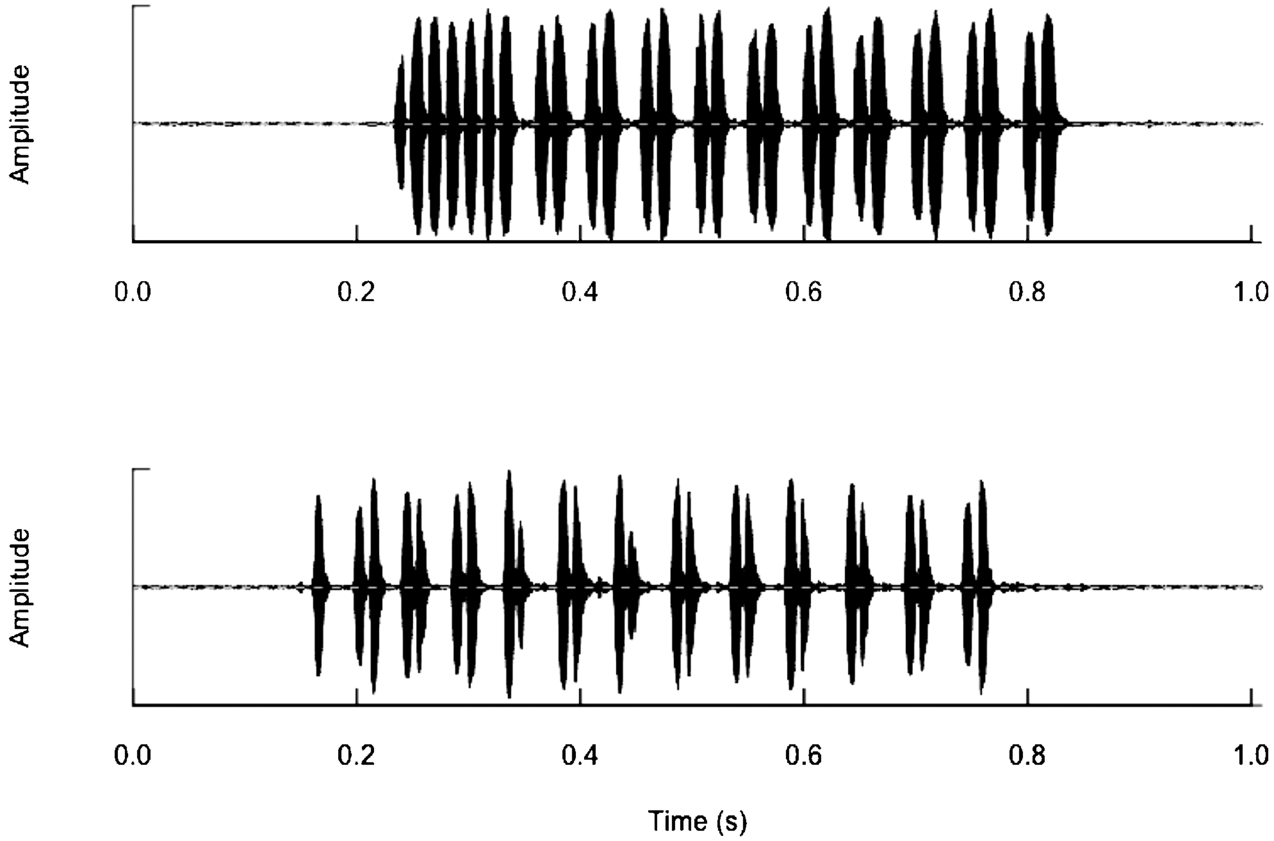

FIGURE 108. One second waveforms of typical calling song of *G. armatus*, same males as in Fig. 107, showing presence (top) and absence (bottom) of an introductory trill in a burst.

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 99 6.85m 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' (S81-44); 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-ii-2008, 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' (S11-92). 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 (S92-62). 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 (S89-63). 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 (S82-89); 1-vii-1994 (S94-33). *Catron Co.,* Reserve, 3-vii-1994, 5770' (S94-50). *Cibola Co.,* El Malpais National Monument, 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-vii-2001, 4420’ (S01-65). *Jeff Davis Co.,* Ft. Davis, 4852’, 1-vii-2015 (S15-67). *Kinney Co.,* Brackettville, 4-vi-1991, 1100’ (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 1420 3.1 m N Farm Road 1018, 10-vii-2013, 15’ (S13-46). **Utah:** *Washington Co.,* La Verkin, 11-ix-2004, 3420’ (S04-121). 1m NE La Verkin, 9-viii-1991, 3700’ (S91-95).

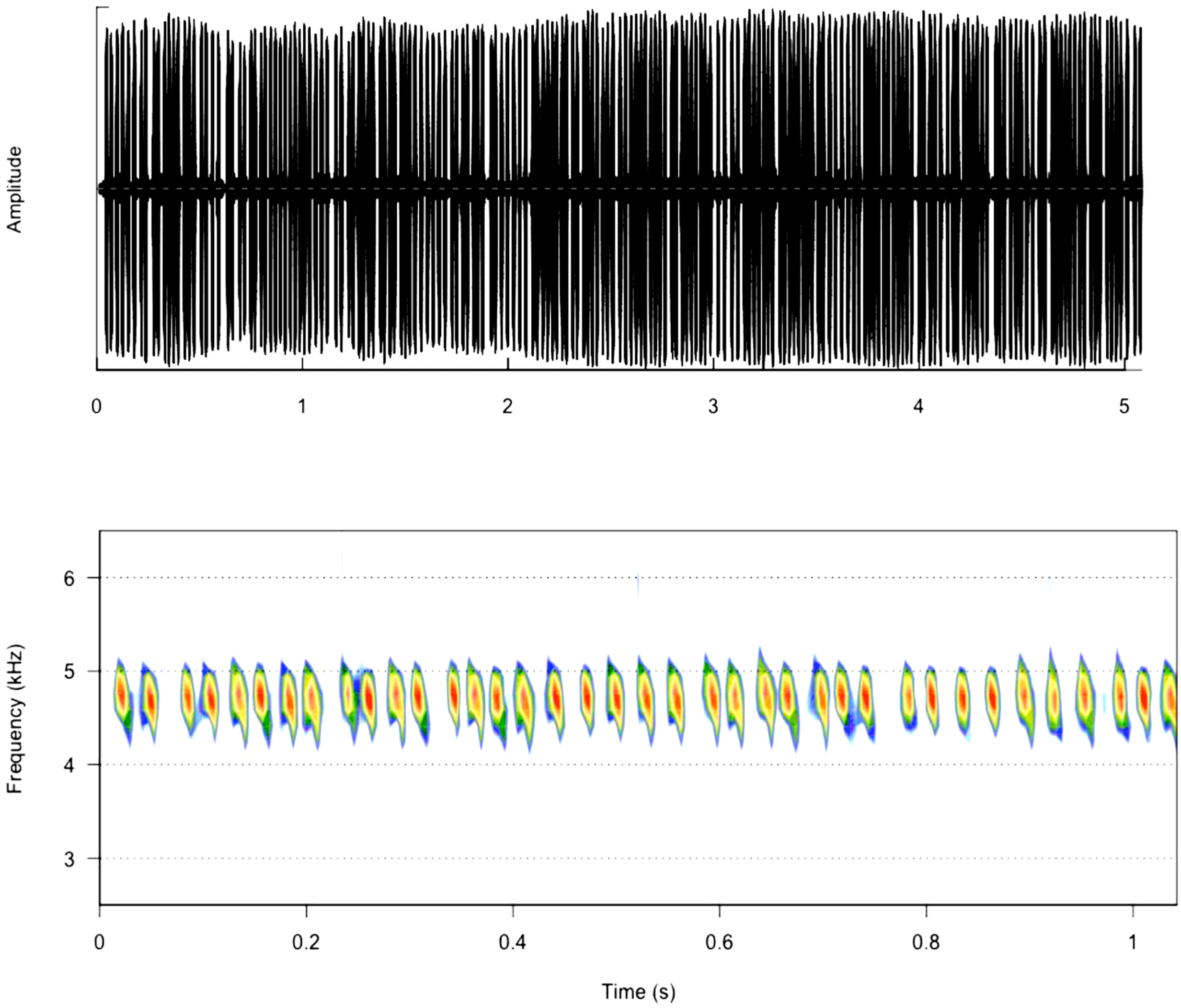

FIGURE 109. Atypical, irregular trill calling song of *G. armatus* (R05-43) Baker, CA (S05-110), at 21.5°C. Top: 5 sec. waveform; Bottom: 1 sec. spectrogram.

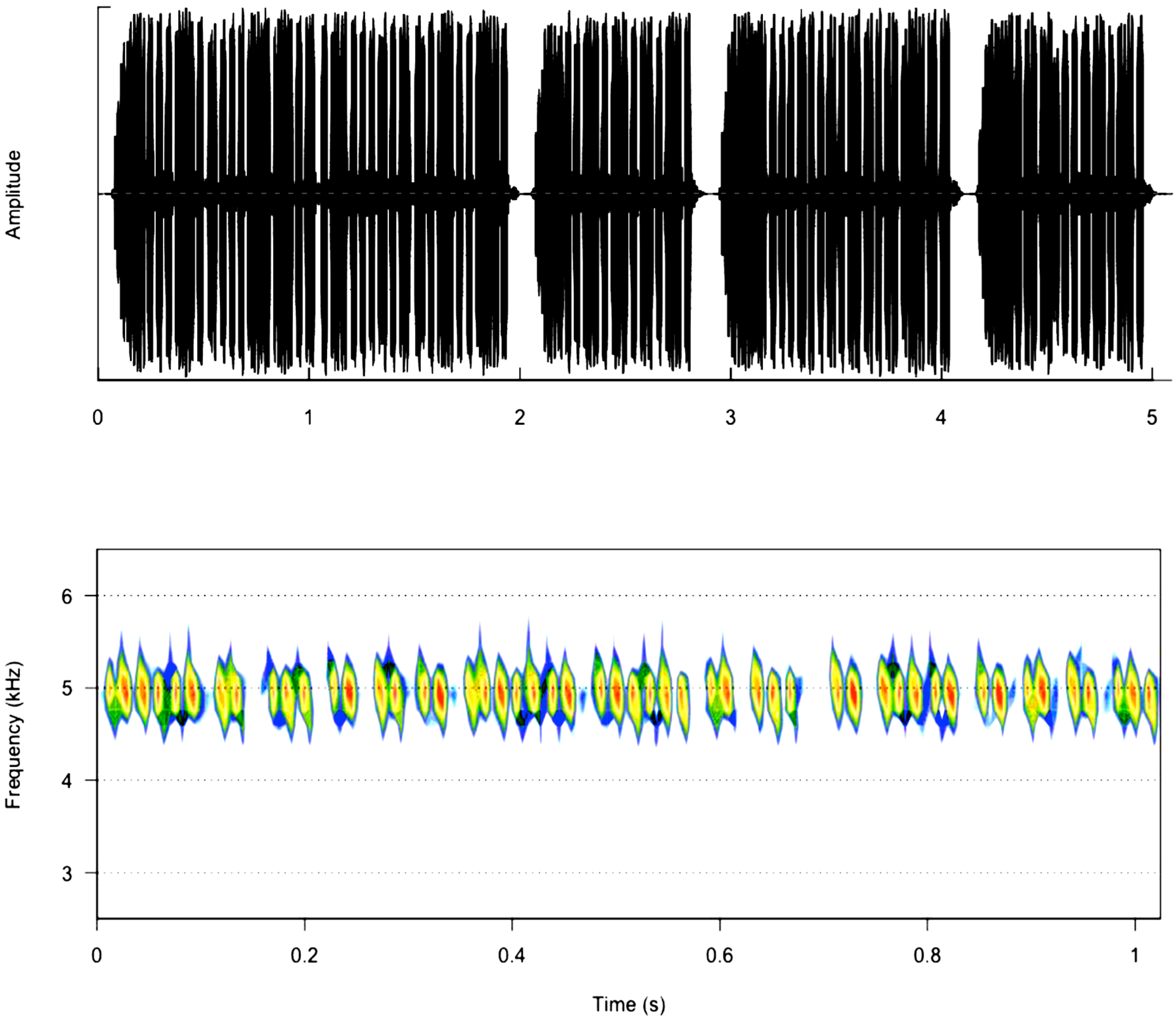

FIGURE 110. Atypical calling song of *G. armatus* (R13-52) Bisbee, AZ, at 24°C, with introductory trill followed by 2-10 pulse chirps. Top: 5 sec. waveform; Bottom: 1 sec. spectrogram.

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 (N = 684 aligned positions) was 98.5 ± 0.87 % within N = 29 *G. armatus*, 99.0 ± 0.77% within N = 34 *G. integer*, and 95.7 ± 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. armatus*, 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 appropriately-singing cricket that we collected was from S87-51, 19 km north Tooele in Tooele Co., and the one male there usually sang with 3p/c (occasionally 2p/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 16S 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 2p/c, then they are probably *G. armatus*. Likewise, several males with no introductory trill and 3p/c are likely *G. integer*. But select *G. armatus*-DNA males can also have no trill and 2p/c and, rarely, no trill and 3p/c. And to complicate matters, males with *G. integer* DNA can have a short introductory trill of 1–3 pulses followed by 2–4p/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 2p/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 2p/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°C and then 2p/c, consistent with *G. armatus*. Five days later in the laboratory at 25°C, this male sang (R91-155) without an introductory trill and with 2–3p/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°C, with no introductory trill and 2p/c. A subsequent recording, at 22.4°, showed an introductory trill and 2 (rarely 3) p/c.

Rare field collected adult males of *G. armatus* sing a pure trill song of 1p/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 3p/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°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).

1964 *Gryllus vernalis* Blatchley. Randell (1964).

Distribution. Known from several central and southern US states (see maps in Capinera *et al*. 2004, Walker 2019), both east and west of the Mississippi River.

Recognition characters and song. Smallest species of *Gryllus*, on average, in US, although some male North Dakota *G. veletis* (from Mirror Pool, Richland Co.) are smaller than the smallest *G. vernalis* males. A morphologically distinctive cricket based on a combination of characters: always with short hind wings, head usually narrower than pronotum (Fig. 118), *song* (Fig. 119, R03-104) usually 3 (rarely 4) p/c, 135–250 c/m, PR 24-31.

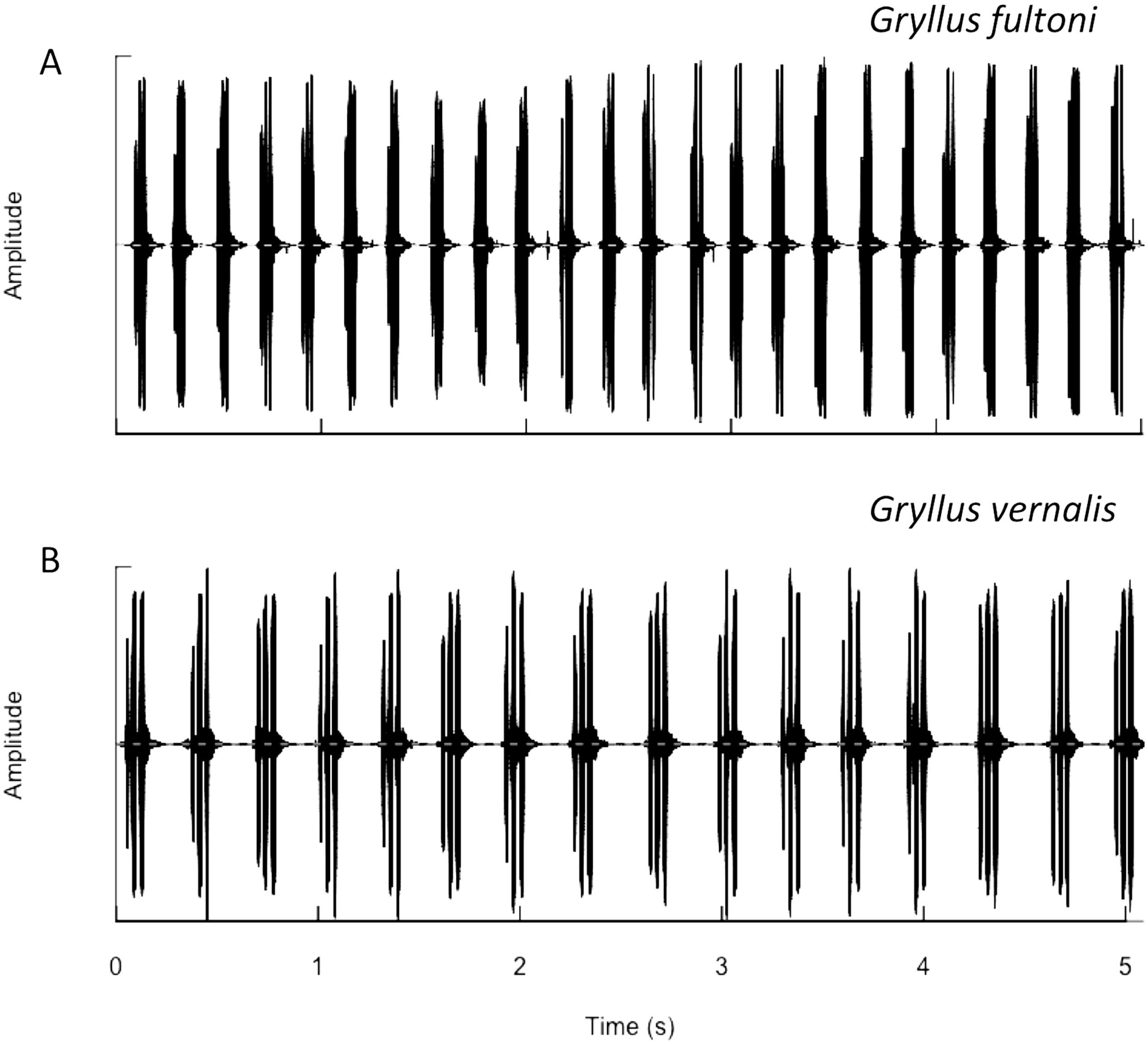

FIGURE 113. Five second waveforms of calling songs of (A) *G. fultoni* and (B) *G. vernalis*. *G. fultoni*: (R03-86) Hocking Co., OH (S03-64), at 25°C; *G. vernalis*: (R03-104) Jefferson Co., MO (S03-56), at 24.5°C.

Differs from sympatric Missouri (S03-56) and Indiana (S03-62) sister species *G. fultoni* in being smaller (Fig. 120), tegmina always black vs. brown and black with tegminal bar in *G. fultoni*, no overlap in file teeth and teeth/mm (Table 1, p. 18), tegmen length, PR slower (can hear difference in field when both species singing at same temperature), and yellow cerci rare (usually the norm in live *G. fultoni*).

Differs from sympatric Iowa *G. veletis* (S03-55) in *G. vernalis* having head frequently narrower than pronotum, proportionately longer cerci, based on body length, smaller size, fewer p/c, and slower PR. Differs from more western, allopatric *G. veintinueve* in no overlap in teeth/mm (Table 1, p. 18), length of cerci, male tegminal length, and multilocus DNA (Fig. 6, p. 28; Gray *et al.* 2019). *G. veintinueve* is only found west of 94° longitude. Differs from allopatric sister species *G. cayensis* because the latter is taciturn and restricted to southern Florida.

Derivation of name. "vernalis" means "of springtime," in reference to its appearance as the first singing *Gryllus* species in Indiana (Blatchley 1903, 1920).

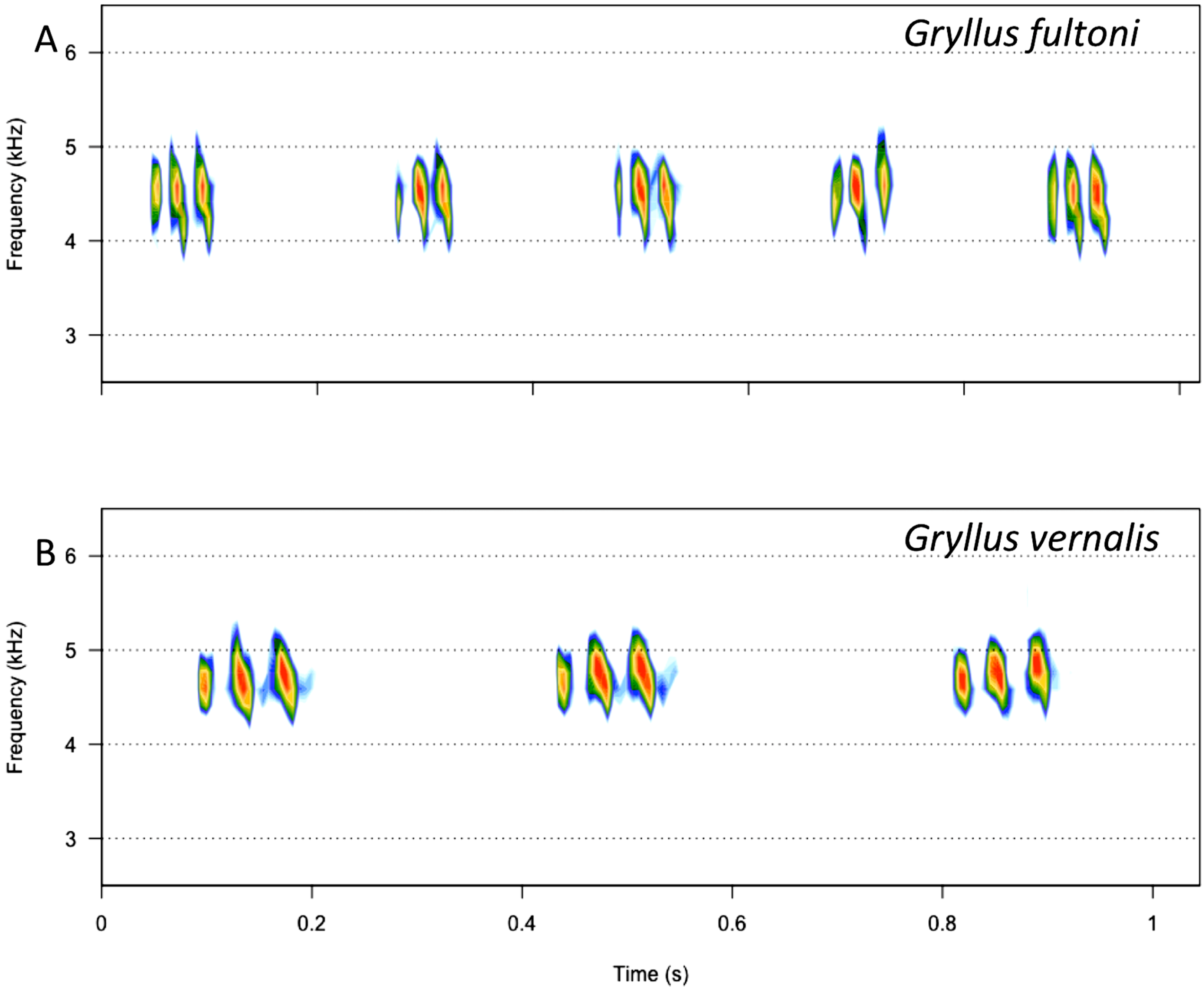

FIGURE 114. One second spectrograms of (A) *G. fultoni* and (B) *G. vernalis*, same males as in Fig. 113.

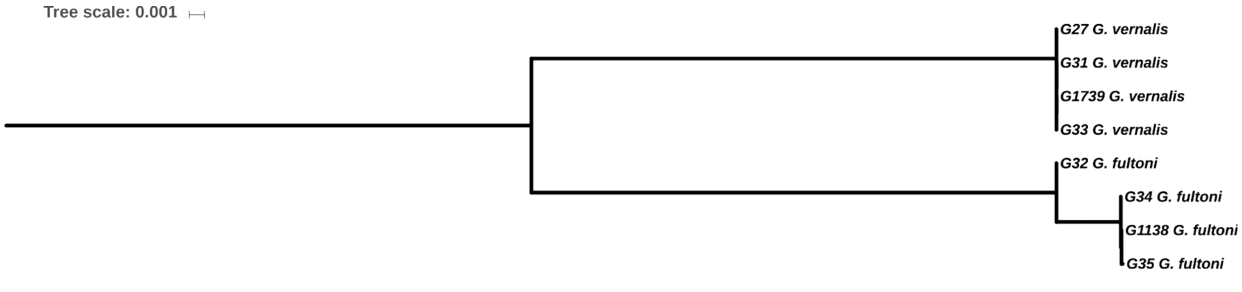

FIGURE 115. ITS2 gene tree. ***G. vernalis*** samples: S03-56 (G27, G1739); S03-62 (G31, G33). ***G. fultoni*** samples: S03-62 (G32, G34); S03-64 (G35), S07-22 (G1138).

Geographic range. (Fig. 121). Some literature citations (e.g. Jang & Gerhardt 2006a, 2006b, for eastern Oklahoma and eastern Texas) probably refer to morphologically similar *G. veintinueve,* a species discussed elsewhere (p. 70) in this paper. Besides our localities (see below), also known from Alabama, Mississippi, and Kentucky (Walker 2019; Jang & Gerhardt 2006a, 2006b).

FIGURE 116. Lectotype female, *G. vernalis*, specimen and labels.

FIGURE 117. Allolectotype male, *G. vernalis,* specimen and labels.

Habitat. An obligate woodland, and edge of woodland, species. Males can frequently be heard singing from undergrowth abutting woodlands but can be difficult to collect even when using oatmeal trails.

Life cycle and seasonal occurrence. No egg diapause. One generation/year. Adults from early May (Blatchley, 1903) until mid-summer, and overwinter as late instars.

Variation. **Head size:** Of the specimens from Indiana near the type locality, 0 of 3 males and 3 of 4 females had the head narrower than the pronotum. From Missouri 5 of 8 males and both females had the head narrower. From Tennessee, 5 of 7 males and all 7 females had the head narrower. No specimens were captured in Iowa or Ohio, although they were heard singing from dense vegetation. **Cerci color:** Rare (1 of 31) individuals with yellow cerci when alive. This color darkens upon death. **Pulses/chirp:** Usually 3 p/c but 1 (S03-56) of 17 recorded males with a rare chirp with 4 pulses. **Are female tegmina widely separated?** Usually, but not always in *G. vernalis*, and this "diagnostic" condition (Blatchley 1903) is also seen in some *G. fultoni* females.

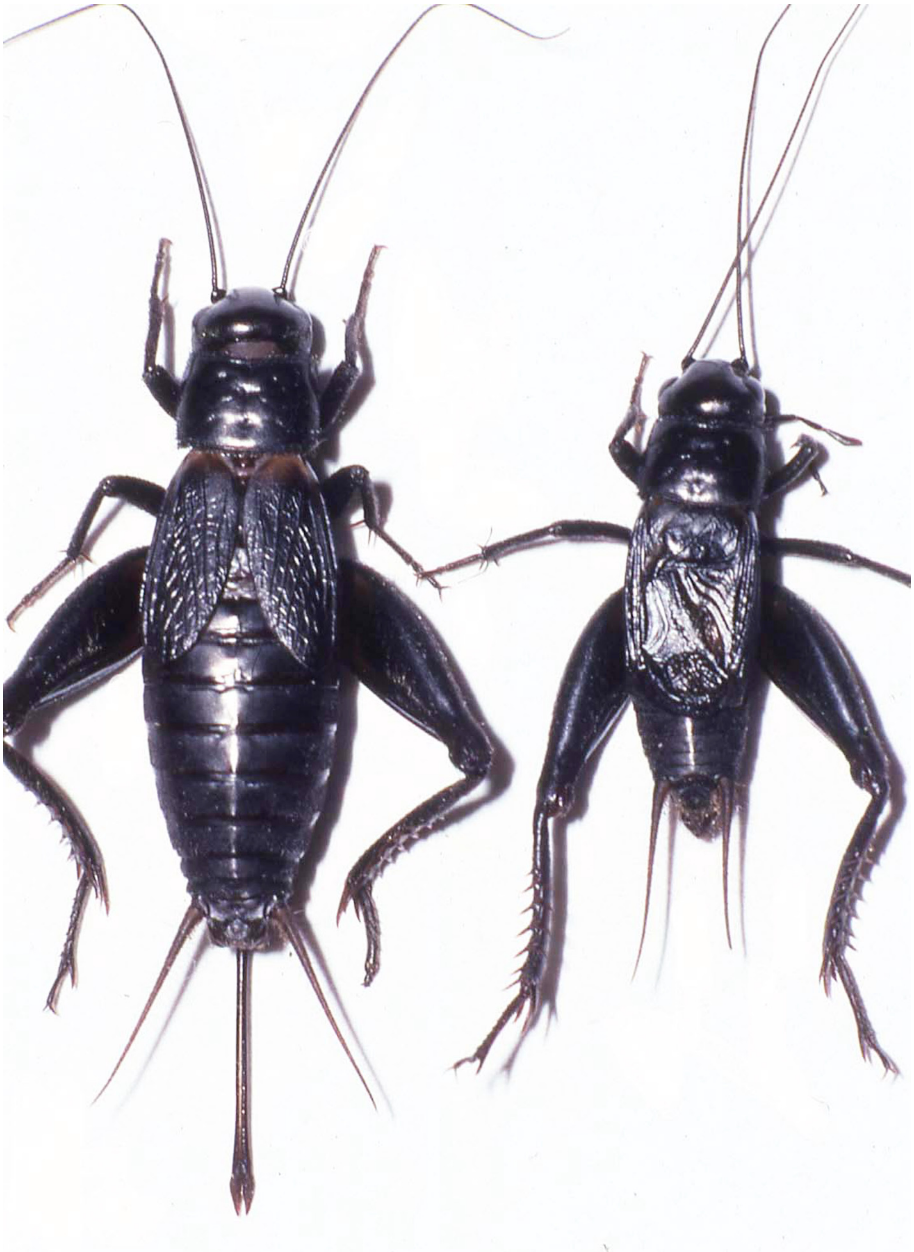

FIGURE 118. Pair of *G. vernalis* from Crawford Co., Indiana (S03-62). Note separation of tegmina of female (left).

Specimens examined. **Arkansas:** Polk Co., Wilhelmina State Park, 17-vi-1995, T.J. Walker, 1♂. **Illinois:** *Johnson Co*., Ferne Clyffe State Park 1.4 m S Goreville, 170m, 8-vii-2014 (S14-35), 2♂, A. & D. Wood. **Indiana:** *Crawford Co*., Hwy 62 11.6 m W of Hwy 135. 750', 4-vi-2003 (S03-62) 3♂ 4♀. **Missouri:** *Jefferson Co*., Edmond A. Babler State Park, 750', 2-vi-2003 (S03-56) 8♂ 2♀. **Tennessee:** *Coffe Co*., Old Stone Fort State Park, 13-v-2003 (S03-57) 7♂ 7♀, Y. Jang.

Song only records. **Iowa:** *Fremont Co*., Waubonsie State Park, 1250' 1-vi-2003 (S03-55). **Ohio:** *Hocking Co*., Hwy 33 9 m S Lanchester, 750' 5-vi-2003 (S03-64).

DNA. We found two 16S clades (Figs 121, 122). Clade 1 included 3 individuals (G31, G33, G440) from near the type locality in Indiana (S03-62). Clade 2 included 4 individuals (G26, G27, G1739, G1740) from Missouri (S03-56); 4 individuals (G28, G1700, G1701, G1738) from Tennessee (S03-57); and 2 individuals (G2754, G2755) from Illinois (S14-35). ITS2 mapping of two Clade 1 individuals (G31 and G33) and two Clade 2 individuals (G27 and G1739) all mapped together (Fig. 115, p. 121). Multilocus G31 (Clade 1, Indiana, S03-62) and G2754 (Clade 2, Illinois, S14-35) have these two 16S clades map together and also identifies *G. fultoni* and *G. cayensis* as sister species (Gray *et al.* 2019).

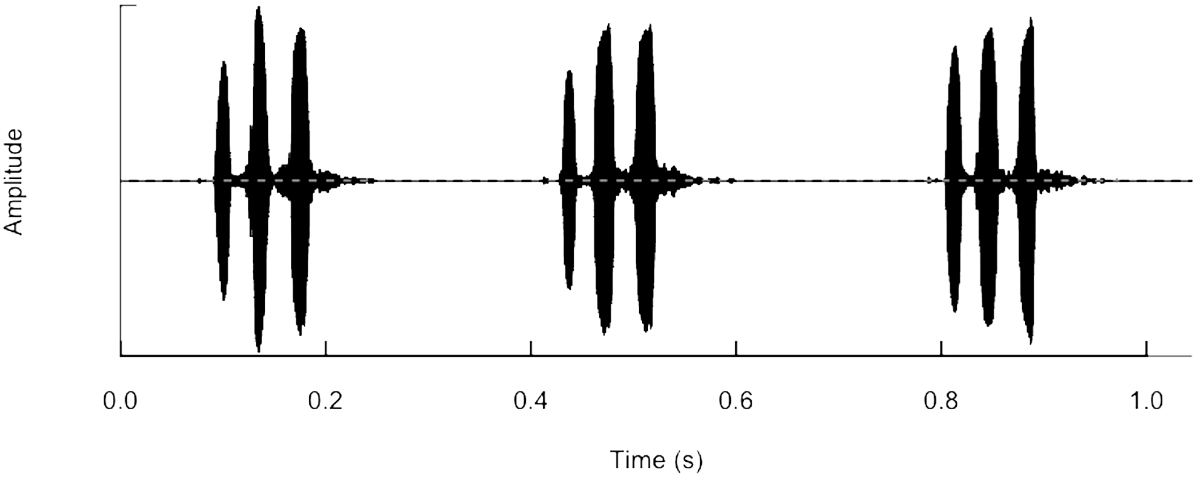

FIGURE 119. Calling song (R03-104) of *G. vernalis* from Jefferson Co., MO (S03-56), recorded at 24.5°C.

FIGURE 120. Size and color comparison of *G. vernalis* (left, S03-56, Jefferson Co., MO) vs. *G. fultoni* (right, S03-62, Crawford Co., IN).

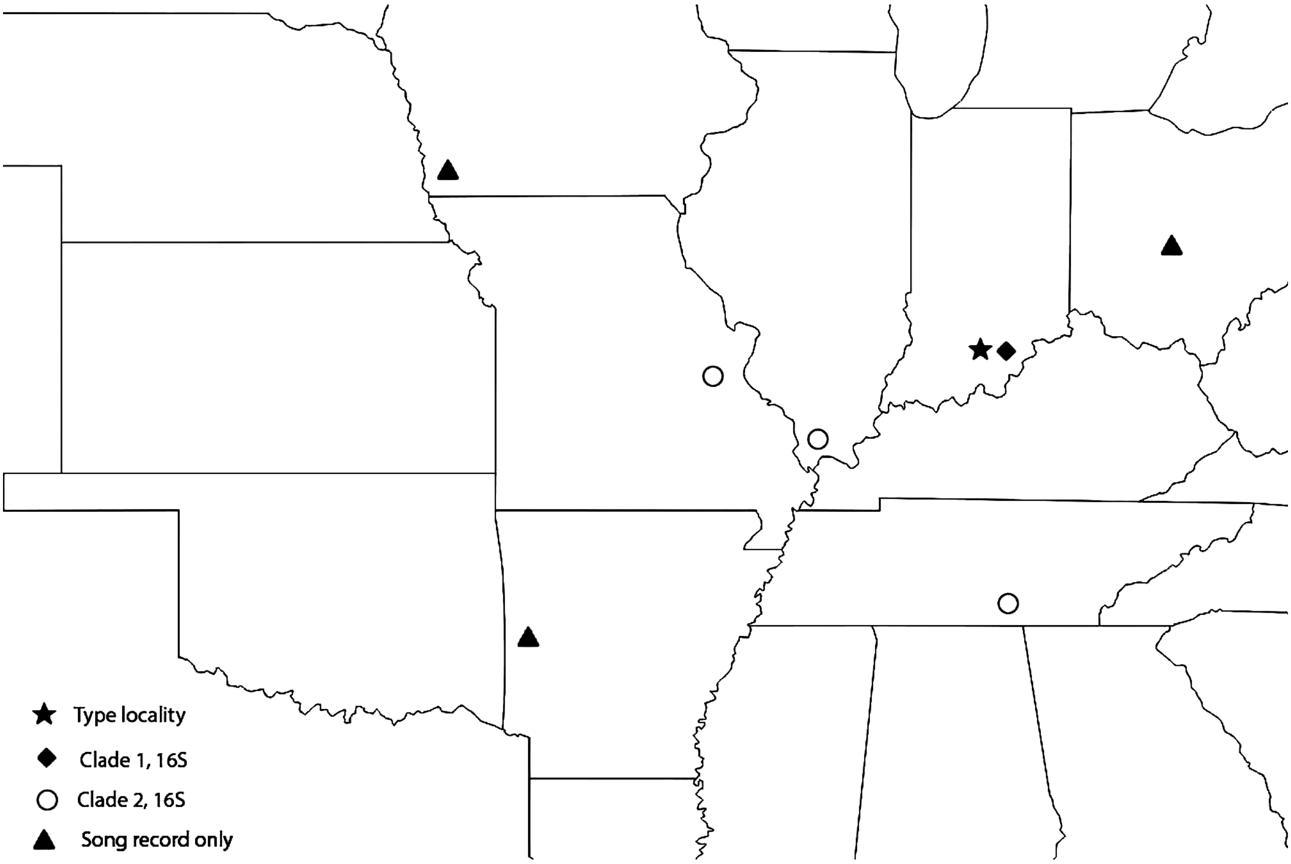

FIGURE 121. Populations of *G. vernalis* that we studied.

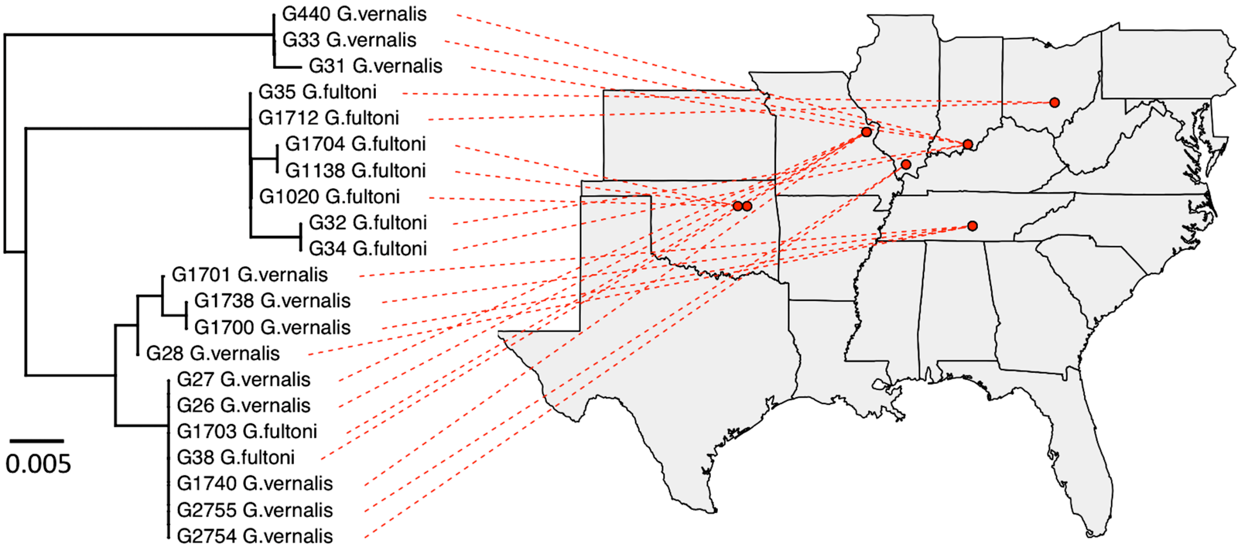

FIGURE 122. 16S gene tree and distribution map showing two 16S Clades for both *G. vernalis* and *G. fultoni* (the latter situation is discussed, below, under *G. fultoni*). ***G. vernalis*** samples: S03-56 (G26, G27, G1740); S03-57 (G28, G1700, G1701, G1738); S03-62 (G31, G33, G440); S14-35 (G2754, G2755). ***G. fultoni*** samples: S01-47 (G1704); S03-56 (G38, G1703); S03-62 (G32, G34); S03-64 (G35, G1712); S07-22 (G1020, G1138).

Discussion. First called the northern wood cricket by Alexander (1957) despite Blatchley's name of "vernalis" meaning "of springtime." In fact, Blatchley discussed (1903, p. 434) how *G. vernalis* is not just the first species of *Gryllus* to sing in the spring but "the first Orthopteran song of the season" appearing as early as May 5th, or about two weeks before *G. veletis* sings in Indiana. However, in 1960, Alexander & Bigelow christened the latter the northern spring field cricket, now simply called the spring field cricket by Walker (2019).

G. vernalis occurs in many localities with either *G. fultoni* and *G. veletis.* With enough searching, we predict that one should find all three taxa sympatric. At such a locality, one could stand and hear and discriminate the three by song and microhabitat as follows: With an air temperature between 18-25° C, i.e. warm enough for males to sing, *G. vernalis* more likely into deeper woods where its individual three pulses/chirp can be counted. *G. fultoni* can be along the forest—adjacent grassland border area where its three pulses/chirp can't be counted because the PR is too high. *G. veletis* would be in the adjacent grassland only and although its pulses are too close together to be counted, one can hear that each chirp contains more than three pulses because of the chirp's longer duration. It is easier to appreciate the differences between *G. fultoni* and *G. vernalis*' pulse rates when the two species are heard singing together.

Near the type locality (S03-62) of *G. vernalis* in Indiana, both *G. vernalis* and *G. fultoni* occurred at high densities within an open area of dense forest that was clear-cut for electrical power lines. The songs of *G. vernalis* were softer than those of *G. fultoni,* not surprising given the shorter tegmina in *G. vernalis*. Many individuals of both sexes of both species were walking on the surface amid various limestone rocks and organic debris.

Jang & Gerhardt (2006a, b; 2007) and Jang *et al*. (2007) document calling song character displacement where *G. vernalis* and *G. fultoni* are sympatric; and aggressiveness related to habitat (Jang *et al.* 2008).

Gryllus fultoni **(Alexander)**

Southern Wood Cricket
Figs 57, 113–115, 122–126, Table 1

1957 *Acheta fultoni*. Alexander (1957). Holotype male (Fig. 123, courtesy of M. O'Brien): Ohio, Hocking Co., Goodhope Township. Deposited at UMMZ. Types also photographed on OSF.
1964. *Gryllus fultoni*. Randell (1964).
'Gryllus #28' of DBW notebooks.

Distribution. East of 98° longitude in southern and central US, to the Atlantic coast and south into Florida.

Recognition characters and song. Small to medium sized cricket, always short hind wings, usually with contrasting yellow cerci when alive, head usually narrower that pronotum (Fig. 124). *Song* (Fig. 125) of 3p/c delivered at 250 to 360 c/m., PR 35–55. Usually lives in woods or on their edges but sometimes in short to long roadside grasses. Some males climb several feet into bushes and tree trunks to sing. One "effective" generation/year (see below under *Life cycle*). Differs from sympatric *G. vernalis* in not being a forest obligate, being slightly larger (Fig. 120), tegmina brown and black with tegminal bar vs. solid black in *G. vernalis*, no overlap in teeth/mm (Table 1, p. 18), PR faster (can hear difference in field when both species singing at same temperature), and yellow cerci common in live individuals (rare in *G. vernalis*). Differs from sympatric *G. veletis* in microhabitat (woods vs. grassland), *G. fultoni* frequently having the head narrower than pronotum, longer cerci that are usually yellow, smaller size, fewer p/c, and faster PR and CR. Differs from sympatric *G. veintinueve* in *G. fultoni* usually having yellow cerci when alive, head narrower than pronotum, faster CR and fewer file teeth, no overlap in its faster PR and different DNA (Fig. 6, p. 28; Gray *et al.* 2019).

Derivation of name. Named, by Alexander, in honor of B. B. Fulton who was the first to recognize this species as distinct.

Geographic range. (Fig. 126). From eastern Texas, Oklahoma, and Kansas through the central US to the Atlantic coast and south into Florida (see maps in Walker 2019; Jang & Gerhardt 2006a, b).

Habitat. Usually in woods or along their borders where they live in leaf litter and can be difficult to collect. Never in open fields. Also in holes in the ground under trees where they are easily flushed with water. Occasionally in short roadside grasses (Kansas, S87-69 & 70) with an open tree cover. In eastern Oklahoma males climb into bushes and trees to sing—we collected males singing 1.5–2m above ground on the side of a tree at Keystone State Park (S88-42) and in Tulsa (S07-22).

Life cycle and seasonal occurrence. No egg diapause (checked from Kansas, S87-70; Oklahoma, S88-42; and Missouri, S00-16), with first field adults in mid-late May. Walker (1974) notes that northern Florida can have second generation *G. fultoni* adults, similar to the situation seen in *G. veletisoides* in California (see p. 195), *G. veletis* in Michigan (Alexander 1957, p. 592), and *G. firmus* in Florida (Walker 1980). The functionality of this second generation in Florida is unknown but apparently non-contributory to the gene pool (T.J. Walker pers. comm. to DBW, 2011).

FIGURE 123. Holotype male (upper) *G. fultoni* and allotype female (bottom), with labels.

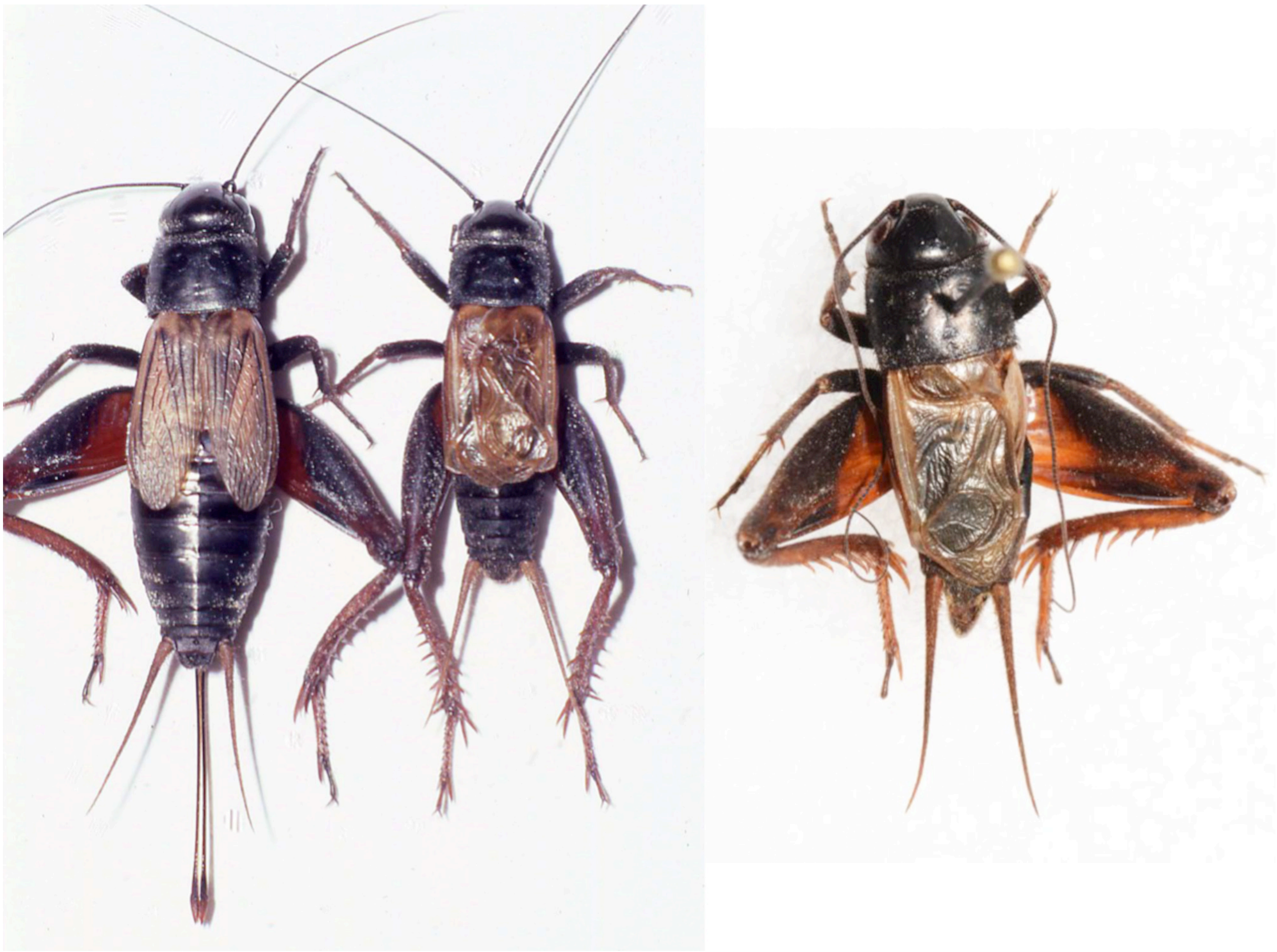

FIGURE 124. Color variation in *G. fultoni*: female (left) and both males (middle and right), all three from Crawford Co., IN (S03-62). Note narrow heads, especially in male on right, and separation of female tegmina.

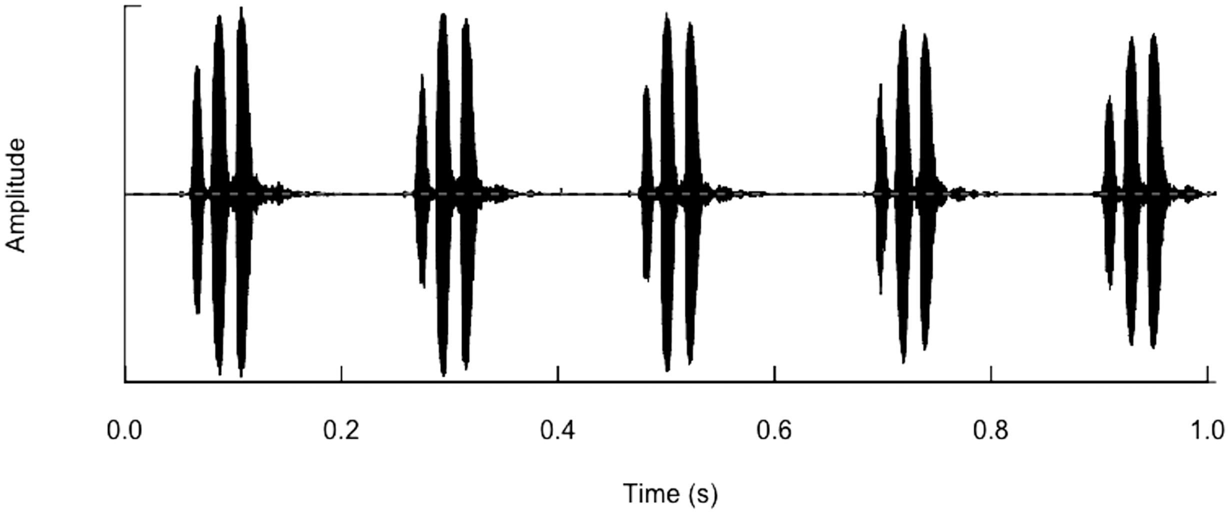

FIGURE 125. Calling song (R03-86) of *G. fultoni* from Hocking Co., Ohio (S03-64), recorded at 25°C.

Variation. **Color:** See Fig. 124 above. **Head width:** 28 of 36 males with head narrower than pronotum while 29 of 31 females with head narrower than pronotum. **Size:** Florida specimens are larger than more northern ones.

Specimens examined. **Arkansas:** *Garland Co.,* Lake Ouachita State Park, 16-vi-1995, T.J. Walker. **Indiana:** *Crawford Co*., Hwy 62 11.6 m W intersection with Hwy 135, 750’, 4-vi-2003 (S03-62). **Kansas:** *Barber Co.,* 1 m

W Medicine Lodge on Hwy 160, 23-vi-1987 (S87-69). 27 m W Medicine Lodge on Hwy 160, 1750’ 23-vi-1987 (S87-70). **Missouri:** *Hickory Co*., Pomme de Terre State Park, 1000’, 20-vii-1993 (S93-49). *Jefferson* Co., Edmond A. Babler State Park, 750’ 2-vi-2003 (S03-56). *Stone Co.,* Table Rock Dam Visitor Center, 31-v-2000 (S00-16) T.J. Walker. **Ohio:** *Hocking Co.* (near type locality), Hwy 33 9 m S Lanchester, 750’, 5-vi-2003 (S03-64). **Oklahoma:** *Ataka Co.,* Jack Fork Mts. 3 m SW Daisy on Hwy 43, 750’, 1-v-1988 (S88-46). *Osage Co.,* near Walnut Creek State Park, 600’ 15-vi-1988 (S88-43). *Tulsa Co.,* Keystone State Park, 600’, 15-vi-1988 (S88-42); Lake Keystone Dam Area 650’, 27-v-2001 (S01-47); Tulsa, at intersection I44 and Hwy 244, 680’, 9-vi-2007 (S07-22); near Tulsa, Exit 238 off I44 2 m E Tulsa city limit, 796’, 15-vii-2013 (S13-68), 36° 09’ 37.4 -95° 47’ 33.1”. **Texas:** *Bastrop Co.,* Bastrop State Park, 700’ 31-v-1991 (S91-23). *Marion Co.,* Caddo Lake State Park, 300’, 18-vi-1993 (S93-42).

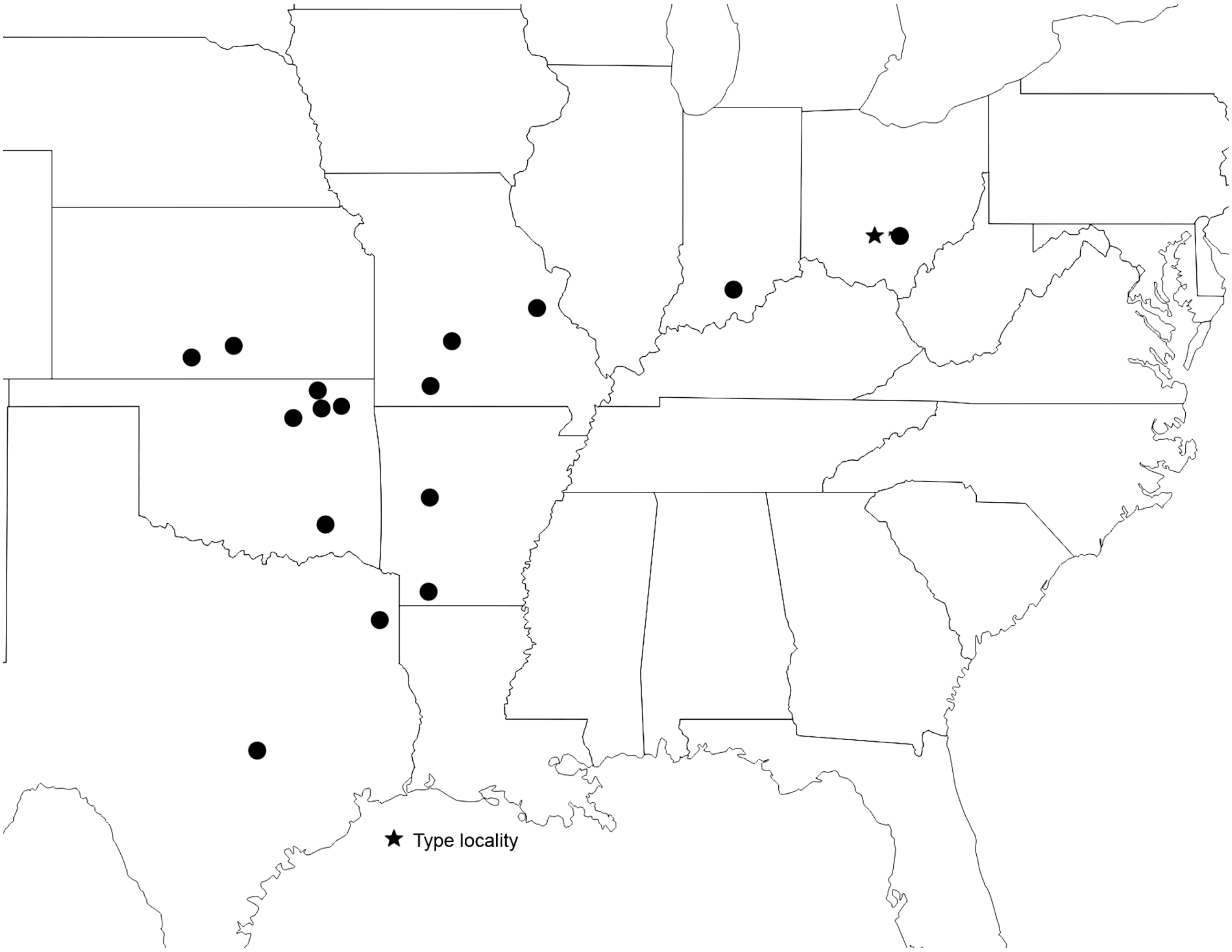

FIGURE 126. Populations of *G. fultoni* that we studied. See Walker (2019) for more eastern localities.

DNA. Multilocus G34 (Indiana, S03-62) sister species with *G. vernalis* and *G. cayensis* (Gray *et al.* 2019). ITS2 shows clear and complete separation between *G. fultoni* and *G. vernalis* (Fig. 115, p. 121), whereas two *G. fultoni* (Fig. 122, p. 125) from Missouri (G38 and G1703, both S03-56) have 16S sequences identical to microsympatric *G. vernalis,* suggesting the possibility of past hybridization.

Discussion. G. fultoni occurs microsympatric in Missouri (S03-56), Indiana (S03-62), and Ohio (S03-64) with *G. vernalis;* in Oklahoma (S88-42, S01-47 and S13-68) with *G. veintinueve*; and in Oklahoma (S13-68) with *G. veletis.* Thus, at the latter Oklahoma locality just east of Tulsa (S13-68), there are 3 *Gryllus* taxa synchronic and microsympatric that can have 3p/c with different PR and CR. Apparently females can discriminate between such small differences in songs.

Although called the southern wood cricket, the distribution of *G. fultoni* extends north of the northern wood cricket, *G. vernalis* (see Fig. 126 and Jang & Gerhardt 2006a, b).

Those males singing in woodlands and grassy areas can be difficult to catch because they sing from under dry leaves and other vegetation. Those males singing in bushes and on tree trucks may jump on approach and get lost in the forest duff. A large butterfly net positioned beneath the male can help in these situations. Aggressiveness in this taxon studied by Jang *et al*. (2008).

Gryllus cayensis Walker

Keys Wood Cricket
Figs 127–129

2001 *Gryllus cayensis* Walker 2001. Florida Ent. 84: 700. Holotype male (Fig. 127); allotype female (Fig. 128) (all courtesy Kyle Schnepp): Florida, Monroe Co., Key Largo. Deposited in FSCA Florida State Collection.

FIGURE 127. Holotype male of *G. cayensis*, with labels.

Distribution. Known only from southern Florida (Walker, 2019), and probably extirpated from the Florida Keys by past mosquito spraying that started in 1972 (Walker 2001).

Recognition characters and song. No calling song. Only woodland inhabiting *Gryllus* species there although *G. assimilis, G. firmus*, and *G. rubens* also occur in southern Florida (Capinera *et al*. 2004).

DNA. Multilocus 2018-002, Florida, Monroe Co., Everglades National Park, Long Pine Key, 14-v-2018. 25.401352° -80.660966°. Closest (Gray *et al.* 2019) to sister species *G. fultoni* and *G. vernalis*.

Discussion. The reader is referred to Walker (2001, 2019) for further information, since our exposure is limited. When DAG looked for them in Everglades National Park, in May, 2018, he was rained out on 3 consecutive nights and felt lucky to get 1 adult female to an oatmeal trail (Fig. 129). At least some individuals survived the area's 2017 flooding from Hurricane Irma.

ALLOTYPE
Gryllus cayensis
T. J. Walker

Monroe Co., Fla.
23 AUG 1958
T.J. Walker, Jr.
Coll. # 2

FIGURE 128. Allotype female of *G. cayensis*, with labels.

FIGURE 129. Photograph of live *G. cayensis* female used in multilocus sequencing.

The Veletis Group

Gryllus veletis (Alexander & Bigelow); *Gryllus planeta* Weissman & Gray, n. sp.

This Group consists of the most geographically widespread US *Gryllus*, *G. veletis*, and a sympatric narrow endemic, *G. planeta*. Songs similar, but *G. planeta* typically with fewer pulses per chirp and slightly faster pulse rate (Figs 130, 131); also, distinguishable by DNA (Fig. 132, Gray *et al.* 2019), morphology and probably habitat.

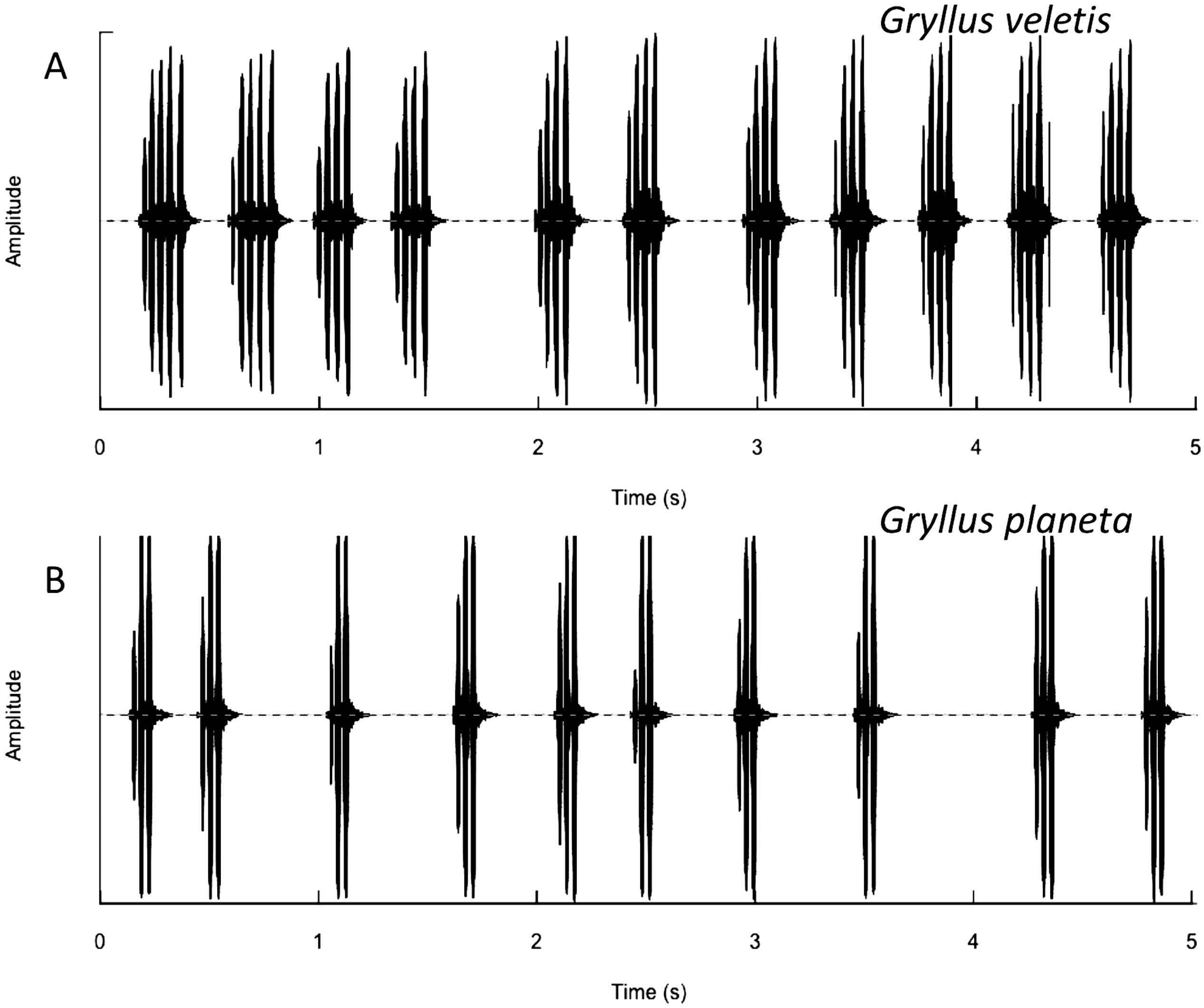

FIGURE 130. Five second waveforms of calling songs of (A) *G. veletis* and (B) *G. planeta*. *G. veletis*: (R03-118) near type locality (S03-58), at 24°C; *G. planeta:* (R15-160) near type locality (S15-61), at 24.9°C.

Gryllus veletis (Alexander & Bigelow)

Spring Field Cricket
Figs 56, 57, 130–151, 205, 206, Tables 1, 2

1960 *Acheta veletis* Alexander & Bigelow. Evolution 14: 335. Type locality: Illinois, Piatt Co. Types in UMMZ (types photographed on OSF and Fig. 133, courtesy of Mark O'Brien).

1964 *Gryllus veletis*. Randell. R.L. 1964. Canadian Entomologist 96:1592.

G. veletis, 'G. eastern veletis', 'G. #27', 'G. #30', 'G. #36', 'G. #43' or 'roadside G.', 'G. pecos', and 'G. utahensis' of DBW notebooks.

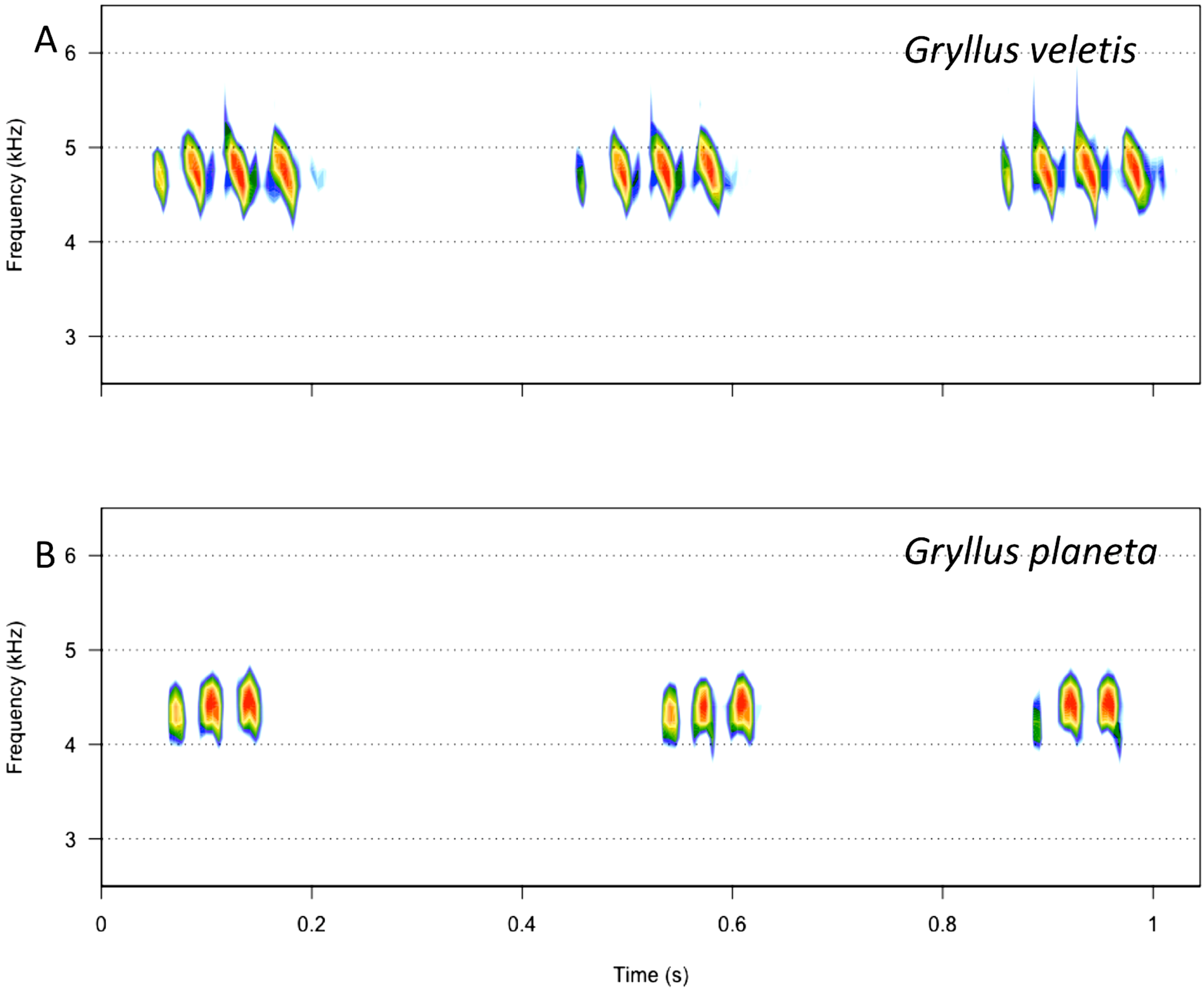

FIGURE 131. One second spectrograms of (A) *G. veletis* and (B) *G. planeta*, same males as in Fig. 130.

Distribution. Most widespread US *Gryllus* species and found in every state except for those in the Southeast (Walker 2019, Capinera *et al.* 2004).

Recognition characters and song. Shortest cerci (along with *G. veletisoides* and *G. pennsylvanicus)* of any US *Gryllus* species. In fact, the cerci are so short that even in old adults, they are frequently intact and taxonomically useful in identification. Most variable cricket for body size (along with the almost equally widespread *G. pennsylvanicus*—see Fig. 32, p. 49) with western Texas specimens around twice the body length of those from North Dakota (Fig. 134). A small to large sized, black except for occasional red area on inside of hind femur, usually short hind winged, wide pronotum, cerci never as long as ovipositor in situ, spring and early summer species usually associated with a vegetation cover such as grass or roadside weeds. *Song* (Fig. 135, R03-118) a slow, usually irregular chirp with 4–5 (range 3–7) p/c and PR generally between 20 to 30 at 25°C. Males can sing during morning hours, especially in spring when evening temperatures are cool, but also during hot afternoon hours (e.g. Blue Springs, Missouri, 21-vi-1993).

Separated from sympatric sister species *G. planeta*, in the Davis Mts. of Texas (S15-62) by habitat (oak woodland for *G. planeta* vs. grassy meadows for *G. veletis*), and smaller, more slender size, with little or no overlap in the following 6 parameters (Table 1, p. 18): *G. planeta* has fewer file teeth, shorter length file, shorter tegmina length and width, shorter ovipositor and shorter hind femur length. Also overlaps in length of cercus with *G. planeta* but when body length size differences compensated for (Fig. 136, all individuals from the Davis Mts., Texas), cerci relatively longer in *G. planeta* even if only by 1–2 mm.

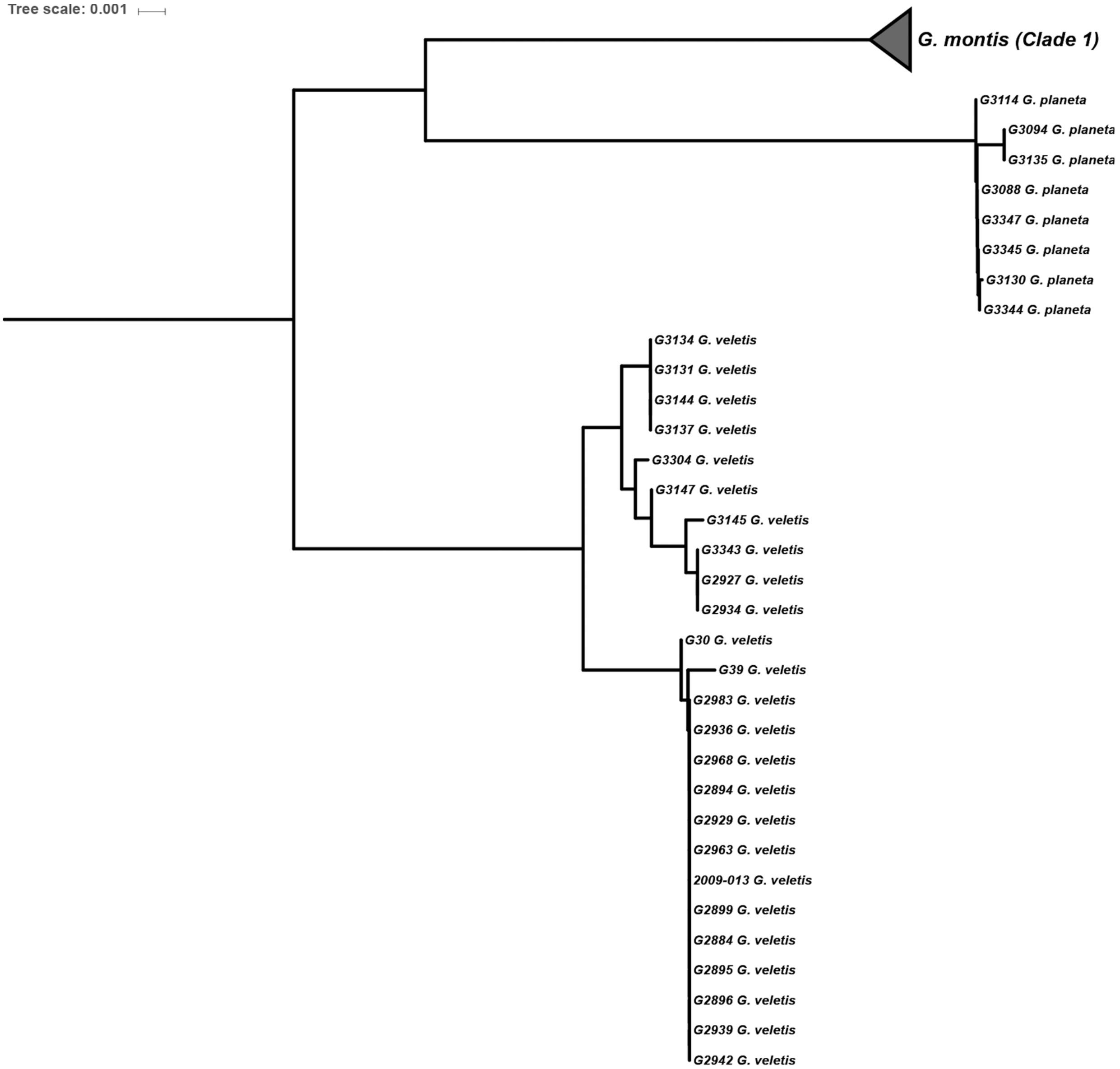

FIGURE 132. ITS2 gene tree. ***G. planeta*** samples: S15-61 (G3088, G3094, G3114, G3135, G3344, G3345, G3347); S15-63 (G3130). ***G. veletis*** samples: S03-58 (G39); S03-60 (G30); S15-9 (G2939); S15-13 (G2884, G2929); S15-16 (G2927, G2934); S15-21 (G2894, G2895, G2896, G2899, G2942); S15-24 (G2936); S15-25 (G2963, G2968, G2983); S15-53 (G3304, G3343); S15-62 (G3131, G3134); S15-67 (G3137, G3144); S15-78 (G3145, G3147); Salt Lake City, UT (2009-013). Most ITS2 sequenced western US *G. veletis* samples match closely with the two eastern US samples from near the type locality, but a few samples from eastern NV, central NM, and west TX are genetically somewhat divergent. ***G. montis*** Clade 1 ITS2 sequences fall within this Group, but alternative placements are supported by different genes and analysis methods (see under *G. montis*, page 201, for discussion).

G. veletis can be separated from the always allopatric, Clade 1 of *G. montis* from the Chiricahua Mts. in southeastern Arizona, by the longer cerci in *G. montis*.

Morphologically most similar to *G. veletisoides* but always allopatric (on different sides of the Sierra Nevada and Cascade Mt. Ranges) and the latter with fewer teeth in file (Fig. 137), but similar length ovipositors (Fig. 138), and ~3.5% divergent in DNA [510 bp of 16S, Tamura-Nei distance, mean ± SD, within N = 54 *G. veletisoides*: 0.001 ± 0.001; within N = 219 *G. veletis*: 0.014 ± 0.015; between *G. veletisoides* and *G. veletis*: 0.038 ± 0.004. 698 bp of ITS2, Tamura-Nei distance, mean ± SD, within N = 10 *G. veletisoides*: 0.0003 ± 0.0006; within N = 25 *G. veletis*: 0.0064 ± 0.0061; between *G. veletisoides* and *G. veletis*: 0.0359 ± 0.0028].

FIGURE 133. Holotype male (left) *G. veletis* and allotype female (right), with labels.

FIGURE 134. Body size variation in *G. veletis*: smallest males (left, S03-52) from North Dakota vs. largest males (right, S03-60) from western Texas. These are typical body sizes at each locality.

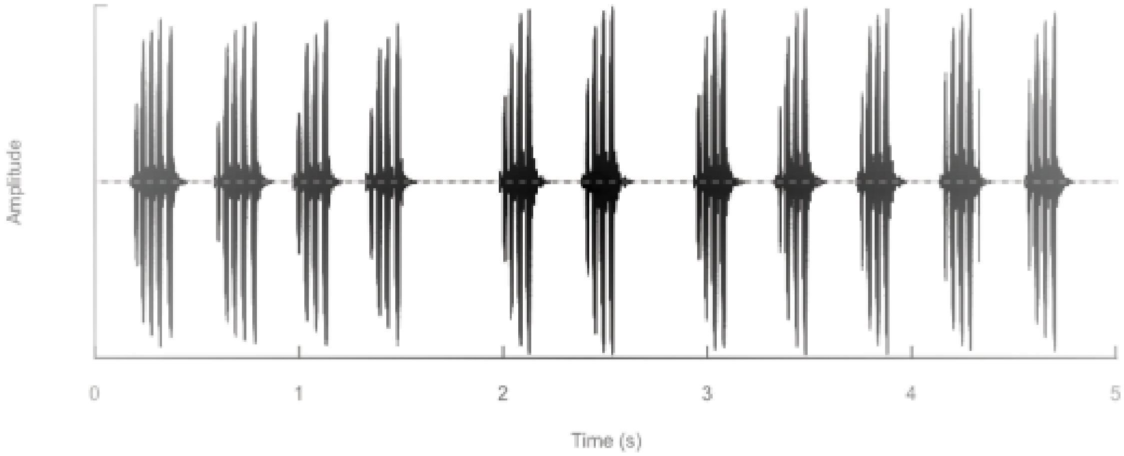

FIGURE 135. Calling song (R03-118) of *G. veletis* from near type locality (S03-58), recorded at 24°C.

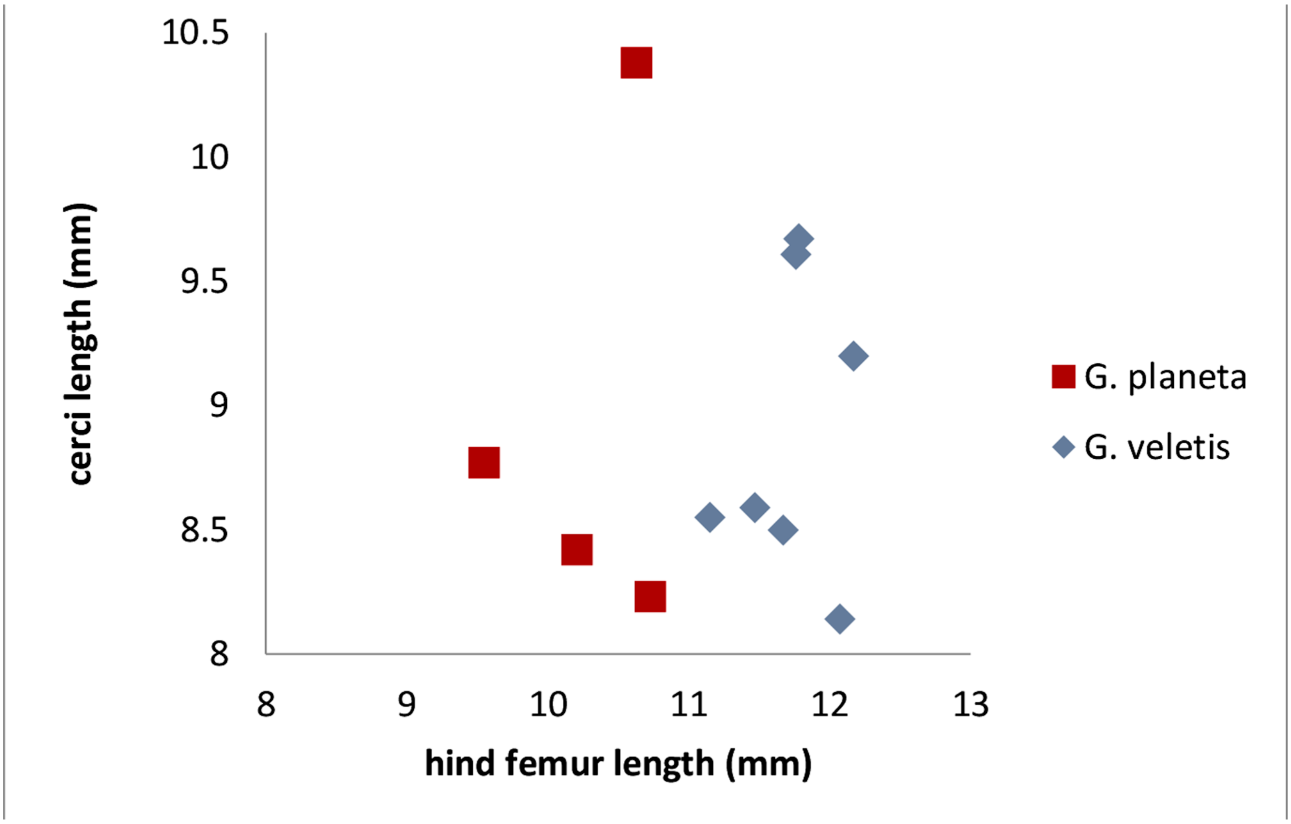

FIGURE 136. Regression of hind femur length vs. cerci length of Davis Mts., Texas, *G. veletis* vs. *G. planeta*, to show separation.

Separated from sympatric and sometimes synchronic *G. pennsylvanicus* where latter has a longer ovipositor (Table 1, p. 18), usually a higher tooth count, longer cerci (Fig. 139), overwinters in the egg stage with first adults appearing in August, and different DNA (721 bp of ITS2 ~5.8% divergent, N = 4 *G. pennsylvanicus* and N = 25 *G. veletis*; Gray *et al.* 2019). More teeth in the file apparently results in a lower pulse rate in *G. pennsylvanicus* that is noticeable in the field when both species are chirping near each other and at similar temperatures.

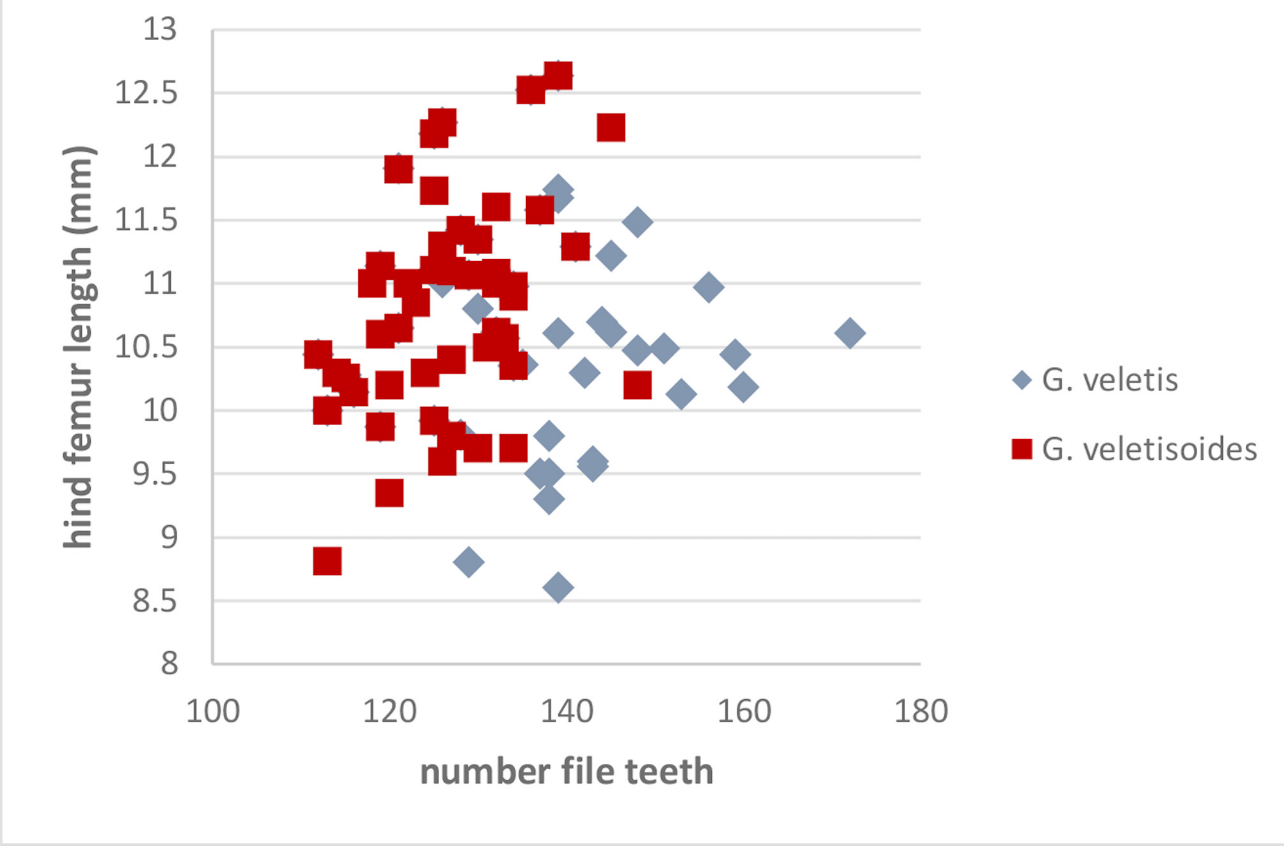

FIGURE 137. Regression of number file teeth vs. hind femur length in *G. veletis* vs. *G. veletisoides.*

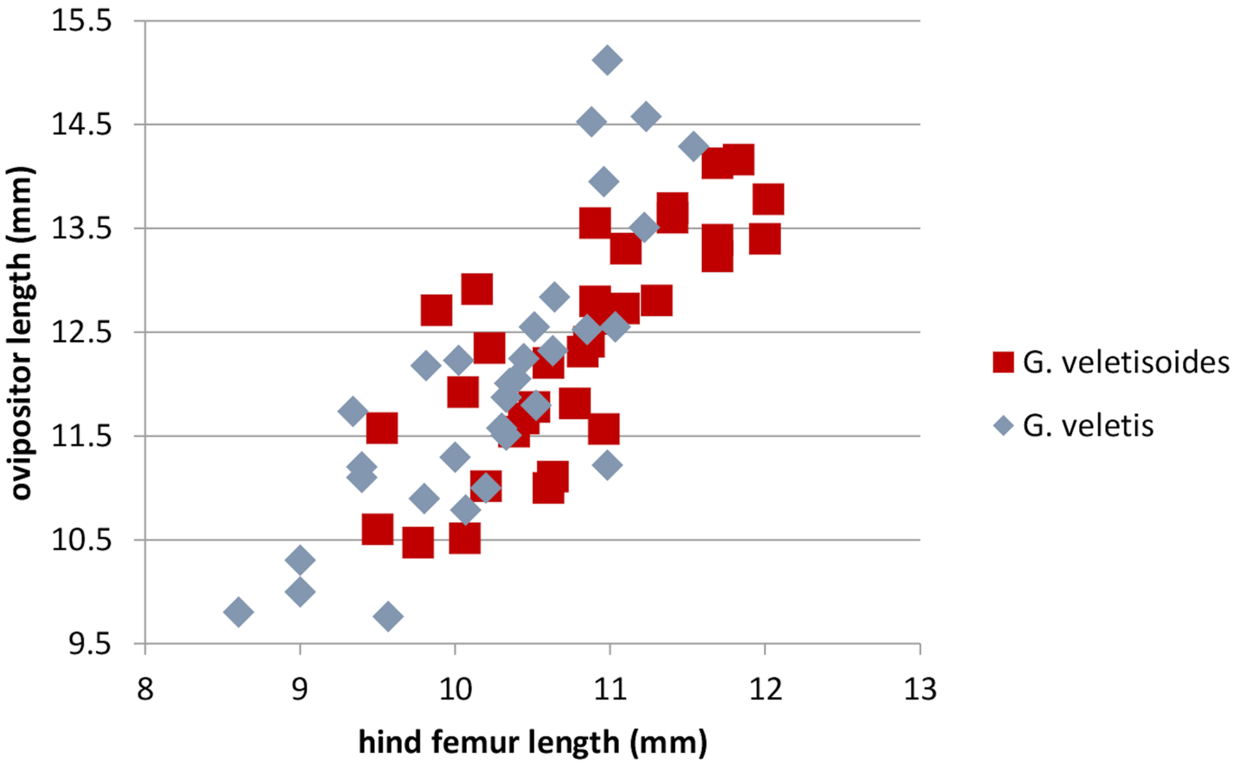

FIGURE 138. Regression of hind femur length vs. ovipositor length in *G. veletis* vs. *G. veletisoides.*

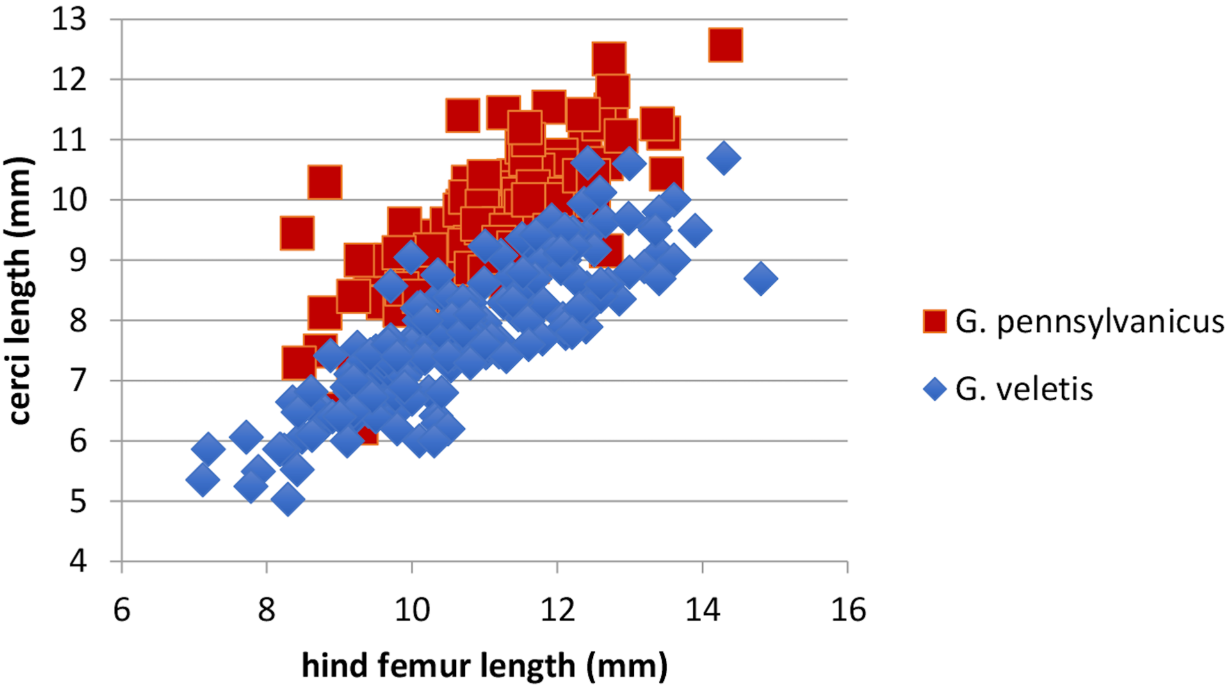

FIGURE 139. Regression of hind femur length vs. cerci length in *G. veletis* vs. *G. pennsylvanicus.*

Separated from faster chirping, microsympatric Clade 4 of *G. montis* near Reserve, NM (S07-53, 54) by longer cerci and narrower pronotum in latter, and DNA (Gray *et al.* 2019). Separated from *G. fultoni*, where *G. veletis* has almost no overlap with the former's faster chirp rate and higher pulse rate, and in *G. veletis,* usually more p/c, lack of yellow cerci, and larger head not narrower than pronotum. Compared to *G. veintinueve*, *G. veletis* is larger in size, has a louder and faster chirp rate, longer tegmina, broader pronotum, and different DNA (Fig. 6, p. 28). Microsympatric with *G. vulcanus* at El Malpais, NM (S07-52), but only at edges of lava flows. The two species are easily separated there by the longer cerci and lower pulse rate in the latter.

Derivation of name. "*veletis*" chosen "in reference to its aggressive behavior" (Alexander & Bigelow 1960) as individuals are more solitary than its 1960 "proposed" sister species *G. pennsylvanicus.* The web site *Latin-dictionary.net* defines "veles" or "velitis" (note spelling difference) as a masculine noun with the following definitions: 1. Guerrilla forces (pl.), irregular bands. 2. Light-armed foot-soldier. 3. Skirmishers. R. D. Alexander (pers. comm. to DBW, August, 2013) stated that he and Bigelow used this modified spelling in *Acheta veletis* (before their taxon was moved to *Gryllus)* "because the 'e' sounds in the two words went together so appropriately."

Geographic range. Fig. 140. See Walker (2019) for more eastern US localities. Probably into adjacent Mexico. Contrary to Alexander & Meral (1967), *G. veletis* does occur in many southwestern US areas without *G. pennsylvanicus* (compare Fig. 140 with Fig. 32, p. 49), but avoids the lower elevation, hotter desert regions.

Habitat. Usually in areas with increased vegetation cover, either natural or planted, around water courses, and on both sandy and loam surfaces. In western Utah, very easy to collect during the daytime, in May, 2015, since almost every area with good grass cover had individuals hiding under boards, rocks, and various items of trash. Rarely at edges of lava flows in New Mexico (S94-41). Also in Oregon at sulfur-saline hot springs (S04-44) and in cracks of saline-saltmarsh grassland (S04-54). From near sea level to over 2440 m (Otero Co., near Cloudcroft, NM). At La Junta, Colorado (S87-65), one singing male on tree trunk 3 m above ground with female nearby and a second female starting to climb up the same trunk. In another tree, one male singing 1 m above ground from under loose bark. At Sedalia, Missouri (S93-51), one male singing 1 m up in shrub. May be riparian associated in otherwise hot dry areas, e.g. *G. veletis* found in moist areas along Deer Creek, Garfield Co., UT (at 1740 m elevation) replaced by *G. saxatilis* within a few meters of transition to dry rocky slopes; the same situation applies in Lodore Canyon on the Green River, Moffat Co., CO (at 1560 m elevation).

Life cycle and seasonal occurrence. No egg diapause: Wanapum Dam Reservoir, WA (S83-42); north of Alturas, CA (S83-48); Sacramento Mts., NM (S83-80 & S85-53); Alpine, TX (S85-59); La Junta, CO (S87-65); near

Farmington, NM (S87-81); west of Medicine Lodge, KN (S88-41); Tulsa, OK (S88-45); Mirror Pool, ND (S88-55); Flagstaff, AZ (S91-75); Kadoka, SD (S97-87); Tooele, UT (S04-107).

One generation/year. Overwinter as late instars with adults first appearing in mid to late spring, even as far north as Mirror Pool, North Dakota (S03-52). Present at Lakin, Kansas (S87-67) on 23-vi-1987 but adults absent here 27-viii-1989 (S89-67) when we only found late instars of *G. veletis* (doubt that they were *G. pennsylvanicus,* which should have already been adult starting in early August) in the same habitat. Alexander & Bigelow (1960) note how "a small percentage (of *G. veletis*) matures without apparent delay (thus accounting for 2nd generation adults), but most require several months." We note possible 2nd generation adults from Jensen, Utah (10-ix-1999, S99-127) and Tooele, Utah (collected 9-ix-2004, S04-107, with no egg diapause in collected females) but late surviving first generation individuals are also a possibility.

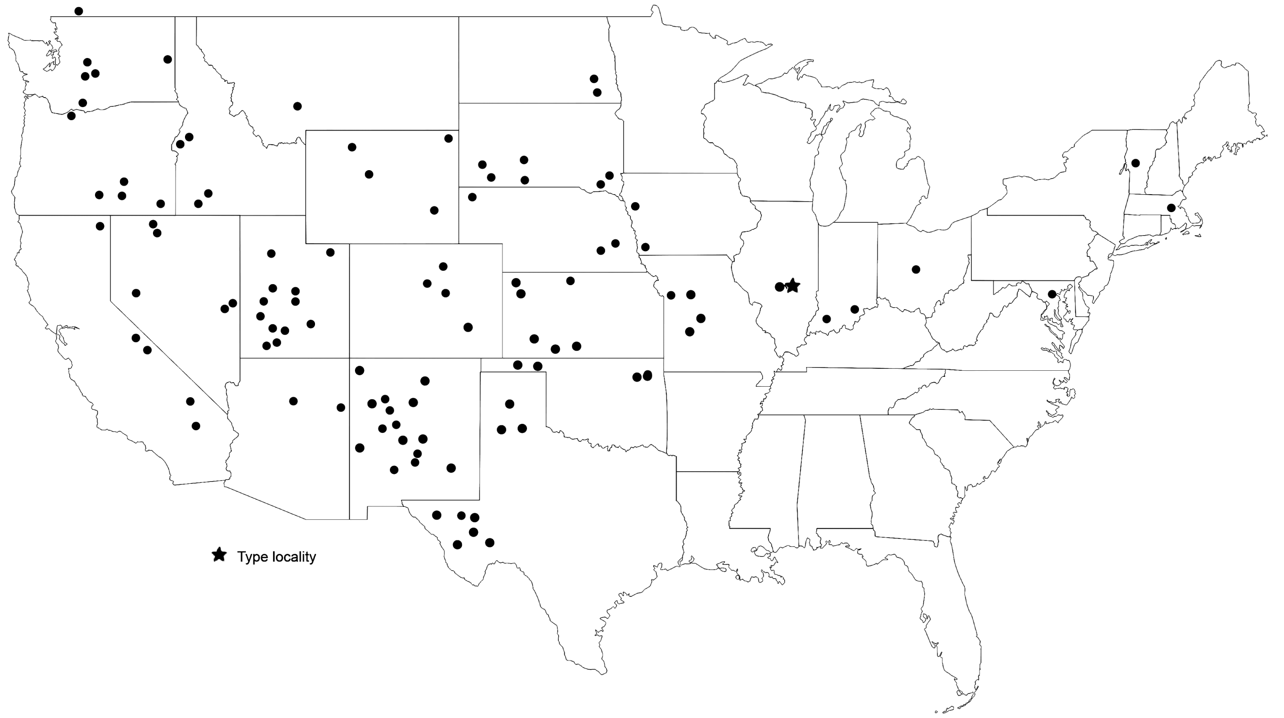

FIGURE 140. Distribution of *G. veletis* specimens that we studied.

Variation. **Body size:** *G. veletis* displays more variation in body size (see Fig. 134) than any US *Gryllus,* and this property has been partially responsible for our confusion as to how many populations are actually *G. veletis*. Individual body lengths, measured immediately upon killing, vary from 13.42/13.70 mm (male/female) from Mirror Pool, North Dakota (S03-52) to 29.5 mm (male from Alpine, Texas, S91-44)/26.78 mm (female from Columbus, Ohio, S03-65). Upon complete drying after pinning, these four individuals, respectively, measured 13.50/11.69 and 23.23/21.42 mm. **Color:** We have a few individuals that are light-colored as discussed by Alexander & Bigelow (1960, p. 337). **Cercus length:** As individuals get larger going north to south, within the US, cercus length also increases. **Female tegmina length:** Individuals, especially those from New Mexico and in populations with large sample sizes, display a range of tegmina lengths where from ½ to the entire female abdomen is covered, and not directly related to the shrinkage associated with drying. **File teeth:** see Fig. 141. Varies from 116 (Pecos, NM, S01-45) to 175 (La Junta, CO, S87-65). **Head size:** Larger males, especially those from New Mexico and Colorado, occasionally have heads much wider than the pronotum. This pattern was not seen in those larger adults (our 'G. #36') from the Alpine-Marathon area of Texas. **Hind wing length:** Of 1091 collected US adults, 200 (18.3%) had long hind wings and 891(81.7%) had short hind wings. Those adults with long hind wings were approximately 60% male. Also see under Discussion. **Songs:** Roswell, NM (S09-58) male with 4-10 p/c (see Fig. 142, R09-73). **Tegmina color:** Guymon, Oklahoma (S88-39 vs. S09-77) and La Junta, Colorado (S87-65 vs. S09-82) show that both 2009 samples have much darker tegmina than the browner 1987 and 1988 samples.

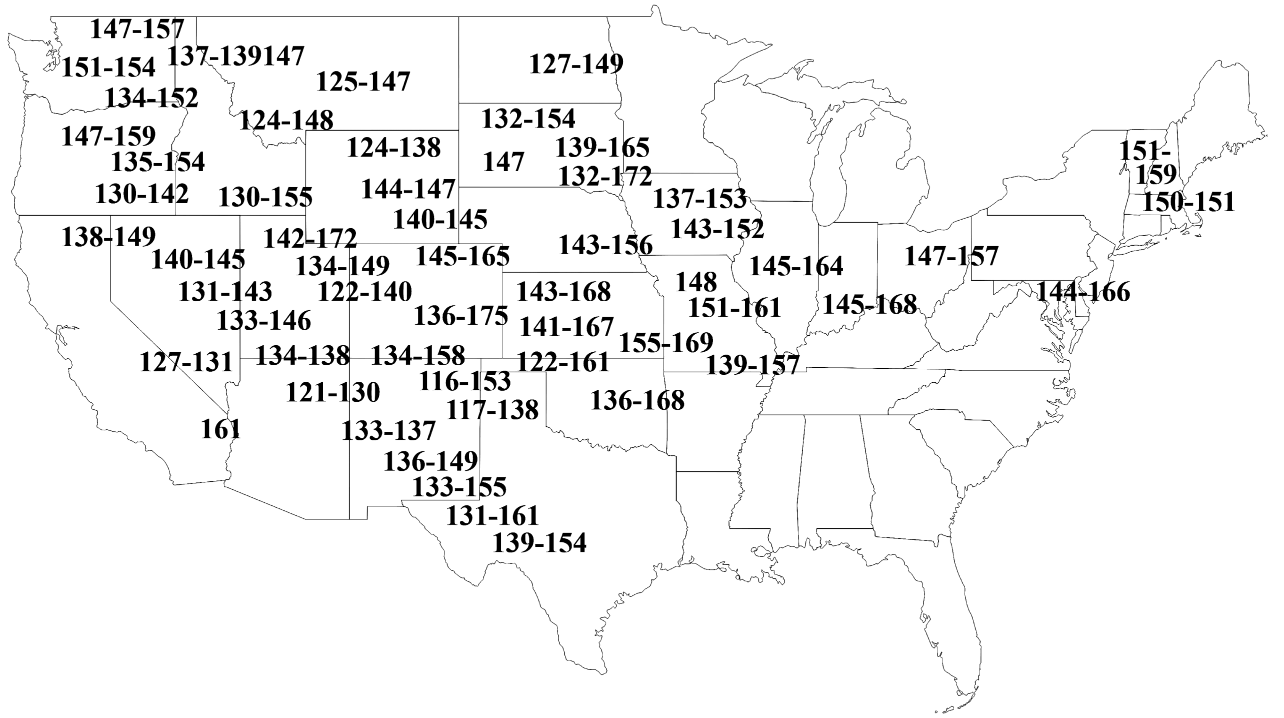

FIGURE 141. Map of *G. veletis* file tooth counts showing geographic variation. Tooth counts vary from 116 (Pecos, NM, S01-45) to 175 (La Junta, CO, S87-65).

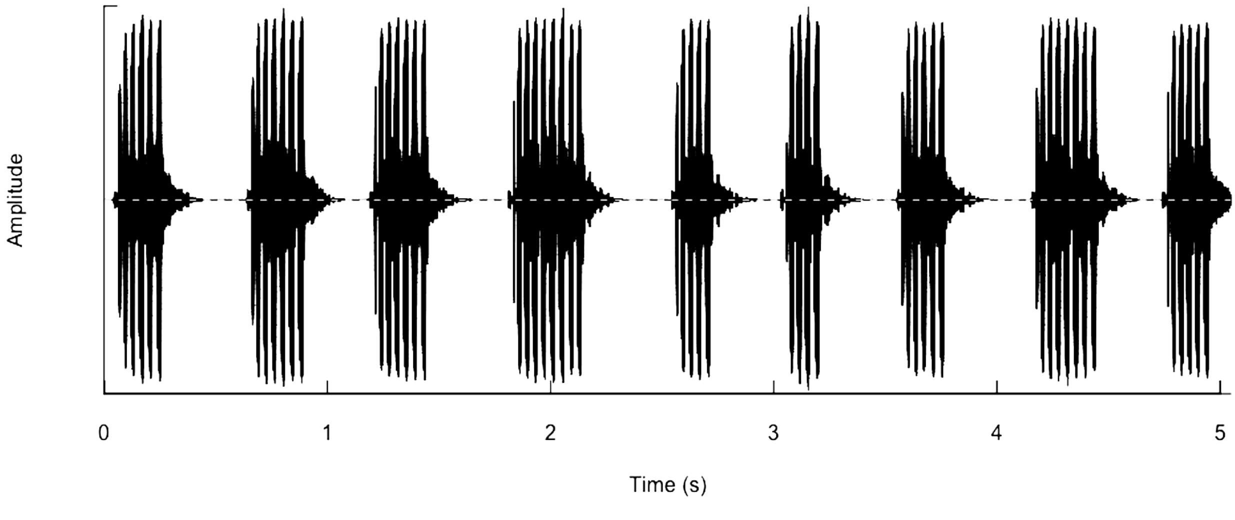

FIGURE 142. Atypical *G. veletis* song with 4-10 p/c (R09-73) from near Roswell, NM (S09-58), recorded at 26°C.

Specimens examined. **CANADA**: **Alberta:** Lethbridge, Old Man River, 3-vi-2001. **British Columbia:** Osoyoos, Haynes Ecological Reserve, 18-vi-2004, 1160' (S04-61 & 62). **USA: Arizona:** *Apache Co.,* St. Johns, 20-v-2001, 5830' (S01-38). *Coconino Co.*, Flagstaff, 5-viii-1991, 6810' (S91-75); 15-vi-2007 (S07-57). **California:** *Inyo Co.,* Bishop, 5-vi-1983, 4140' (S83-56). 9 m N Bishop, 4-vi-1983, 4700' (S83-55). Lone Pine, 5-vi-1983, 3700' (S83-58). *Modoc Co.,* 9.1 m N Alturas, 3-vi-1983, 4600' (S83-48). *San Bernardino Co.,* Barstow, 28-vi-2003, 2300' (S03-73). **Colorado:** *Boulder Co.,* Boulder, 30-vi-2007, 5800-7200' (S07-72). *Jefferson Co.,* 9.3 m W Golden, 26-vii-1997, 6440' (S97-75). *Larimer Co.,* Ft. Collins, 3-viii-1997 (S97-112). *Otero Co.,* La Junta, 22-vi-1987, 4200' (S87-65); 2-vii-2009 (S09-82). **Idaho:** *Elmore Co.*, Mt. Home, 26-vi-2014 (S14-31). 1.5 m W Hill City, 16-v-2000, 5040' (S00-8). 34 m E Mt. Home, 16-v-2000, 5520' (S00-7). *Owyhee Co.*, Mt. Home, 7-vi-1996, 3260' (S96-41). 2 m N Bruneau, 2900' (S04-40). 2 m S Bruneau, 7-vi-1996, 2600' (S96-37). *Valley Co.*, 6 m S Donnelly, 18-v-2000, 4700' (S00-12). *Washington Co.,* Andrus Wildlife Management Area, 11-v-1998, 3000' (S98-41). **Illinois:** *DeWitt*

Co., Clinton, 3-vi-2003, 820' (S03-58). 3 m SE Clinton, 3-vi-2003, 850' (S03-59). **Indiana:** *Floyd Co.,* Georgetown, 4-vi-2003, 500' (S03-63). *Spencer Co.,* Dale, 4-vi-2003, 700' (S03-60). **Iowa:** *Freemont Co*., Waubonsie State Park, 1-vi-2003, 1250' (S03-55). Monona Co., Lewis and Clark State Park, 1-vi-2003, 1140' (S03-54). **Kansas:** *Barber Co*., Medicine Lodge, 23-vi-1987, 1550' (S87-68). 27 m W Medicine Lodge on Hwy 160, 14-vi-1988, 1750' (S88-41). *Comanche Co.,* at junction of Highways 160 and 183, 14-vi-1988 (S88-40). *Kearny Co.,* Lakin, 23-vi-1987, 2950' (S87-67). *Norton Co.,* near Edmond 23-vi-1993, 2900' (93-55). *Sherman Co.,* Sherman Co. State Park, 24-vi-1987, 3500' (S87-73). Goodland, 24-vi-1987, 3500' (S87-74). **Maryland:** *Prince George Co.,* College Park, 30-v-2004, 500' (S04-35). **Massachusetts:** *Berkshire Co.,* 29-vii-2006, 1700' (S06-67). **Missouri:** *Hickory Co*., Hermitage, 20-vi-1993, 1000' (S93-50). Pomme de Terre State Park, 20-vi-1993, 1000' (S93-49). *Jackson Co.,* Kansas City, 8-viii-2002, 860' (S02-54). *Pettis Co.,* Sedalia, 20-vi-1993, 950' (S93-51). **Montana:** *Gallatin Co.,* Bozeman, 15-vii-2004, 4450' (S04-66). **Nebraska:** *Dawes Co.,* 3 m E Crawford, 3-vii-2009, 3680' (S09-88). *Fillmore Co.,* Geneva, 7-viii-2002, 1420' (S02-51). *Lancaster Co.,* Lincoln, 7-viii-2002, 940' (S02-52). **Nevada:** *Humboldt Co*., Paradise Valley, 8-vi-1996, 4600' (S06-42). *Elko Co.*, Angel Creek Camp, Ruby Mts., 6600', 16-vi-2002, (DAG 2002-011). *White Pine Co.,* Baker, 5300', 9-vi-1996 (S96-49); 23-v-2015 (S15-16). 4.7-5.0 m W Baker, 9-vi-1996, 6520' (S96-46 & 47a). **New Mexico:** *Apache Co.,* Springerville, 20-v-2001 (S01-42). St. Johns, 20-v-2001, 5830' (S01-38). *Bernalillo Co.,* Tijeras Canyon ~2 m W Tijeras, 6600-6900', 3-5-vii-2019, S19-37 & S19-38, DC & K Lightfoot. UNM Campus, 13-vi-1994 (S94-33). 6 m NE Cedar Crest, 7035', 12-vii-2015 (S15-78) DC Lightfoot. Manzanito Mts., Carolino Canyon, 7500', 19-vii-2008 (S08-53) DC Lightfoot. *Catron Co.,* Apache Creek, 3-vii-1994, 6420' (S94-49). Reserve, 3-vii-1994, 5770' (S94-50); 2.1-2.2 m SW Reserve, 3-vii-1994, 5920-6120' (S94-51 & 52); 20-v-2001 (S01-40); 14-vi-2007 (S07-53). *Chaves Co.,* Roswell, 28-vi-2009, 3800' (S09-58). Hwy 82 near Elk, 28-vi-2009, 5840' (S09-57). *Cibola Co.,* El Malpais National Monument, Hwy 117 at 31 m S I40, 18-viii-1993, 7200' (S93-71 & 73); 1-vii-1994 (S94-40 & 41); 14-vi-1996, (S96-68); 14-vi-2007 (S07-51 & 52). Grants, 18-viii-1993, 6340' (S93-74); 1-vii-1994 (S94-43); 13-vi-1996 (S96-67). Hwy 117 at 35 m S I40, 14-vi-2007, 6870' (S07-51). Hwy 53 at mile-post 61, 13-vi-1996, 7800' (S96-66). *Eddy Co*., Guadalupe Mts., Dog Canyon 30-vii-2003, 6289'. *Lincoln Co.,* Carrizozo Rec Area, 2-vii-1994, 5560' (S94-47). Valle del Sol Municipal Golf Course, 13-vi-2007, 5320' (07-45). 12 m W Capitan, 2-vii-1994, 7060' (S94-45). *Otero Co.,* 1.8 m W Cloudcroft, 29-vi-1983, 8300' (S83-80); 7-vi-1985 (S85-53). 5 m E Cloudcroft, 30-v-2011, 8200' (S11-24). *San Juan Co.,* Farmington, 19-vi-1987 (S87-81). 12 m W Farmington, 19-vi-1987, S87-81, DC Lightfoot. *San Miguel Co.,* Pecos, 21-v-2001, 6944' (S01-45). Pecos National Historic Park, 21-v-2001, 7280' (S01-44). Pecos National Monument, 6-x-1994 (S94-106). Hwy 63 at mile-post 7.3, 21-v-2001, 7440' (S01-46). Hwy 25 at Exit 307, 21-v-2001, 7270' (S01-43). *Socorro Co.,* Los Pinos Mts., Goat Draw, 16-viii-1993, 6440' (S93-69). Sevilleta National Wildlife Refuge, 21-vi-1995, 5400' (S95-50), DC Lightfoot. *Valencia Co.,* 1 m S Los Lunas Bridge, 1-vii-1994 (S94-44). **North Dakota:** *Richland Co.,* Mirror Pool, 30-vi-1988, 1030' (S88-55); 31-v-2003, 46° 32.963' -97° 19.310' (S03-52). **Ohio:** *Franklin Co.,* Columbus, 5-vi-2003, 800' (S03-65). **Oklahoma,** *Texas Co.,* Guymon, 13-vi-1988, 3380' (S88-39); 1-vii-2009 (S09-77). Optima Wildlife Refuge 15 m E Guymon, 1-vii-2009, 3120', 36° 41' 49.8" -101° 9' 36.3" (S09-76). *Tulsa Co.,* Tulsa, near intersection Hwy 244 and I44 around 5828 W. Skelly Dr., 232m, 36° 04' 56.7" -96° 02' 58.0", 15-vi-1988 (S88-45); 23-vi-1993 (S93-57); 15-vii-2013 (S13-67); Near Exit 238 off I44, 2 m E Tulsa city limit, 15-vii-2014 (S13-68), 796', 36° 09' 37.4" -95° 47' 33.1". **Oregon:** *Harney Co.,* Alvord Hot Springs, 13-vi-2004, 4000' (S04-44). Burns, 2-vi-1997, 4020' (S97-51). 23.5 m S Burns, 14-vi-2004, 4000' (S04-48). *Jackson Co.,* Phoenix, 1500', 24-ix-2004 (S04-132). *Lake Co*., 16-vi-2004, 4500' (S04-54). *Sherman Co.,* 0.7 m SE Biggs, 31-v-1997, 220' (S97-47). **South Dakota:** *Jackson Co.,* Badlands National Park, Cedar Pass Overlook, 22-vi-1993, 3100' (S93-53); 3-vii-2009 (S09-89). Kadoka, 30-vii-1997, 2200' (S97-87). *Jones Co.,* Murdo, 22-vi-1993, 2600' (S93-54). *Minnehaha Co.,* Sioux Falls, 1-vi-2003, 1450' (S03-53). *Yankton Co.,* Lewis and Clark Lake, 21-vi-1993, 1500' (S93-52). **Texas:** *Brewster Co.,* Alpine, 9-vi-1985, 4200' (S85-59); 5-vi-1991 (S91-44); 12-vi-2007 (S07-41); 2-vii-2015 (S15-73). Marathon, 12-vi-2007, 3840' (S07-40). 22 m E Marathon, 12-vi-2007, 3850' (S07-35). *Culberson Co.,* Hwy 10 25 m E Van Horn, 29-vi-2009, 4780', 31° 4' 20.4" -104° 23' 21.8" (S09-63). *Jeff Davis Co.,* Davis Mts., 1.1 m below Observatory, 6246', 1-vii-2015 (S15-62). Fort Davis, Ft. Davis National Historic Site, 4852', 1-vii-2015 (S15-67). 1 m SW Ft. Davis, 6-vi-1991, 4800' (S91-46). **Utah:** *Beaver Co.,* Beaver, 5878', 23-v-2015 (S15-20). Milford, 4990', 24-v-2015 (S15-19). Minersville, 19-iv-1999, 5140' (S99-11). *Garfield Co.,* Boulder, 24-iv-2006, 6580' (S06-18). Panguitch, 19-v-2001, 6560' (S01-35); 23-iv, 2006 (S06-17). *Juab Co.,* Eureka, 5800', 19-iv-1999 (S99-8); 23-v-2015 (S15-13). Nephi, 5200', 10-ix-2004 (S04-115); 24-v-2015 (S15-23). *Kane Co.,* Hwy 89 9.3 m SSW Long Valley Junction, 19-v-2001, 6740' (S01-34). Road to Zion Narrows, 18 m NE Springdale, 10-

vi-1996, 6740’ (S96-51). *Millard Co.,* Delta, 4670’, 23-v-2015 (S15-14). Fillmore, 4920’, 31-vii-1992 (S92-102). Fillmore, Canyon Rd. 0.9 m E Business I15, 4920’ 18-v-2001, 38° 57.728’ -112° 18.439’ (S01-30). 8.5 m NW Fillmore, 18-v-2001, 4450’ (S01-28). Lava fields near Flowell, 19-iv-1999, 4520’ (S99-10); 18-v-2001 (S01-29). *Salt Lake Co.,* Riverton, 4500’, 24-v-2015 (S15-24). Salt Lake City, near Airport, 24-v-2015 (S15-25); Salt Lake City, Avenues residential area, 19-v-2009. *Sanpete Co.,* Manti, 5515’, 24-v-2015 (S15-23). 1.4 m SW Manti, 21-iv-1999, 5660’ (S99-17). 11 m N Manti, 21-iv-1999, 5700’ (S99-18). *Sevier Co.,* Richfield, 5300’, 24-v-2015 (S15-21). Salina, 17-viii-2009, 5300’ (S09-122). *Tooele Co.,* James Walter Fitzgerald Wildlife Management Area, 5200’, 23-v-2015 (S15-12). Stockton, 5200’, 30-vii-1992 (S92-93); 23-v-2015 (S15-11). Tooele, 5200’, 9-ix-2004 (S04-107); 23-v-2015 (S15-10). *Uintah Co.,* Jensen, 10-ix-1999, 4740’ (S99-127). *Wayne Co.,* Hanksville, 11-vi-1996, 4500’ (S96-60). **Vermont:** *Addison Co.,* Middlebury, 23-v-2009 (S09-16). **Washington:** *Grant Co.,* Wanapum Dam Reservoir, 1400’, 1-vi-1983 (S83-42). Ephrata, 30-v-1997, 1240’ (S97-46). Grand Coulee, 30-v-1997, 1400’ (S97-43). Lake Lenore, 19-vi-2004, 1020’ (S04-60). Moses Lake, 21-vi-2014, S14-18). *Lincoln Co.,* 2.5 m SE Grand Coulee, 30-v-1997, 1640’ (S97-42). **Wyoming:** *Crook Co.,* Aladdin, 4-vii-2009, 3780’ (S09-90). *Fremont Co.*, Shoshoni, 18-vii-2011, 4849’ (S11-72). 11 m N Shoshoni, 18-vii-2011, 4788’ (S11-71). *Park Co.,* Cody, 16-vii-2004, 5140’ (S04-73). *Platte Co.,* Guernsey, 27-vii-1997, 4000’ (S97-80). Near Guernsey, Road 270 3.9 m N Hwy. 26, 12-ix-1999, 4300’ (S99-139).

DNA. Multilocus G30, from near type locality of *G. veletis,* Spencer Co., Indiana (S03-60); and multilocus G2958, ‘Gryllus utahensis’, Nephi, UT (S15-23) comprise one close pair within *G. veletis*. Multilocus G1345, our ‘Gryllus #27’, Guymon, OK (S09-77); and multilocus G3075, our ‘Gryllus #36’, Alpine, TX (S15-73) comprise a second close pair within *G. veletis*. All are sister species (Gray *et al.* 2019) to *G. planeta.* See Discussion below for consideration of whether or not DNA supports further sub-division of this widespread species.

Discussion. Our initial sorting of this species resulted in six different, geographically separate “species.” Further efforts to delineate these “species” boundaries, using morphological and genetic properties, were unsuccessful probably, in large part, due to the vast geographical area and ecological diversity covered and the fact that just one (or perhaps two) species seems to be involved. As an example, adult females of *G. veletis* from near the most northern limits in North Dakota are small and very agile while their western Texas conspecifics are large and so bulky (including males) that they jump poorly, if at all.

Nevertheless, it seems prudent to briefly discuss those characters that in certain populations gave us pause, as to species identification, so that further investigations can be directed here:

1. We initially (1987) considered a “Great Plains” grouping (our ‘Gryllus #27’) from south-eastern Colorado, western Oklahoma, and Kansas to be distinct from *G. veletis* based upon the usual presence of long hind wings. For example, we found that 10 of 12 from La Junta, CO (S87-65); all 20 from Lakin, KS (S87-67); 3 of 4 from Medicine Lodge, KS (S87-68); all 11 from Goodland, KS (S87-74); and 21 of 23 from the town of Guymon, OK (S88-39 and S09-77), had long hind wings, loud songs, were very colonial, and at high, outbreak densities in these towns. More widespread collecting in nearby central Missouri in 1993, showed that this pattern was geographically limited since all 22 Missouri adults, about half from within towns, had short hind wings. The final tally for this 3-state region, within towns only, was that 65 out of 70 (93%) individuals had long hind wings. This pattern contrasts with ~12.5% long hind wings for *G. veletis* in the rest of its US distribution, both within and outside of towns. For ‘natural’ Optima Wildlife Refuge, Oklahoma (S09-76), 15 m E Guymon, 7 of 8 adults had short hind wings.

2. We initially considered individuals from around Tulsa, Oklahoma (our ‘G. #30’) to be distinct because males generally have fewer p/c and a more regular, faster chirp rate. But in comparison with our other US *G. veletis,* we find no consistent characters, including DNA, to separate them.

3. We initially considered individuals from western Texas (including Alpine, Marfa, Marathon, Davis Mts. and Amarillo—our ‘Gryllus #36’) to be distinct because adult females are so large and bulky, that they cannot hop. Additionally, when the males in these western Texas populations are compared with those male *G. veletis* from throughout New Mexico (our ‘Gryllus #43’), we find the heads in New Mexico to be wider, relative to pronotum width, than those of the larger males from Texas. It is doubtful that the few Texas adults that have long hind wings can fly because of their weight.

4. Sequencing of the 16S gene in individuals from western Utah revealed a second, distinctive clade (see Fig. 143), which we initially called ‘G. utahensis’. Subsequent ITS2 and multilocus sequencing revealed that all of these individuals were consistent with *G. veletis* from Illinois and Indiana (near type locality), and that individuals in two Utah populations (Tooele, S15-10 and Richfield, S15-21) contained both haplotypes.

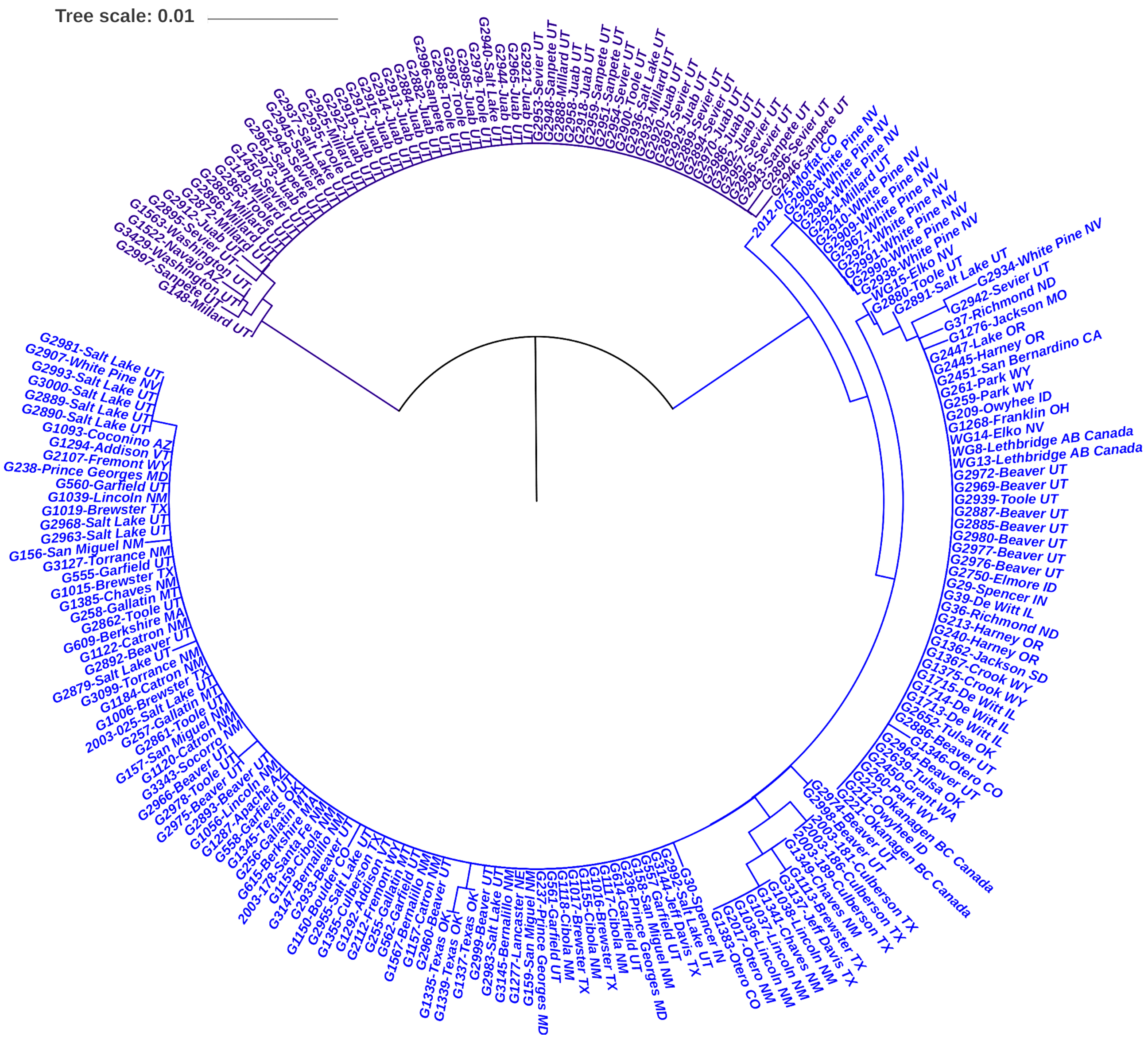

FIGURE 143. Radial 16S gene tree showing large and distinct 16S clade (in purple) in central Utah. Labels indicate County and State; the '**G. utahensis**' 16S clade is in purple, whereas geographically widespread ***G. veletis*** samples (including other Utah samples) are in blue.

Despite our unwillingness now to further subdivide *G. veletis*, we do note strong subdivision within the nuclear ITS2 gene (see Fig. 132) consistent with the two-pairs of the four samples in the multilocus tree. ITS2 similarity based on Tamura-Nei distances was 99.1 ± 0.76 within individuals from NV, NM, TX, and OK (n=10), 99.4 ± 0.45 within individuals from IN, IL, and UT (n=15), but 94.09 ± 0.26 between these groups.

G. veletis and *G. pennsylvanicus* are sympatric over much of their northern US distribution. Because the former overwinters as a late instar and the latter as an egg in obligate diapause, they mature and sing at different times in the subsequent spring and summer. They may have a brief period of synchronicity but such has only been studied in detail in Michigan (Alexander & Meral 1967), and even then, complete resolution was difficult because of morphological similarity between the two taxa and almost identical songs, although Alexander & Bigelow (1960) noted that *G. pennsylvanicus* females tend to have longer ovipositors than *G. veletis*. We were consequently surprised to find the two species synchronic and easy to distinguish, based on pulse rate, number of file teeth, and length of ovipositor at localities in South Dakota, Nebraska, Missouri, and Utah (Table 2). For instance, at Kadoka, SD (S97-87), both *G. veletis* and *G. pennsylvanicus* adults were singing on 30-vii-1997 although most individuals of the latter were several molts to adult. Our 2 collected adult male *G. veletis* had 134 and 138 teeth with laboratory recorded pulse rates of 25-35, at 23°C and 26.5°C, respectively. These rates were faster than the 4 male *G. pennsylvanicus* collected as late

TABLE 2. Where *G. veletis* and *G. pennsylvanicus* are synchronic and can be separated.

Species	Locality	Stop number(s)	Collection date(s)	file teeth	teeth/mm	Pulse rate	ovipositor length (mm)
G. veletis	Hanksville, UT	S96-60	11-vi-1996	130–144	40–43	27.8–29.4	none
	Kadoka, SD	S97-87	30-vii-1997	134–138	40–40.6	25–35	11.7
	Jensen, Utah	S99-127	10-ix-1999	141–143	46.1–46.2	25–29.4	none
	Geneva, NB	S02-51	7-viii-2002	156	43.3	25	none
	Lincoln, NB	S02-52	7-viii-2002	143–148	37.6–41.1	20.8	none
	Kansas City, MO	S02-54	8-viii-2002	148	43.5	25	none
G. pennsylvanicus	Hanksville, UT	S92-109, 98-88, 99-119, 04-128	1-viii-1992, 11-ix-1998, 9-ix-1999, 12-ix-2004	173-214	40.4–51.8	12.5–17.9	14.4–19.4
	Kadoka, SD	S97-87	30-vii-1997	149–171	39.8–44.4	17.9–21.7	17.6 x 2
	Jensen, Utah	S99-127	10-ix-1999	173–177	39.8–40.7	13.2–16.1	16.1
	Geneva, NB	S02-51	7-viii-2002	174–200	44.3–51.3	10.9–17.2	17.81–19.36
	Lincoln, NB	S02-52	7-viii-2002	169	45.7	not recorded	20–22.29
	Kansas City, MO	S02-54	8-viii-2002	163–171	49.4	16.7–20.8	none
G. pennsylvanicus, but not known if *G. veletis* also occurs sympatric	Oklahoma City, OK	S02-48	6-viii-2002	211–223	51.9–53.4	10.4–14.3	none
	Salina, KS	S02-49	7-viii-2002	161–215	43.7–55.2	13.9–20	18.03–21.93
	Concordia, KS	S02-50	7-viii-2002	174–199	45.8–56.5	11.7–13.5	16.14–17.15
	Millersville, MO	S02-58	9-viii-2002	195	56.5	16.7	none
	Rifle, CO	S09-109	15-viii-2009	168–191	41–45.2	10–15.6	16.71–18.06

instars (we were unable to collect any adult males) and that molted to adults in mid-late August: they had 149-171 teeth and laboratory recorded pulse rates between 17.9-21.7, at 22.5-25°C. Interestingly, teeth/mm were essentially the same: 40.0-40.6 in the 2 *G. veletis* males and 39.8-44.4 in the 4 *G. pennsylvanicus* males. But these pulse rate differences were easily appreciated in the field when the two taxa were singing together at similar temperatures. We also collected 1 adult female *G. veletis* with a short ovipositor, long tegmina, and no egg diapause when compared to those female *G. pennsylvanicus* collected as nymphs and that molted to adult 2 weeks later in mid-late August. A similar situation existed at the 5 other Nebraska, Missouri, and Utah localities listed in Table 2, although we were never at Hanksville at the right time of year to document potential synchronicity. Likewise, the 5 localities from Oklahoma, Kansas, Missouri, and Colorado, where *G. pennsylvanicus* also has increased numbers of file teeth when compared with surrounding areas, do not have documented populations of *G. veletis*, but we suspect they do exist if we had been there earlier in the season. We wonder if these increased number of file teeth in *G. pennsylvanicus* are a reflection of character displacement in areas where the 2 taxa have overlap in singing adult males? In any case, these localities should be compared, for synchronicity between these 2 taxa, with the areas around Chadron, NB (S97-83 and 97-84), where, on 28-vii-1997, we collected 2 adult males and many late instars that yielded 9 *G. pennsylvanicus* males with 139-166 teeth, 39.7-48.8 teeth/mm, and pulse rates of 19.2-25, and 1 adult female and several late instars that yielded 5 *G. pennsylvanicus* females with ovipositor lengths of 14.0-16.0 mm. While we didn't collect or hear any *G. veletis* there, we did see many small *Gryllus* nymphs that could be recently hatched *G. veletis.* Perhaps the 2 species around Chadron are not synchronic, or minimally so, so that character displacement doesn't occur there?

Where it occurs, *G. veletis* is usually the most common field cricket, with apparent outbreaks, in towns, of mostly long hind winged individuals, occurring in certain Colorado, Kansas, and Oklahoma localities in 1987, 1988 and 2009. This finding is in contrast to reports of typically solitary individuals for more eastern US populations (summarized in Alexander & Bigelow 1960). We frequently find nymphs and adults of *G. veletis*, in normal population-size years, congregating together under objects in spring and early summer and infrequently associated with specific burrows. Because most of the western US dries out in the summertime, resulting in deep substrate cracks and suitable refuges, burrows may be less necessary for shelter. Eastern populations, where summer rains can be more significant and substrate cracks rare, could find burrows more important.

Although males in different populations can vary by over 100% in body length (Figs 144, 145, 146), showing a distinct north to south size cline, we find no similar differences in tooth file architecture with reference to number of teeth (Figs 141, 147). Because southern males are much larger than northern males, they also have correspondingly longer files (Fig. 148). If tooth density remained the same going south, then files would contain many more teeth, a situation not seen (Fig. 147). We do find that the density of file teeth increases (Fig. 149) going northward. Given that the PR (Fig. 150) and dominant frequency remain essentially the same throughout *G. veletis'* range, this suggests that the larger southern males apparently close their wings faster (over a longer file with fewer teeth/mm) in order to have a constant pulse duration and a constant dominant frequency.

Preliminary hybridization studies conducted in 2003 between California virgin *G. veletisoides* and virgin *G. veletis* from the Midwestern US produced the following results: 3 females from Indiana crossed with Fresno, CA, males—two females had documented matings (with passed spermatophores) but only one of the two females laid eggs. The female in the third pairing laid eggs but no eggs from any female hatched. One female, from Illinois, mated with a Fresno, CA, male and laid eggs but none hatched. One female from Iowa matched with a male from Los Gatos, CA, laid eggs (never saw a passed spermatophore) but they never hatched. As controls, an Indiana female mated with a North Dakota male produced lots of eggs that hatched while a North Dakota female that mated with an Illinois male produced eggs that didn't hatch.

G. veletis appears in the literature as an example of allochronic speciation (Alexander & Bigelow 1960), studies on calling, movement, parasites, age, and mating (Alexander & Meral 1967; French & Cade 1987; Zuk 1987, 1988; Thomson & Bertram 2014), genetics of wing morphology and diapause (Bégin & Roff 2002), changes in calling songs as males age (Fitzsimmons & Bertram 2011), and freeze tolerance adaptations (Toxopeus *et al.* 2018).

Tachinid fly *Exoristoides johnsoni* emerged from adult males from Utah (S96-50 and S96-51), Nebraska (S97-83), and South Dakota (S03-53), the latter from a penultimate instar male.

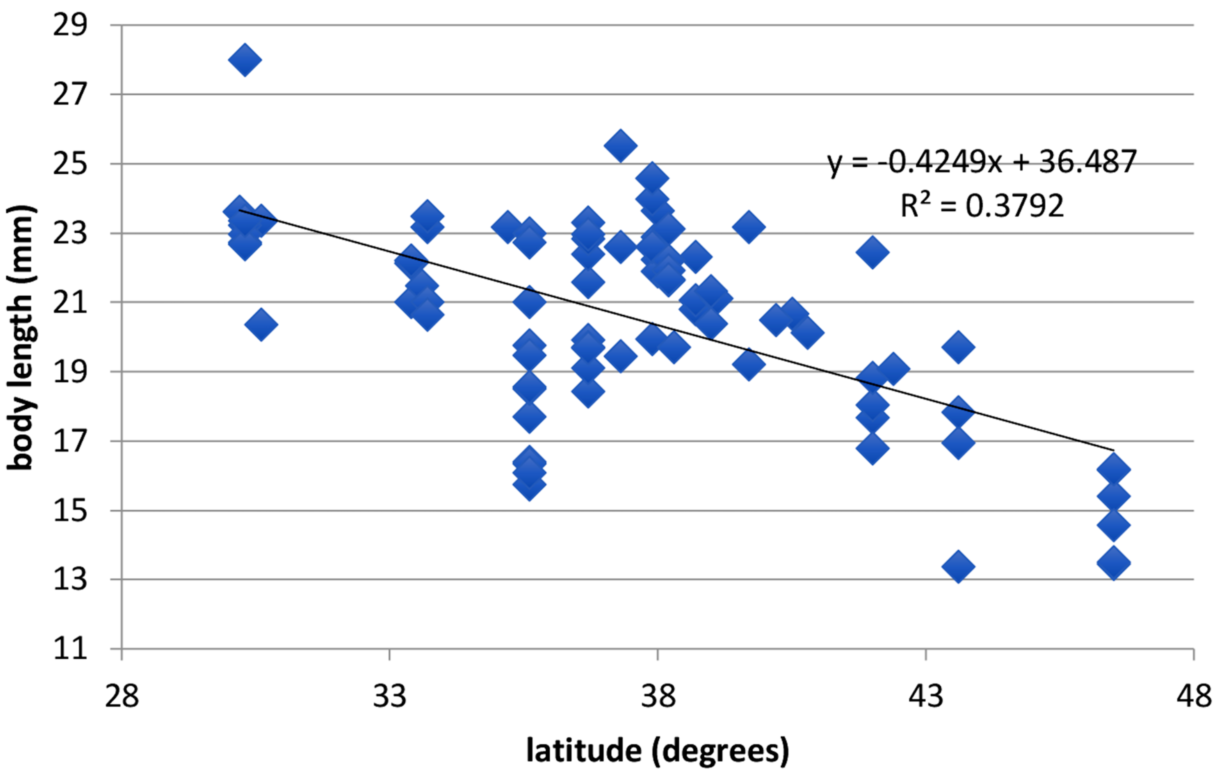

FIGURE 144. Regression latitude vs. body length in *G. veletis.*

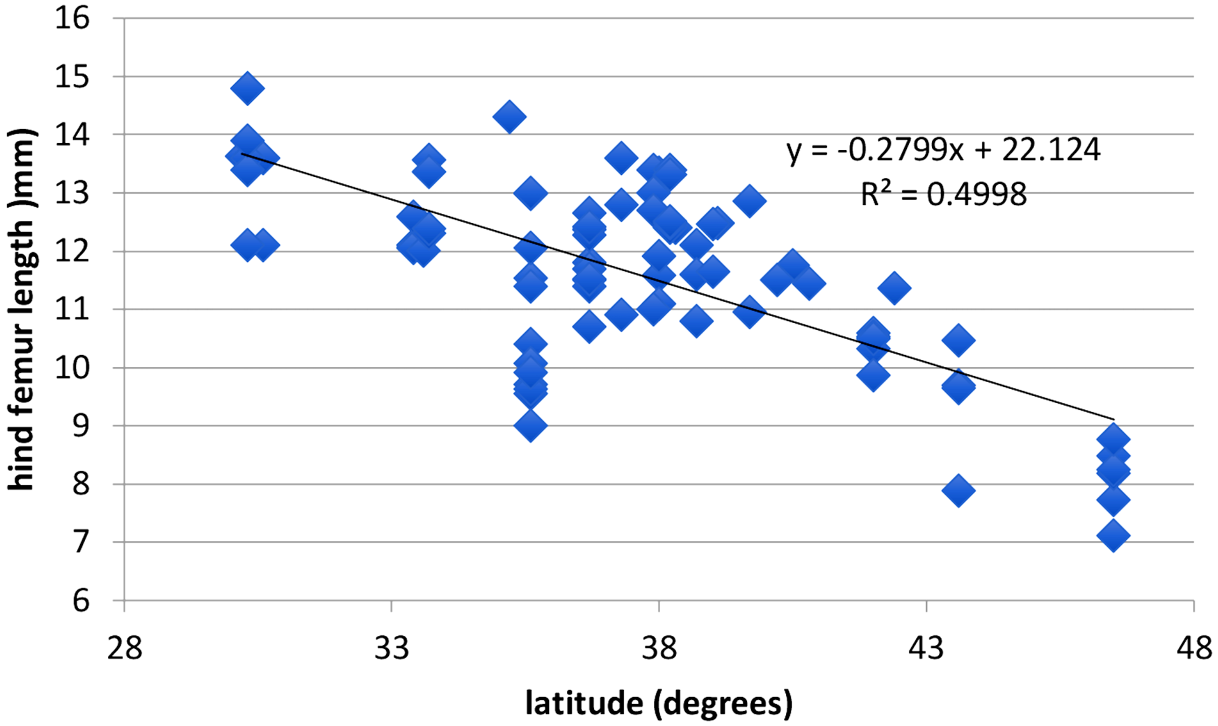

FIGURE 145. Regression latitude vs. hind femur length in *G. veletis.*

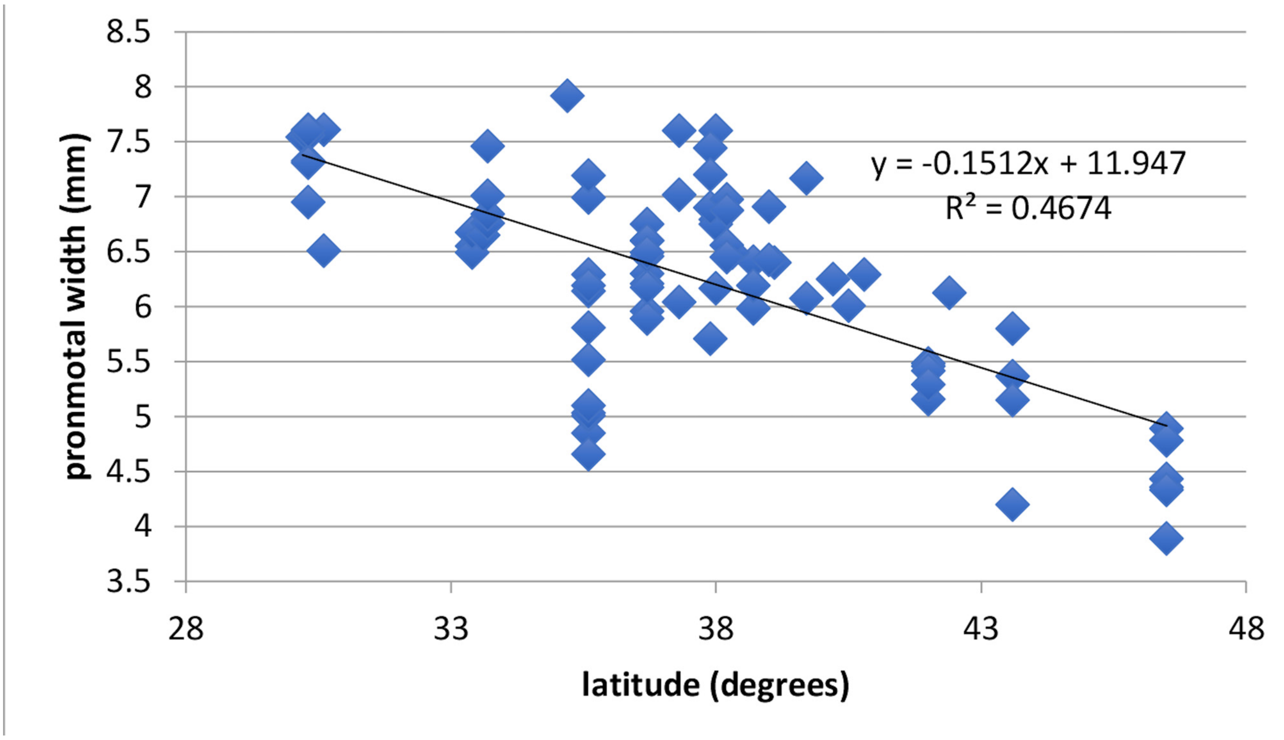

FIGURE 146. Regression latitude vs. pronotal width in *G. veletis*.

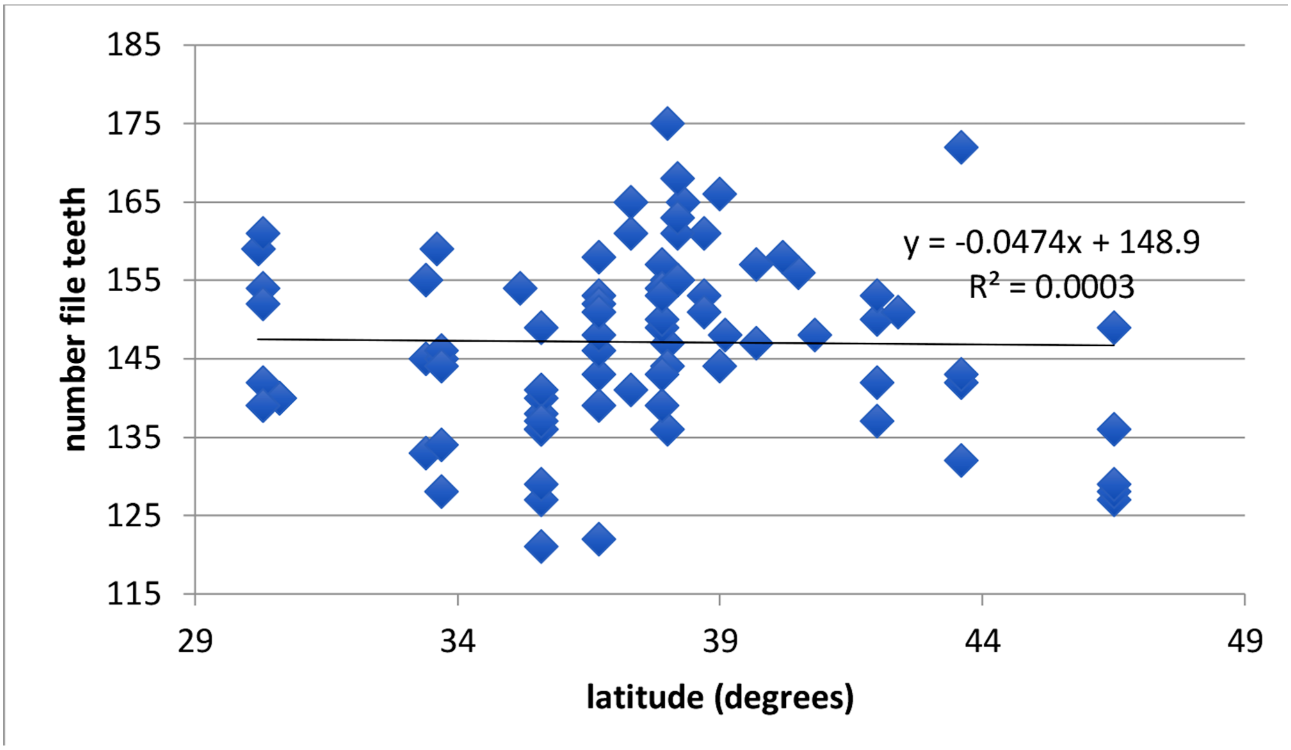

FIGURE 147. Regression latitude vs. file teeth number in *G. veletis*.

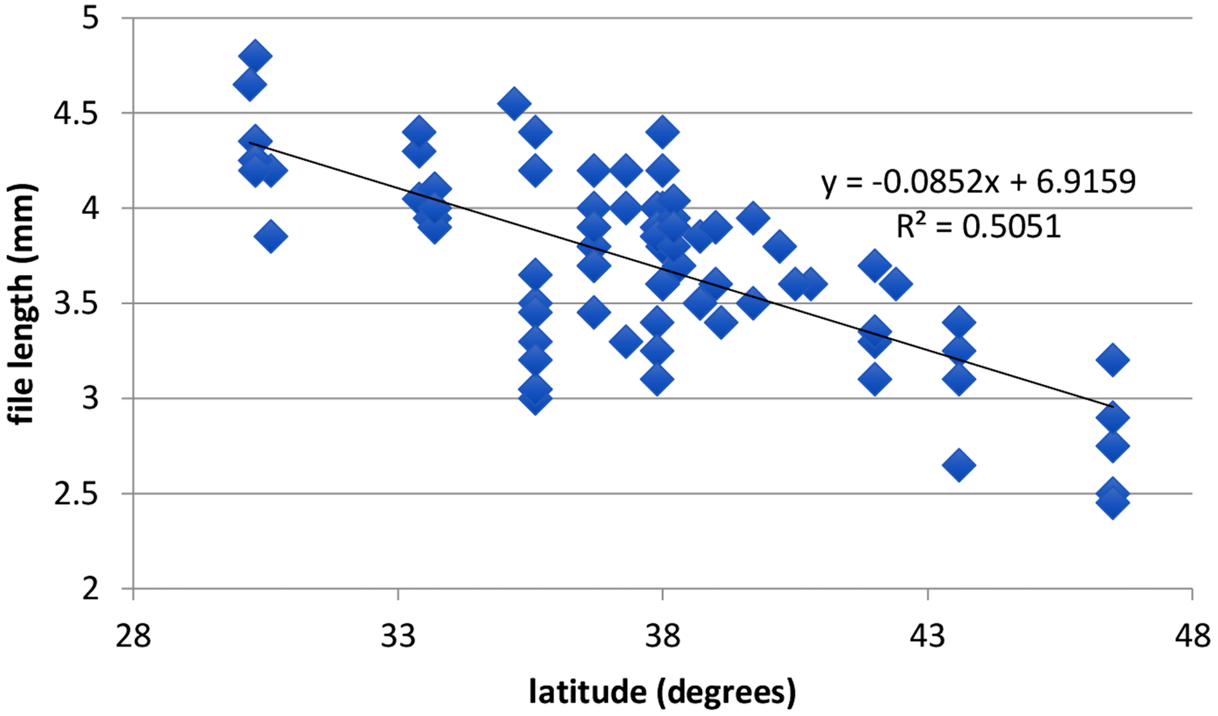

FIGURE 148. Regression latitude vs. file length in *G. veletis*.

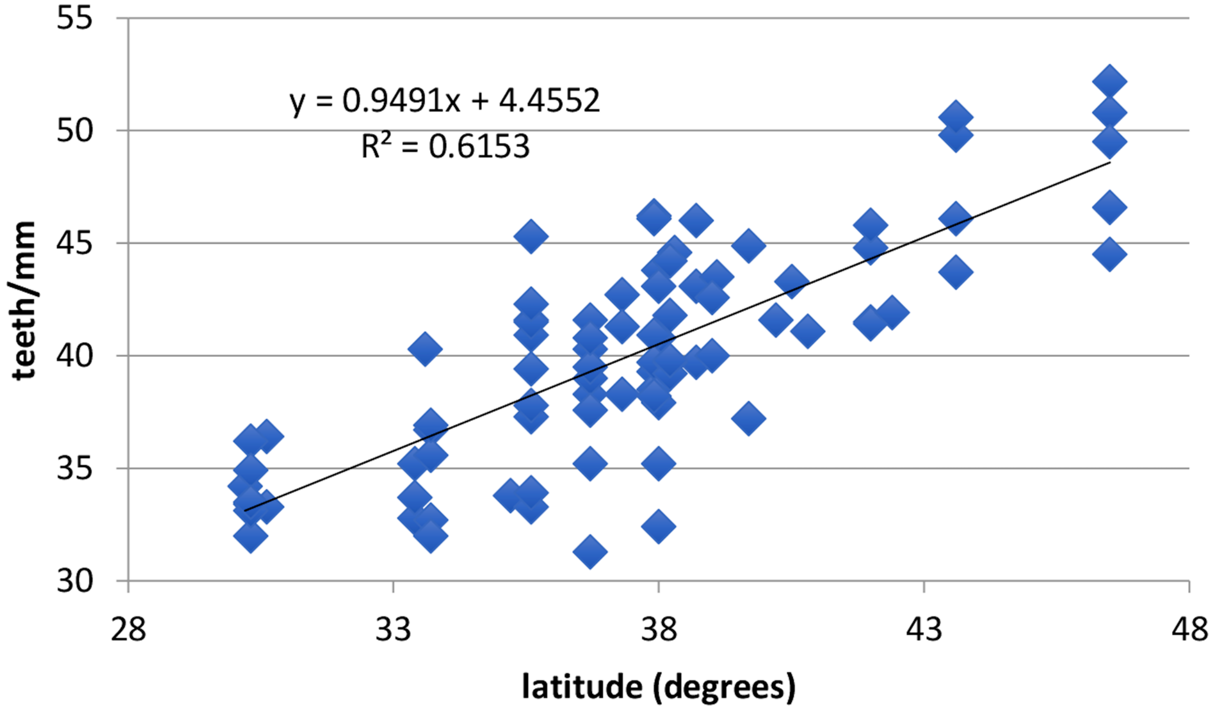

FIGURE 149. Regression latitude vs. teeth/mm in *G. veletis.*

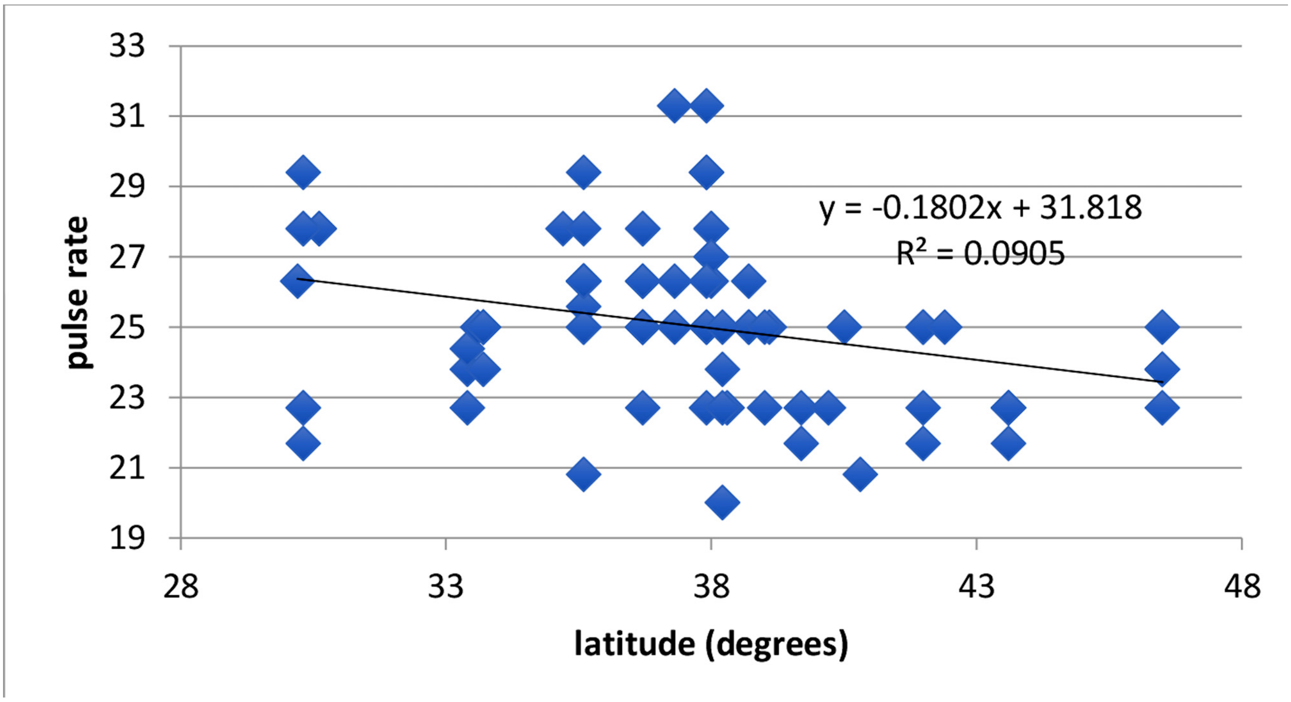

FIGURE 150. Regression latitude vs. pulse rate in *G. veletis*.

Gryllus planeta **Weissman and Gray, n. sp.**

McDonald Observatory Wood Cricket

Figs 130–132, 136, 151–154, 205, Table 1

Distribution. Known only from the sky island oak-woodlands of the Davis Mountains in west Texas, around the area of the McDonald Observatory.

Recognition characters and song. *G. planeta* is microsympatric with each of the other three slow chirping *Gryllus* species in the Davis Mts., but with only one species at a time. A small-medium body length, narrow, black (except for inside of hind femur), always short hind winged, cricket characterized by short cerci (Fig. 151). *Song* (Fig. 152) a slow chirp with 3 p/c, 150-200 c/m, and a PR of around 27 at 25°C. Morphologically most similar to western Texas *G. veletis* (microsympatric at S15-62) but generally separated by habitat (oak woodland vs grassy meadows), smaller, more slender size, and no overlap in the following 6 parameters (Table 1, p. 18): *G. planeta* has shorter file length with higher tooth density, shorter tegmina length and width, shorter ovipositor and shorter hind femur length even where they occur microsympatric. Also overlaps in length of cercus with *G. veletis* but when body length size differences compensated for (Fig. 151), cerci relatively longer in *G. planeta* even if only by 1-2 mm.

Genetically different from *G. veletis* for multilocus (Gray *et al.* 2019) and ITS2 (Fig. 132) but similar for 16S (Fig. 143). Separated from microsympatric *G. transpecos* (Davis Mts., S15-61) by 6 mostly non-overlapping characters (Table 1, p. 18): shorter cerci length in *G. planeta*, number of teeth, file length, tegminal length and width, and faster chirp rate in addition to genetics (different multilocus, 16S and ITS2 gene profiles). Separated from microsympatric *G. longicercus* (Davis Mts., S15-63) by non-overlapping (Table 1, p. 18) number of teeth, file length, teeth/mm, cerci length, PR, and DNA. *G. planeta* is morphologically similar to other narrow, small, spring-adult, black, slow chirping, allopatric western *Gryllus* species, such as *G. montis* (nearest population ~500 km west in Chiricahua Mts., Arizona) and *G. saxatilis* (nearest population ~1000 km west in Arizona) but, except for *G. veletis, G. planeta* can immediately be separated in the field on the basis of its short cerci and restricted geographic distribution. Also, similar to New Mexico, Organ Mountains sky island endemic *G. sotol*, ~280 km to the NW, but can be separated by cerci length, DNA, habitat, and maturation time (summer for *G. sotol* vs. spring for *G. planeta*).

Holotype. Male (Fig. 153). Texas, Jeff Davis Co., Davis Mts., Mt. Locke, McDonald Observatory, in oak woodland at base of Otto Struve Telescope, 1-vii-2015. 6747’, 30° 40’ 16.82” -104° 01’ 24.76”. D.B. Weissman & D.W. Weissman. S15-61, R15-189, G3114. 16S GenBank accession # MK446549; ITS2 GenBank accession #

MK441918. BL 20.16, HF 10.63, LC 10.38. Right tegmen removed: 128 teeth, file length 2.8, TL 9.4, TW 3.9. Deposited CAS, Entomology Department #19269.

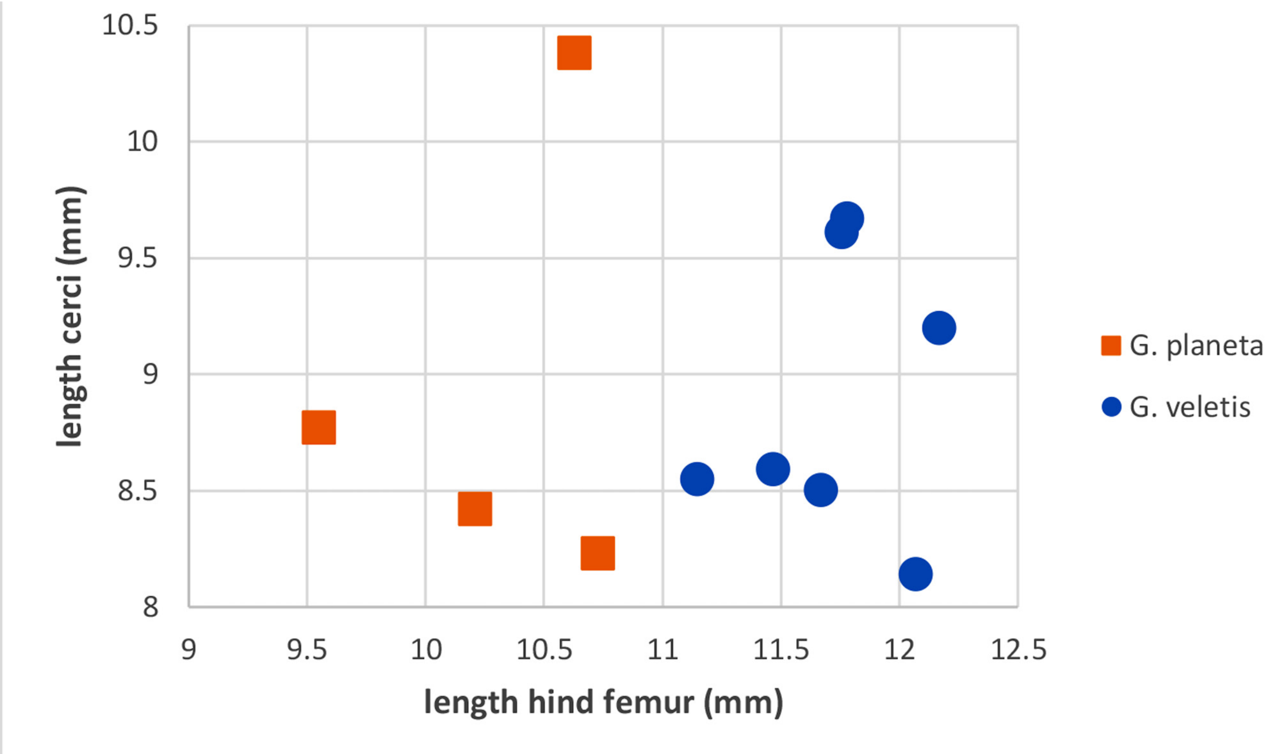

FIGURE 151. Regression hind femur length vs. length cerci in *G. planeta* vs. *G. veletis*, in the Davis Mts., TX, showing separation between these sympatric species.

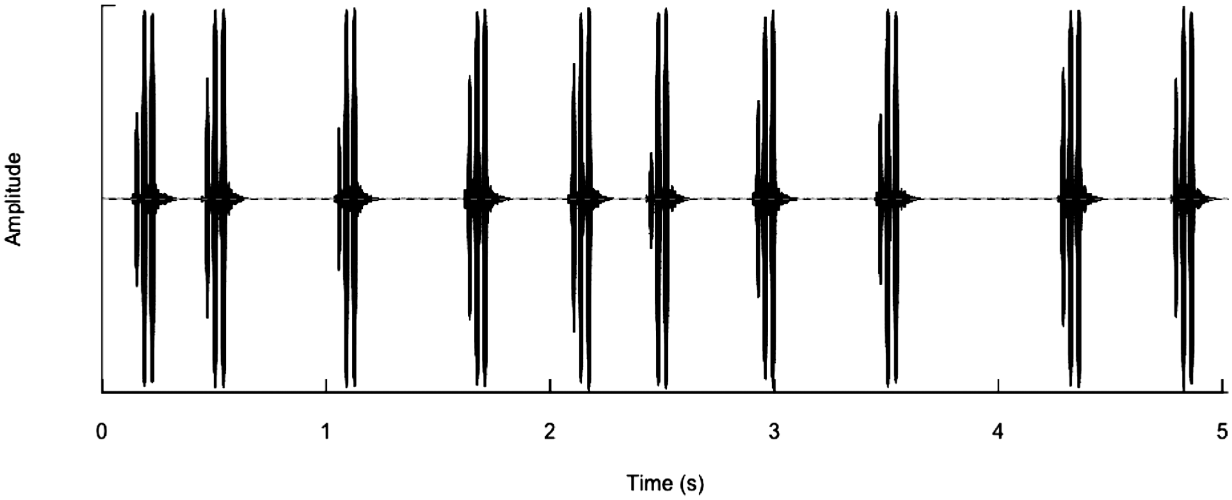

FIGURE 152. Calling song (R15-160) of *G. planeta* from the type locality (S15-61), recorded at 24.9°C.

Paratypes. (Total: 5♂ 3♀). **Texas**, Jeff Davis Co., Davis Mts., Mt. Locke, 6747’, same data as holotype, S15-61, 3♂ 3♀; 6246’; open mowed field 1.1 road miles below Telescope, 1-vii-2015, S15-62, 30° 40’ 51.03” -104° 01’ 22.78”. D.B. Weissman & D.W. Weissman, 1♂; 6073’, rocky road cut 2.7 road miles below Telescope, 1-vii-2015, S15-63, 30° 39’ 57.79” -104° 02’ 10.41”. D.B. Weissman & D.W. Weissman, 1♂.

Derivation of name. “planeta” from Latin (masculine) for planet or planetary, in reference to its only known occurrence being from 1851-2056 m elevation on Mt. Locke in the Davis Mountains, site of the McDonald Observatory operated by the University of Texas at Austin. The highest elevation of 2056m is at the base of the Otto Struve Telescope which is also the highest state maintained road in Texas.

Geographic range. (Fig. 154) Known only from the Davis Mts.

FIGURE 153. Holotype male (left) *G. planeta.* Female (right) also from type locality.

Habitat. From 1851m to 2056m elevation. At Telescope (S15-61), most common *Gryllus,* and microsympatric with *G. transpecos*, under short oaks with a fairly open canopy. Several collected there walking around with males singing in the open or from cracks in stone wall. Farther down the mountain (S15-62), 1 male singing with more common *G. veletis* in an open field but his microhabitat not noted. Still farther down the mountain (S15-63), 1 male singing in area of rocky road cut with locally more common *G. longicercus*.

Life cycle & seasonal occurrence. Egg diapause not checked but probably absent given the presence of apparently old adults, as indicated by broken cerci, in early summer specimens. No nymphs seen on 1-vii-2015. Given elevation, probably 1 generation/year.

Variation. Nothing significant except for measurements in Table 1, p. 18.

DNA. Multilocus G3088, type locality. Nearest relative is *G. veletis* (Astral analysis) or Clade 1 of *G. montis* (see G2416 and G2464 in concatenated analysis, Gray *et al.* 2019), the latter two both from the Chiricahua Mts. in eastern Arizona. In the Davis Mts., all individuals verified as to species by ITS2, to insure separation from *G. transpecos*, since if cerci damaged in the latter, can be confused with *G. planeta* due to some overlap in several morphological characters (see under "Recognition characters").

Discussion. Our field attention was first called to this cricket, on the top of Mt. Locke (S15-61), by cerci that seemed 1-3 mm too long for *G. veletis* but not long enough for microsympatric *G. transpecos*. While under mountain top tree canopy is not a typical habitat for *G. transpecos, G. veletis* is known from such areas, such as Cloudcroft, NM. We subsequently collected obvious *G. veletis* 150 m lower (S15-62) on our elevational transect. At the latter site, *G. veletis* were much larger than those *G. planeta* from higher up but the cerci of these *G. veletis* were still shorter than those of the smaller *G. planeta* (see Fig. 151). Critically, at S15-62, we collected one much smaller male which morphologically agrees with *G. planeta* (see "Recognition characters"). Our first genetic efforts with mitochondrial 16S showed no difference between *G. planeta* and *G. veletis*, but ITS2 clearly separated the two taxa, which then revealed the many physical characters that also separate them. When the paratype series of *G. planeta* was collected in early July, the situation was complicated, by damaged cerci in microsympatric *G. transpecos* (probably reflecting their old adult age), which then resembled, in length, those of *G. planeta*. Thus, ITS2 was run on all paratype individuals to confirm identity. The calling songs of *G. planeta, G. veletis*, and *G. transpecos* are indistinguishable from one another in the field, despite them being microsympatric in places. Perhaps if we knew beforehand which species we were listening to, then better field identification might be possible.

G. planeta, along with *G. chisosensis* and *G. sotol*, are all sky island, geographically restricted taxa, occupying cooler, wetter, and more biologically diverse habitats than the surrounding Chihuahua Desert (Cullen, 2015). The Davis Mountains receive 51 cm of rainfall a year, contrasted with 25 cm a year in the surrounding Desert (Cullen, 2015).

The Davis Mountains were created about 35 million years ago by the same volcanic thrust that formed the front range of the Rockies.

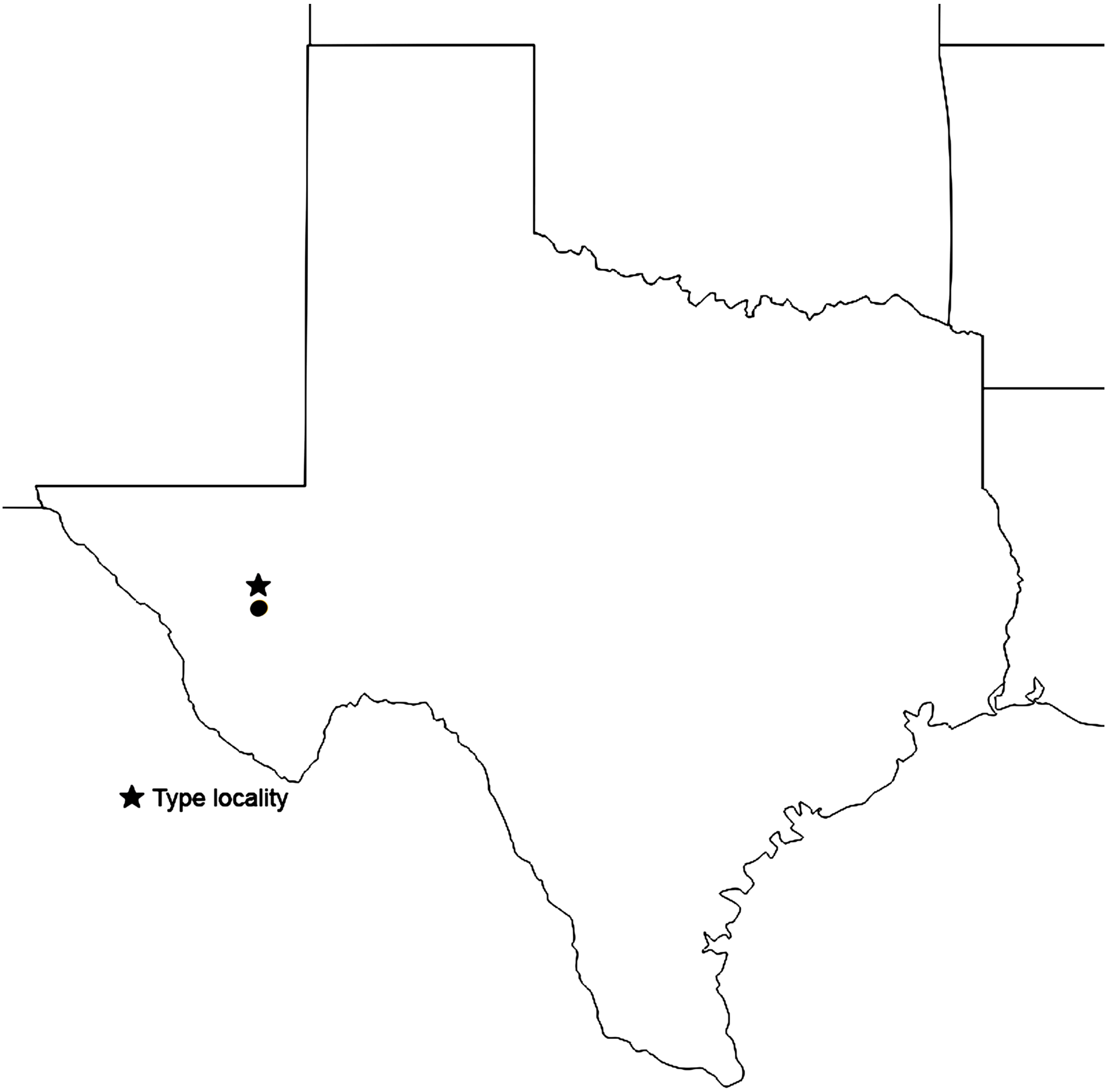

FIGURE 154. Known distribution of *G. planeta*.

The Vocalis Group

Gryllus vocalis Scudder and *Gryllus cohni* Weissman

Sister species of field crickets: *G. vocalis* typically associated with mesic areas (including human watered landscapes) and with riparian areas in the interior western US; *G. cohni* in the Sonoran Desert from Arizona into Mexico. Song a fast series of regular (3 pulses/chirp, *G. vocalis*) or highly irregular (*G. cohni*) numbers of pulses (Figs 155, 156). Well separated by ITS2 (Fig. 157).

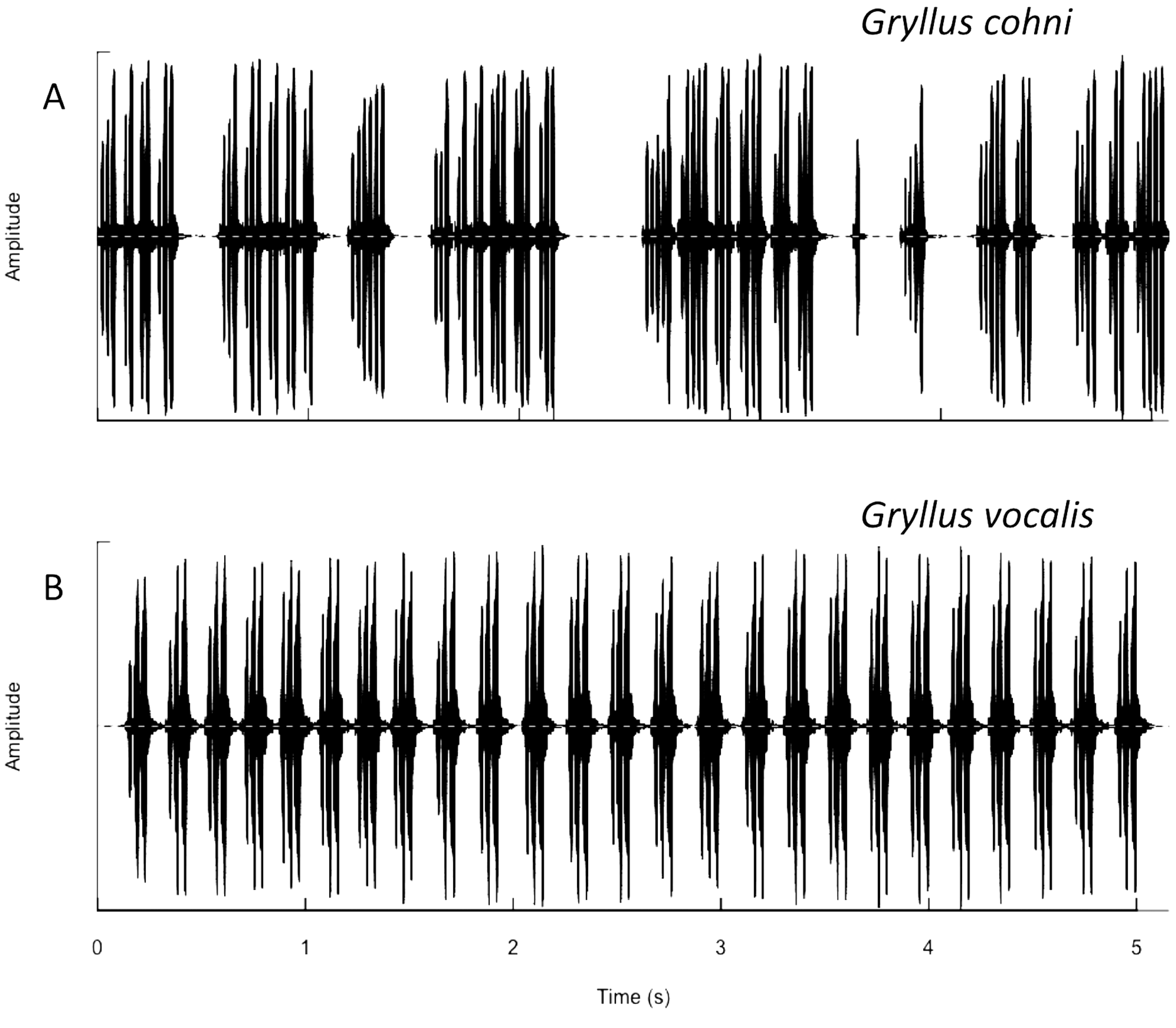

FIGURE 155. Five second waveforms of calling songs of (A) typical *G. cohni* and (B) *G. vocalis*. *G. cohni*: (R15-289) Pima Co., AZ (S15-108), at 25.3°C; *G. vocalis*: (R09-17) San Diego Co., CA (S09-18), at 23.5°C.

Gryllus vocalis Scudder

Damp-Loving Field Cricket
Figs 155-163, Table 1

1901 *Gryllus vocalis* Scudder, Psyche 9: 268. Lectotype male (Fig. 158), courtesy of J. Weintraub) designated by Weissman *et al*. (1980): “L. Angeles, Calif., July 29, 1897. *Gr. vocalis*, Scudder’s type 1901. Red type label, type 14070.” Deposited in ANSP.

1902 *Gryllus alogus* Rehn. Proc. Acad. Nat. Sci. Philadelphia 54: 726. Holotype female: “Albuquerque, 1902. N. M. T.D.A. Cockerell/Red type label *Gryllus alogus* Rehn Type No. 5067.” Adult type (Fig. 159, courtesy of J. Weintraub) with black head and pronotum, pronotum hirsute, tegmina tan, hind wings short, all legs orange brown. Head narrower than pronotum. Some brown-red markings in area of lower face. Body 17.2, hind femur 10.9, ovipositor 14.8, head width 5.2, pronotum width 5.7, pronotum length 3.4.

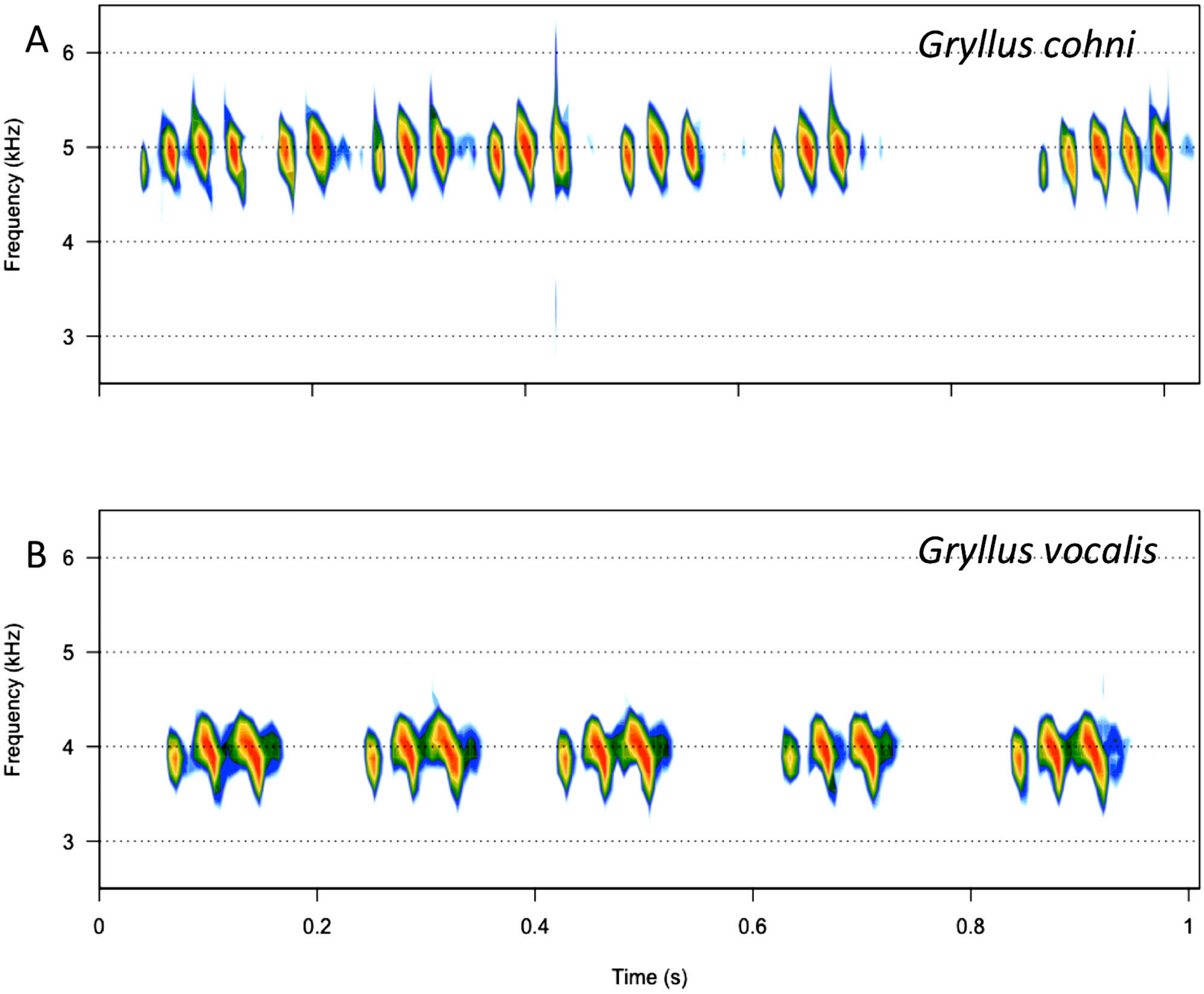

FIGURE 156. One second spectrograms of (A) *G. cohni* and (B) *G. vocalis*, same males as in Fig. 155.

Because the holotype is a female without intact cerci, we don't have the benefit of male file characters or cerci length to help in determining which species this is. The following five *Gryllus* species occur either in the city of Albuquerque or its vicinity (we considered a geographical area wider than Albuquerque since many old collecting localities were frequently "assigned" to the nearest town): *G. armatus, G. longicercus, G. veletis, G. lightfooti*, and *G. alogus*. We eliminate *G. armatus* because the body colors of the holotype of *G. alogus* are different, her pronotum is too long and hirsute, and she has short hind wings. We eliminate *G. longicercus* because the ovipositor to hind femur ratio in New Mexico specimens (Fig. 160) is wrong, the pronotum is hirsute, and the head is narrower than the pronotum, the last two qualities not seen in *G. longicercus*. We eliminate both *G. veletis* and *G. lightfooti* because their pronotums are not hirsute or minimally so, and the body, tegmina, cerci and legs of the latter two taxa are generally black and not orange brown, as in the holotype. This elimination process leaves only *G. alogus*. Deposited in ANSP. **New synonymy.**

1981 'Gryllus IV', Rentz & Weissman (1981).
'Gryllus #10, #18', 'arizonensis' and *alogus* of DBW notebooks.
'Regular stutter-triller' of Sakaguchi & Gray (2011).

Distribution. Widespread (Fig. 163) across the Southwestern US from southern California up along the eastern side of the Sierras, through southwestern Nevada, southern Utah, Arizona, New Mexico, and east to Big Bend, Texas.

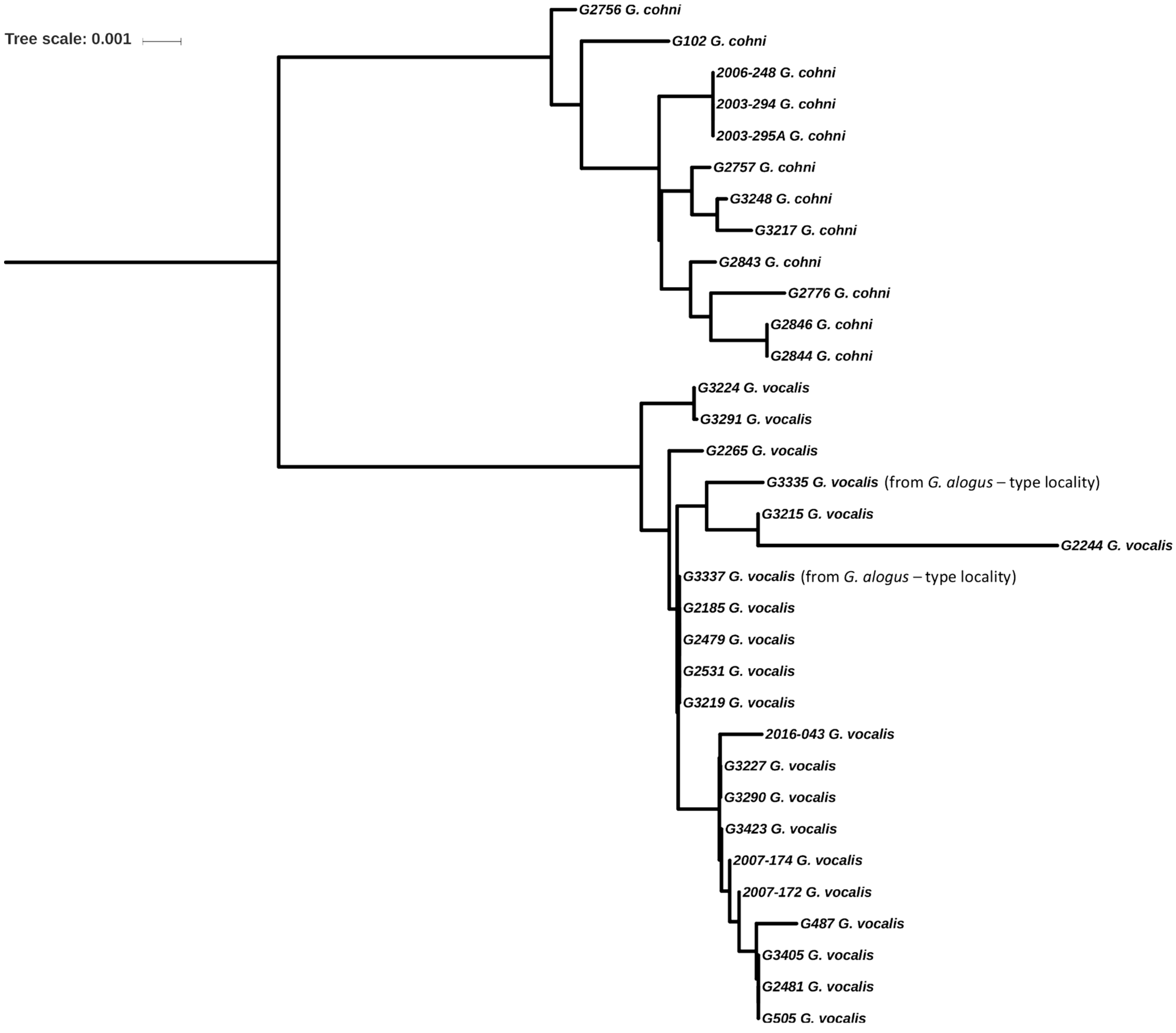

FIGURE 157. ITS2 gene tree. ***G. cohni*** samples: S95-81 (G102); S14-53, 20 km S Mazatlán, Mexico (G2756, G2757, G2776, G2843, G2844, G2846); S15-107 (G3248); S15-108 (G3217); Cordes Junction, Yavapai Co., AZ (2003-294, 2003-295A); Bloody Basin x Pueblo la Plata, Agua Fria National Monument, Yavapai Co., AZ (2006-248). ***G. vocalis*** samples: S05-68 (G487); S05-99 (G505); S11-102 (G2185); S12-20 (G2244); S12-26 (G2265); S13-13 (G2531); S13-14 (G2479); S13-16 (G2481); S15-110 (G3215); S15-111 (G3219, G3224, G3227, G3290, G3291); S16-18 (G3405); S16-28 (G3423); Wet Beaver Creek Campground, Yavapai Co., AZ (2007-172, 2007-174); California State University Northridge, Los Angeles Co., CA (2016-043). ***G. alogus***, type locality, Albuquerque, NM (G3335, G3337).

Recognition characters and song. While geographically widespread, *G. vocalis* has a narrow microhabitat and is almost always associated with wet, verdant habitats such as coastal salt marshes (Cardiff by the Sea, S80-48, 49), along seasonal (Whitewater, S09-21 and Agua Fria, S13-14) and year-round streams (Furnace Creek, Death Valley, S80-32, S83-60, S03-36; and Zion National Park, S01-33), in seasonal ponds with *Distichlis* salt grass (7.2 km N Beatty, NV, S80-34), and in gardens (Gila Bend, S15-111) and artificially watered areas. Medium to large crickets that almost invariably have a dark head, pronotum and tegmina (Fig. 161) from coastal California east to the borders of the Mohave Desert, while those from Owens Valley (Big Pine and Bishop) are also dark. East of the Mohave Desert, individuals in most populations usually with dark heads and pronotum but light colored tegmina. *Song* (Fig. 162, R09-17) unique within the western US: 3 p/c (range 2-4), PR 23-45 at 25°C, 5-10 c/s evenly delivered. Their song can only be confused with certain western US individuals of *G. cohni* from central-southern Arizona and we extensively discuss how to separate the 2 taxa on p. 162. Males singing at 30+°C in Gila Bend, sounded more like

G. armatus than *G. vocalis* because of their increased chirp rate and shortened pulse period when that warm. *G. vocalis* and *G. cohni* are apparently only microsympatric at Ajo, Arizona (S98-72). Song of 3p/c also similar to more eastern *G. fultoni* and *G. vernalis* but CR faster in *G. vocalis* and nowhere sympatric. Distinguished from allopatric *G. veintinueve* by faster chirp rate and almost non-overlapping and faster pulse rate in *G. vocalis*, in addition to different DNA.

FIGURE 158. Holotype male *G. vocalis*, with labels.

FIGURE 159. Holotype female of *G. alogus*, with labels.

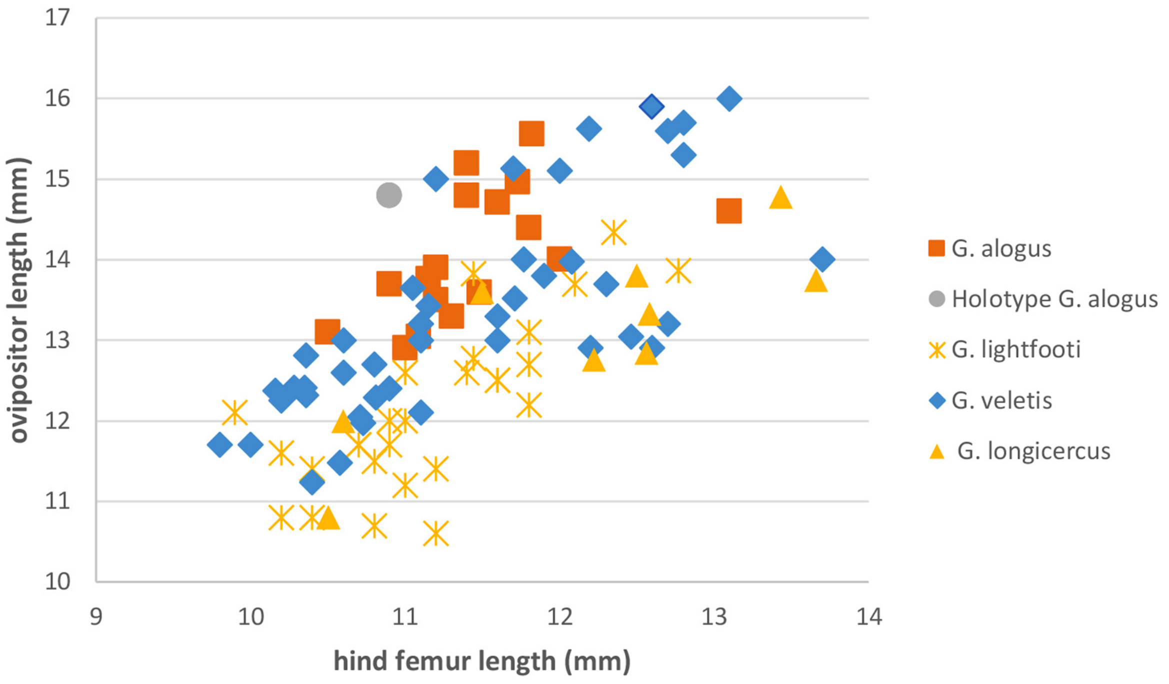

FIGURE 160. Regression of hind femur length vs. ovipositor length for all *Gryllus* species in the Albuquerque, NM, area, which is the type locality of *G. alogus*.

Derivation of name. "voco" is Latin for call, perhaps referring to the distinctive fast chirp rate and loud calling song of this species. Which raises the interesting question of who collected the lectotype and did this person subsequently relate such information to Scudder? In 1896, Scudder developed Parkinson's disease (aka paralysis agitans) and started to prepare for his decline and demise (Mayor 1919), such that we assume that he did not visit Los Angeles in July, 1897 when the lectotype was collected. Scudder retired in 1902 and died in 1911. No further collection information is available at ANSP (J. Weintraub, pers. comm. to DBW, June, 2018).

Geographic range. Fig. 163. Also into northern Baja California Norte, Mexico.

Habitat. Individuals with an impressive temperature tolerance and almost always associated with wet habitats: Salt marshes (Cardiff by the Sea, S80-48, 49) and freshwater marshes (Shoshone, S85-27), irrigated gardens, cultivated ivy, along desert streams and ponds and, rarely, in railroad track rocks (near UC Riverside, S03-40). In San Diego (S97-60), 1 male singing 3m above ground in hole in tree with a long hind winged female near him. In a nearby palm tree, another male singing from 1.5m above ground. At coastal Ballona Wetlands (Los Angeles Co., S92-58) in ice plant on sandy substrate. While easy to approach, singing males can be very difficult to collect because they sing from dense vegetation. Oatmeal trails and checking under available rocks and trash can assist in such situations.

Life cycle and seasonal occurrence. No egg diapause: **Arizona:** S15-111 (Gila Bend). **California:** S92-60 (Shoshone), S95-112 (Big Pine), S03-73 (Barstow). **Nevada:** S90-44 (Cottonwood Cove). Apparently one or two generations/year depending on locality. In coastal California, a definite late winter—early spring species probably with one generation/year as those March, Orange Co. specimens (S05-28 and S05-29) were collected as late instars and no adults were heard after June at these localities.

S. Gershman (pers. comm. to DAG, 18-xi-2014) reports for inland and warmer Riverside, California: "I found a few calling males (of *G. vocalis* at the UCR Botanic Garden—S03-39) even in the winter. Here's what I think is happening. Eggs do not diapause under summer conditions in the lab. Eggs are fairly constant in development time. Adults do not differ much in longevity. But, even in the lab under constant light and temperature, there is a huge range in development times of nymphs. Under lab summer conditions, some *G. vocalis* go from hatching to adult in 2 months. Others take more than 6 months. I assume that this spread causes individuals in nature to emerge as adults at random times throughout the year."

Nevertheless, we have the following late summer collections in southern California: 3 adult males on 7-ix-2001 at Sepulveda Basin Wildlife Refuge in Los Angeles Co.; 1 adult male 11-ix-1977 in Orange in Orange Co.; and 2 adult males on 8-ix-2005 at Afton Canyon in San Bernardino Co. We wonder if certain California localities might have sporadic second-generation adults, as discussed for *G. veletisoides* (see p. 195), which make no genetic contribution to future generations.

In contrast, interior western US *G. vocalis* are often abundant in late summer and fall, e.g. at Zion National Park, Utah, 5-7-ix-2008, 5♂ 11♀. DAG recorded the following data for near Los Lunas, NM (S94-44 and S94-100), in 1994, which suggests 2 generations/year: Collecting in the last 2 weeks of June and the first 2 weeks of July showed adults abundant with some 80 collected. On July 25th, only one adult female seen; on August 8th, 8 adults; August 10th, 12 adults; August 23rd, 20 adults; August 24th, 35 adults; September 6th, 36 adults. In central Arizona, DAG has also observed both spring and fall adults: Agua Fria National Monument, Bloody Basin Road at Agua Fria river, Yavapai Co., 2 males 27-iii-2005, 2 females 1 nymph 16-iv-2010; Wet Beaver Creek Campground, Yavapai Co., 3 males 9 females 8-viii-2007; Oak Creek Canyon, Manzanita Campground, Coconino Co., 2 males 18-viii-2004.

FIGURE 161. Typical color in *G. vocalis,* this male from Shoshone, CA (S03-37).

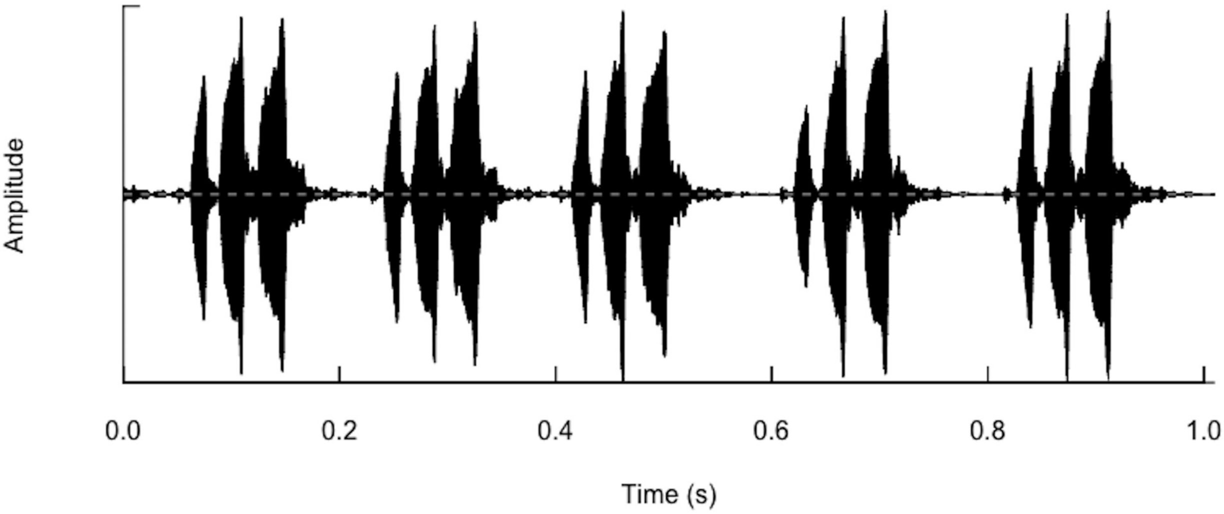

FIGURE 162. Calling song (R09-17) of *G. vocalis* from San Diego Co., CA (S09-18), recorded at 23.5°C.

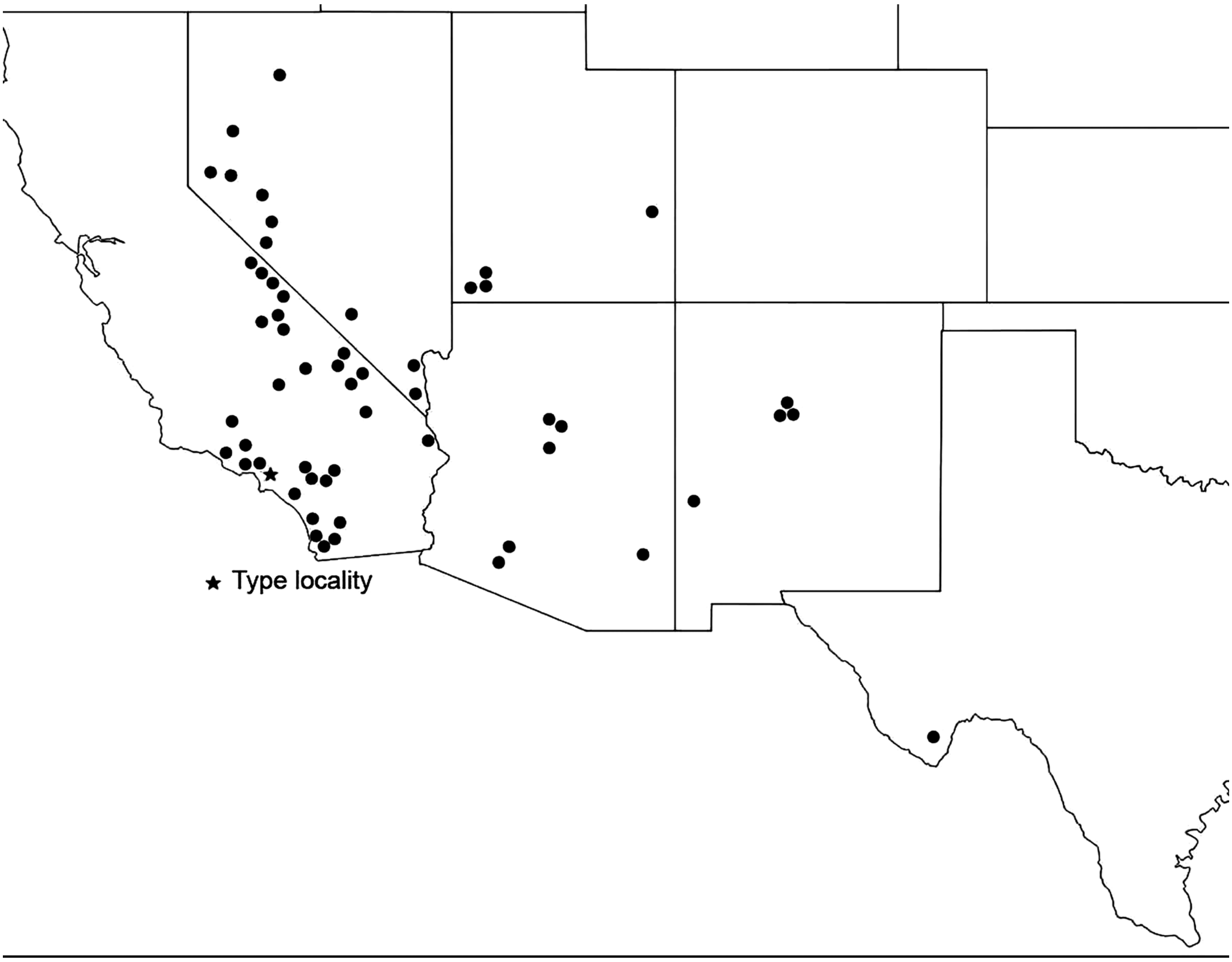

FIGURE 163. Known US distribution of *G. vocalis.*

Variation. **Pronotal hirsuteness**: variable resulting in shiny to dull surfaces within many populations. **Color:** varies as discussed under "Recognition characters." Of 10 males and 3 females from Death Valley (S80-32 & S83-60), all 10 males and 1 female had light colored tegmina with male pronotums ranging from reddish to solid black.

In a large 1994 survey at Las Lunas, NM, DAG found most individuals with dark brown pronotums, although some definitely reddish. **Hind wing length:** All 80 first generation field (i.e. those collected before 8-viii-1994), Las Lunas, NM, individuals, with short hind wings. Second generation field individuals collected there after 8-viii-1994, showed 26 of 58 males and 22 of 53 females with long hind wings. All 7 individuals from Cottonwood Cove (S90-44) had long hind wings. Of 33 males and 19 females from the type locality of *G. alogus* (Albuquerque, NM), all but 2 females had short hind wings. All 16 males and 49 females from along permanent stream at Agua Fria (S13-14) had short hind wings. All 8 males and 9 females from the watered garden area at McDonald's in Gila Bend, Arizona, had long hind wings. One female was dealate. **Song:** males in some populations have long series of chirps (Albuquerque, S85-52) while others (Gila Bend, S15-111) have more broken up songs. **Tegmina length:** variable within and between populations.

Specimens examined. (Total: 333♂ 216♀). **Arizona:** *Coconino Co.,* Sedona, 4500', 15-vi-1990 (S90-49) 1♂; 5-viii-1991 (S91-78) 5♂; 30-vi-1994 (S94-35) 1♂. *Graham Co.,* 4.5 m S Safford, 3180', 10-vi-2012 (S12-20) 1♂. *Maricopa Co.,* Buckeye, 840', 18-ix-2011 (S11-102) 1♂. Gila Bend, garden area at McDonald's, 32° 56' 38.5" -112° 43' 57.5", 712', 1-viii-2009 (S09-103) 3♂; 18-ix-2011 (S11-101) 1♂; 30-vii-2015 (S15-111) 4♂ 10♀. Hwy 85 E Goodyear, 980', 31-vii-1981 (S81-46) 3♂. *Yavapai Co.,* Agua Fria National Monument, stream crossing 4.9 m SE of pavement end, 989m, 34° 15' 27.57" -112° 03' 50.5", 27-iii-2005, 2♂; 16-iv-2010, 2♂; 12-vi-2012 (S12-26) 1♀; 31-v-2013 (S13-14) 16♂ 49♀. Wet Beaver Creek Campground, 8-viii-2007, 3♂ 9♀. Hwy 179 eastern side Sedona, 4000', 31-v-2013 (S13-16) 2♂. **California:** *Inyo Co.,* Big Pine, 10-ix-1995, 4000' (S95-112) 1♂ 1♀. Bishop, 5-vi-1983, 4450' (S83-56) 1♂; 28-viii-2005 (S05-99) 3♂. 9 m N Bishop on Hwy 395, 1430m, 4-vi-1983, (S83-55) 13♂ 1♀; 26-vi-1992 (S92-64) 4♂ 5♀. Death Valley National Park, Furnace Creek, -190', 23-vi-1980 (S80-32) 5♂ 3♀; 5-vi-1983 (S83-60) 5♂; 5-v-2003 (S03-36) 1♀. Little Lake 20 m S Olancha, 3400', 5-v-2003 (S03-33) 8♂ 7♀. Lone Pine, 3650', 5-viii-1978 (S78-117) 1♂, 29-viii-2005 (S05-105) 1♂. Shoshone, 12-iii-1985 (S85-27) 2♂ 6♀; 25-vi-1992 (S92-60) 10♂ 10♀; 5-v-2003 (S03-37) 3♂ 3♀. Hwy 127 0.6 m N Shoshone, 1600', 6-vi-1983 (S83-61) 13♂ 6♀. 3 m W Lone Pine on Whitney Portal Rd, 5-viii-1978 (S78-119) 1♂. *Kern Co.,* Frazier Park, 16-vi-1978, 4600', 1♂. Kern River area across from CSU Bakersfield, 5-viii-1980 (S80-70) 1♂. Mojave, 2757', 5-viii-1988 (S88-70) 2♂. *Los Angeles Co.,* Ballona Wetlands, 24-vi-1992 (S92-58) 6♂ 2♀. CSU Northridge, 810', 8-v-2003, (S03-47) 3♂; early April, 2004 (S04-27) 2♂ 1♀. Malibu near Big Rock and Rockport Rds., 26-vi-1976, 2♂ 1♀; Malibu Canyon Rd. near Pacific Coast Hwy, 1-vii-1976, 1♂. Santa Monica Mts., Cold Creek, 2-v-2002, 3♂ 2♀. Sepulveda Basin Wildlife Refuge, 7-ix-2001, 3♂. Sherman Oaks, 28-vi-1976, 2♂. *Mono Co.,* 9 m N Laws at western base of White Mts., 26-vi-1992, 4500' (S92-63) 5♂ 4♀. *Orange Co.,* Costa Mesa, Talbert Nature Preserve, 15-iii-2005, 20' (S05-28) 1♂. Irvine near UCI Medical Center, 6-iv-1978, 2♂ 2♀. Newport Beach, Backbay Rd., 7-vii-1976, 5♂ 6♀. Orange, 9-iv-1978, 7♂ 1♀; 11-ix-1977, 1♂. Peters Canyon Regional Park, 16-iii-2005, 620' (S05-29) 1♂. *Riverside Co.,* Riverside, mid-July, 2001 (S01-96) 2♂ 1♀. UC Riverside Botanic Garden, 6-v-2003 (S03-39) 6♂. Near UC Riverside, railroad tracks, 6-v-2003 (S03-40) 2♂. Whitewater Canyon ca. 2.5 m N I10, 1-iv-1978, 1300' 2♂ 2♀; 26-v-2009 (S09-21) 1♂. *San Bernardino Co*., Afton Canyon, Mojave River, 1400', 35.03920° -116.38260°, 2-v-2004, 4♂ 4♀; 1-v-2005 (S05-50) 7♂ 4♀; 8-ix-2005, 2♂. Barstow, 2300', 16-viii-1998 (S98-58) 1♂; 28-vi-2003 (S03-73) 1♀. Cherry Valley, 4-iv-1991, 4000' (S91-12) 1♂ 1♀. Rancho Cucamonga, 10-iii-1998 (S98-9B) 1♂. San Bernardino Mts., Mill Creek Ranger Station, 25-vii-1981 2800' (S81-27) 1♂. *San Diego Co.,* Camp Pendleton, 10-vii-1976, 4♂ 1♀. Cardiff by the Sea, Manchester Ave., 27 & 28-vi-1980 (S80-48, 49) 28♂ 15♀; 7-v-2003 (S03-42) 3♂. San Diego, Mission Bay Hilton, 18-vi-1994 (S94-34) 3♂ 1♀; 5-vi-1997 (S97-60) 5♂ 1♀. Hwy 79 0.8 m S Warner Springs, 26-v-2009, 3000' (S09-18) 2♂. Hwy 79 23.8 m E 15, 17-iii-2005, 2820' (S05-32) 1♂ 1♀. Hwy S22 2.1 m W Anza Borrego, 4000' ,17-iii-2005 (S05-34) 2♀. *Ventura Co.,* Ojai Valley Swim and Spa Club, 3-iv-1999, 1000' (S99-5) 2♂. **Nevada:** *Churchill Co.,* Fallon, Churchill Community Hospital, 4000', 16-ix-1998 (S98-95) 5♂ 1♀. Hwy 95 2.5 m N Fallon, 3900', 21-vi-2005 (S05-69) 1♂ 1♀. Hwy 50 Alt. 12.8 m NW Fallon at Bench Rd intersection, 19-iii-1993, 3900' (S93-7) 2♂ raised from 9 collected mid-instars. *Clark Co.,* Cottonwood Cove, 800', 14-vi-1990 (S90-44) 3♂ 4♀. Echo Bay, Lake Mead, 1600', 7-vi-1989 (S89-33) 2♂. *Lyon Co.,* 0.5 m N Fernley on Hwy 50, 4-vi-1983, 1311 m (S83-51) 1♂. *Mineral Co.,* Hwy 95 near Mina, 4600', 3-vii-2005 (S05-68) 2♂. *Nye Co.,* Hwy 95 0.5 m N Beatty, 20-vi-2005 (DL05-16) 1♂ 1♀. Hwy 95 4.5 m N Beatty, 3500', 24-vi-1980 (S80-34) 1♂. **New Mexico:** *Bernalillo Co.,* Albuquerque, 5300', late May, 1984 (S84-25) 6♂; 6-vi-1985 (S85-52) 5♂ 6♀; 18-vii-1985 (S85-95) 4♂; 13-vi-1986 (S86-34) 12♂ 9♀; 23-vi-1993 (S93-59) 7♂ 5♀. Rio Grande Nature Center, June, 2005, D.C. Lightfoot, 1♂; 11-vii-2012, DC Lightfoot, 5♂. *Catron Co*., Village of Reserve, 5770', 3-vii-1994 (S94-50) 4♂ 2♀. *Sierra Co.,* Caballo Reservoir State Park, 7-vi-1986 (S86-38) 3♂ 1♀. *Valencia Co.,* Los Lunas, 1 m S Los Lunas Bridge, 1-vii-1994 (94-44) 2♀; early September, 1994 (S94-100) 6♂ 5♀. **Texas:** *Brewster Co*., Big Bend National Park, Rio Grande Village, 2100', 9-vi-1985 (S85-56) 5♂ 2♀; 5-vi-1991 (S91-43) 3♂ 2♀. **Utah:** *Grand Co.,* Moab, 25-iv-2006 (S06-21) 4♂. *San Juan Co.,* 12 m W Farmington, 19-vi-1987 (S87-80) 1♂. Rest station 12 m S Moab, 21-vi-1987 (S87-59) 4♂ 4♀. *Washington Co.,* Hurricane, 3420', 20-iv-1999 (S99-12) 1♂ 3♀. La Verkin, 3420', 11-ix-2004 (S04-121) 1♂. Springdale, 4000', 9-viii-1991 (S91-94) 2♂. St. George, 3040', 19-v-1995 (S95-39) 6♂ 1♀. Zion National Park, near turnoff to Zion Narrows, 4200', 19-v-1995 (S95-38) 1♂; Zion Museum, 3980', 19-v-2001 (S01-33) 2♀. 1 m W entrance to Zion National Park, 4060', 10-vi-1996 (S96-56) 1♀.

Uncertain placement. **Arizona:** *Pima Co.,* Ajo, plaza area, 520m, 20-viii-1998 (S98-72) 1 male (R98-28). This long hind winged male has 3p/c delivered evenly and probably represents *G. vocalis.* If true, this site is the only documented locality where *G. cohni* and *G. vocalis* occur microsympatrically. Hwy 85 13 m N Ajo, 1255', 30-vii-2015 (S15-110) 1 female. This female has ITS2 DNA that agrees with *G. vocalis* despite the absence of water. No males heard singing in area.

Song records only. **Nevada:** *Pershing Co.,* Rye Patch State Recreational Area, 4050', 27-vi-1992 (S92-67) 3 males heard. **California:** *Ventura Co*., McGrath State Beach, 24-vi-2007.

DNA. ITS2 and multilocus 2016-036, Los Angeles Co., type locality of *G. vocalis*; G3335, Albuquerque, NM, type locality of *G. alogus;* and G3227 from Gila Bend, AZ (S15-111), locality of 'G. arizonensis' all map together (Gray *et al.* 2019) and are all sister species to multilocus *G. cohni* G101, Baja California Sur, type locality (S95-81); G2776 Mazatlán, Mexico (S14-53); and 2016-041 Agua Fria National Monument. We caution that *G. cohni* type locality leg G101, used in both 16S and multilocus sequencing, was removed, in 2003, from a pinned specimen, eight years after collection. In both sequences, the leg mapped consistent with other *G. cohni* and near sister species *G. vocalis* specimens. A singleton male from 7.2 km S Safford (S12-20, G2244) had a unique 16S haplotype but mapped with all other *G. vocalis* for ITS2 gene.

Discussion. We initially divided *G. vocalis* into four groups mainly separated by geographic regions. We discuss our early thinking here so that future researchers can revisit these results and reexamine some of our uncertainties. *G. vocalis* (with a type locality of Los Angeles, California) was defined by Weissman *et al*. (1980) as those dark 3p/c crickets in southern coastal California that extended through the Mohave Desert and into the Owens Valley east of the Sierras. *G. alogus* (aka 'G. #18') (with a type locality of Albuquerque, New Mexico) is a light colored 3p/c cricket of the Rocky Mountains that extends southeast into Big Bend, Texas. 'G. #10' is the light colored 3p/c cricket that occurs in the northern Mojave Desert, Great Basin Desert and Arizona between *G. vocalis* and *G. alogus*. 'G. arizonensis' was restricted to Gila Bend, AZ, where all individuals had long hind wings. While 1 out of 7 Gila Bend males had a broken song, although still with 3p/c, his ITS2 DNA, along with 5 other adults from there, all clustered with *G. vocalis* (Fig. 157). Thus, after failing to find physical or genetic characters to reliably separate these initial groupings, we merged them. On the other hand, we still see a definite dichotomy in that almost all individuals of *G. vocalis* discussed in Weissman *et al.* (1980), are dark colored with probably one generation/year; while almost all specimens to the east, including those from the Mohave Desert, are light colored and some may have two generations/year. We were also able to cross one male of *G. vocalis* from Riverside Co. (S03-39) with a female of 'G. #10' from Inyo Co. (S03-37) and got good egg hatches.

At Furnace Creek in Death Valley National Park, there were good numbers of *G. vocalis* singing in both 1980 and 1983, but only one male was heard in 2003 (Weissman *et al*. 2012). While *G. vocalis,* and sympatric *G. staccato, G. saxatilis,* and *G. armatus*, which we also heard on earlier visits, were all declining there, non-native *Acheta domesticus,* which was rare in the early 1980's, had increased significantly and suggests competitive exclusion.

Tachinid *Ormia ochracea* emerged from adult males collected at S91-78 (Sedona), S92-58 (Ballona Wetlands), S98-95 (Fallon—with 2 of 5 males parasitized), and S13-14 (Agua Fria—2 of 12 males parasitized). Most interestingly, from a mid-instar nymph collected under a cow pie on 19-iii-1993 (S93-7 at 20.6 km NW Fallon), a dead adult tachinid *Exoristoides johnsoni* was present in the rearing container on 6-v-1993. It is unknown when the larvae emerged from the cricket but this may represent a mechanism whereby tachinids can pass the winter at localities that experience freezing winter temperatures.

Gershman (2009, 2010) discussed aspects of mating in *G. vocalis.* Sandford (1987) studied aggression with crickets from Oklahoma: his '*G. alogus*' is uncertain, but not *G. vocalis* or *G. alogus* as understood here (because out of range) while his '*G. integer*' is probably *G. texensis*.

Gryllus cohni Weissman

Irregular-Trilling Field Cricket
Figs 155–157, 164–169, Table 1

1980 *Gryllus cohni* Weissman, Transactions of the American Entomological Society 106: 339. Holotype male (Fig. 164): Mexico, Baja California Sur, 0.5 km W Hwy 1 km 8 sign W La Paz, 16-vii-1978. S78-59, R78-90. Type in CAS, Entomology type # 13220.
'Gryllus irregularis', G. #20 of DBW notebooks.
Arizona stutter triller of Sakaguchi & Gray (2011).

FIGURE 164. Holotype male of *G. cohni*, with labels.

Distribution. Known from south-central Arizona and Mexican states of Sonora, Sinaloa, Nayarit, Jalisco and the Cape Area of Baja California Sur.

Recognition characters and song. Small to medium sized, small headed, usually long hind winged, pronotum moderately hirsute and slightly dull (Figs 164, 165). *Song* variable, which can make for difficult identification, but usually an irregular "trill" (Fig. 166, 2003-295, R15-289) with groupings of 1 to 13 pulses and a PR between 22 and 41 at 25°C. Some males (Fig. 167, R14-36) with much longer, uninterrupted trills. Some individuals, mainly from central Arizona, with sections where their pulses clustered in threes (see Fig. 167, recording 2006-260), resembling the song of morphologically indistinguishable sister species *G. vocalis*. Nevertheless, songs of *G. cohni* can be distinguished from those of *G. vocalis* since the latter produces long uninterrupted bouts of 3 pulse chirps, with little or no variation in pulse number, and pulses never grouped into trills as seen in other sections of recording 2006-260. The two-sister species are also usually separated ecologically with *G. vocalis* around moist environs and *G. cohni* in drier, more open desert situations. Both taxa were found microsympatric at only one location—a semi-garden area in Ajo, AZ (S98-72), although several subsequent visits to both Ajo and Why failed to yield more specimens of either. Additionally, *G. vocalis* usually with short hind wings and a shiny pronotum and frequently at high densities in riparian corridors (see under *G. vocalis)* while *G. cohni* rarely common anywhere. *G. cohni* distinguished from other western US trilling *Gryllus* species as follows: From Arizona *G. regularis*, which is a larger, broader cricket with a shiny pronotum and short hind wings whose pulses are uniformly spaced and not grouped; females somewhat separable by ovipositor length relative to pronotal width (Fig. 168). From Arizona *G. staccato*, a larger cricket whose calling song can vary from an irregular trill with a faster pulse rate of 70-110, variable pulses/chirp, and different DNA. From Texas and eastward medium to large *G. rubens*, which has long series (> one second) of regularly-spaced trills delivered with a PR less than 60. From larger eastern New Mexico and eastward *G. texensis* that has regularly-spaced trills delivered with a PR >70. Rare western *G. integer* trill but with PR >70. Lastly, at very warm (>35°C) nighttime summer temperatures (easily reached in Ajo and Why, AZ) *G. cohni* males, when mainly singing with 3-4 p/c, can sound like *G. armatus.* They can be easily separated by recordings made closer to 25°C with differences in pulse rate and chirp rate diagnostic. Where they occur with *G. multipulsator* and *G. staccato* (e.g. near Mazatlán, S14-53), females too similar to separate except by DNA.

FIGURE 165. Female *G. cohni* from Pima Co, AZ (S98-71).

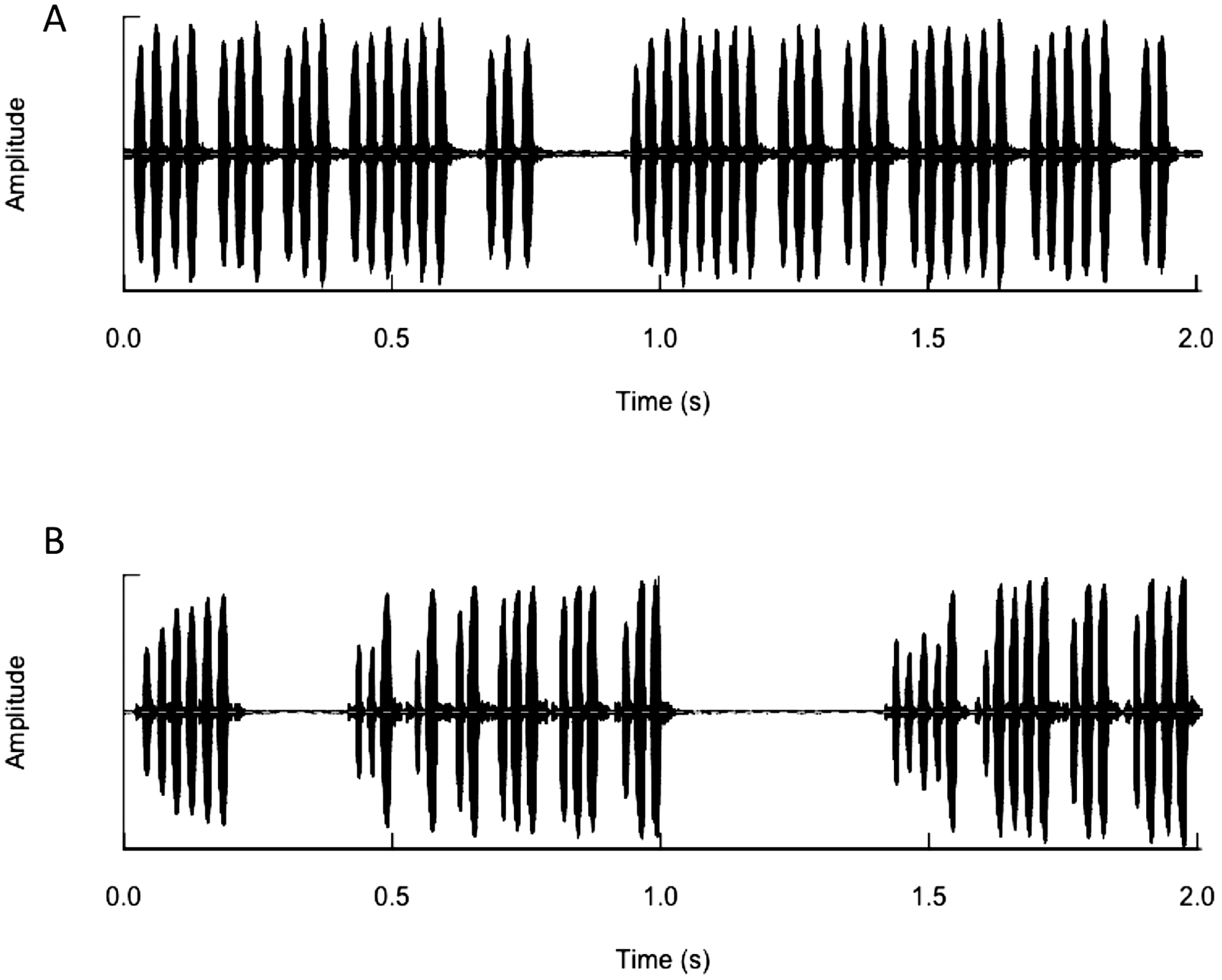

FIGURE 166. 'Typical' songs of *G. cohni* illustrating the extreme variability in pulse numbers both within and among individuals. (A) 2003-295 Cordes Junction, Yavapai Co., AZ, at 22.0°C. (B) R15-289 Pima Co., AZ (S15-108), at 25.3°C.

Specimens examined. (Total: 64♂ 27♀). **MEXICO.** *Baja California Sur*, 0.5 km W Hwy 1 km 8 sign W La Paz, 16-vii-1978 (S78-59) 3♂ (including holotype) 7♀; 31-xii-1978 (S79-16) 2♂; 21-iv-1979 (S79-84) 1♂; 25-viii-1995 (S95-81) 2♂. First wash along road to Miraflores, off Hwy 1, 24-iv-1979 (S79-95) 1♂. *Jalisco,* Club Med Playa Blanca, Rincon de Careyes ~55 road km N Manzanillo, 29-xii-1984 (S85-1) 13♂ 4♀. Puerto Vallarta, 29-iii-1983 (S83-13) 2♂. *Nayarit,* Hwy 200 1.6 km NE turnoff for Alta Vista, km post 78.3, 26-vi-2011, 320', 21° 07' 57.4" -105° 10' 01.3" (S11-50) 1♂. *Sinaloa*, Mazatlán, 11-viii-1999 (S99-87) 1♂. ~20 km S Mazatlán, 23-vii-2014, 110', 23° 11' 49.4" -106° 11' 37.7" (S14-53) 6♂ 1♀. Hwy 40 2 km NE Hwy 15, 11-viii-1999 (S99-86) 2♂. *Sonora,* Alamos, 18-vii-2006, 390m, 27.0257338° -108.9403527° (DAG 2006-215) 2♂. Hermosillo, 24-vii-1990 (S90-77) 1♂. San Carlos Bay, Club Med, 22-29-iii-1986 (S86-15) 6♂. 12 km W San Carlos, 25-vii-1990 (S90-78) 2♂. **USA**. **Arizona**. *Pima Co*., Ajo, north end town, 520m, 20-viii-1998 (S98-74) 6♂. Ajo, plaza area, 520m, 20-viii-1998 (S98-72) 2♂. Sells, 29-vii-2015 (S15-107) 1♂. Why, 530m, 20-viii-1998 (S98-71) 1♂ 6♀. Hwy 86 4.4 m NW Sells, 31° 57' 25.4" -111° 56' 46.4" 2276', 29-vii-2015 (S15-108) 1♂. *Yavapai Co.,* Agua Fria National Monument, Perry Mesa near intersection Bloody Basin Rd and Pueblo La Plata Rd, 3657', 34° 14' 8.56" -112° 01' 45.34", 16-viii-2006, DAG 2006-243, 4♂, 1 last instar male and 1 last instar female; 11-ix-2007, 1♂ 1♀; 11-ix-2012 6♀. Forest Service Road 525 west of Sedona, 4507', 16-viii-2004, 34.91855° -111.91090° 2♀, I17 near Cordes Junction, gas station, 6-viii-2003, 34° 19' 41.6" -112° 07' 8.3" (DAG 2003-294, 2003-295) 3♂.

Song records only. **MEXICO.** *Sinaloa,* Concordia, 320', 11-viii-1999 (S99-85) 2♂. El Fuerte, 23-vii-2006, 800', 26.42099° -108.61774° (2006-224) 1♂.

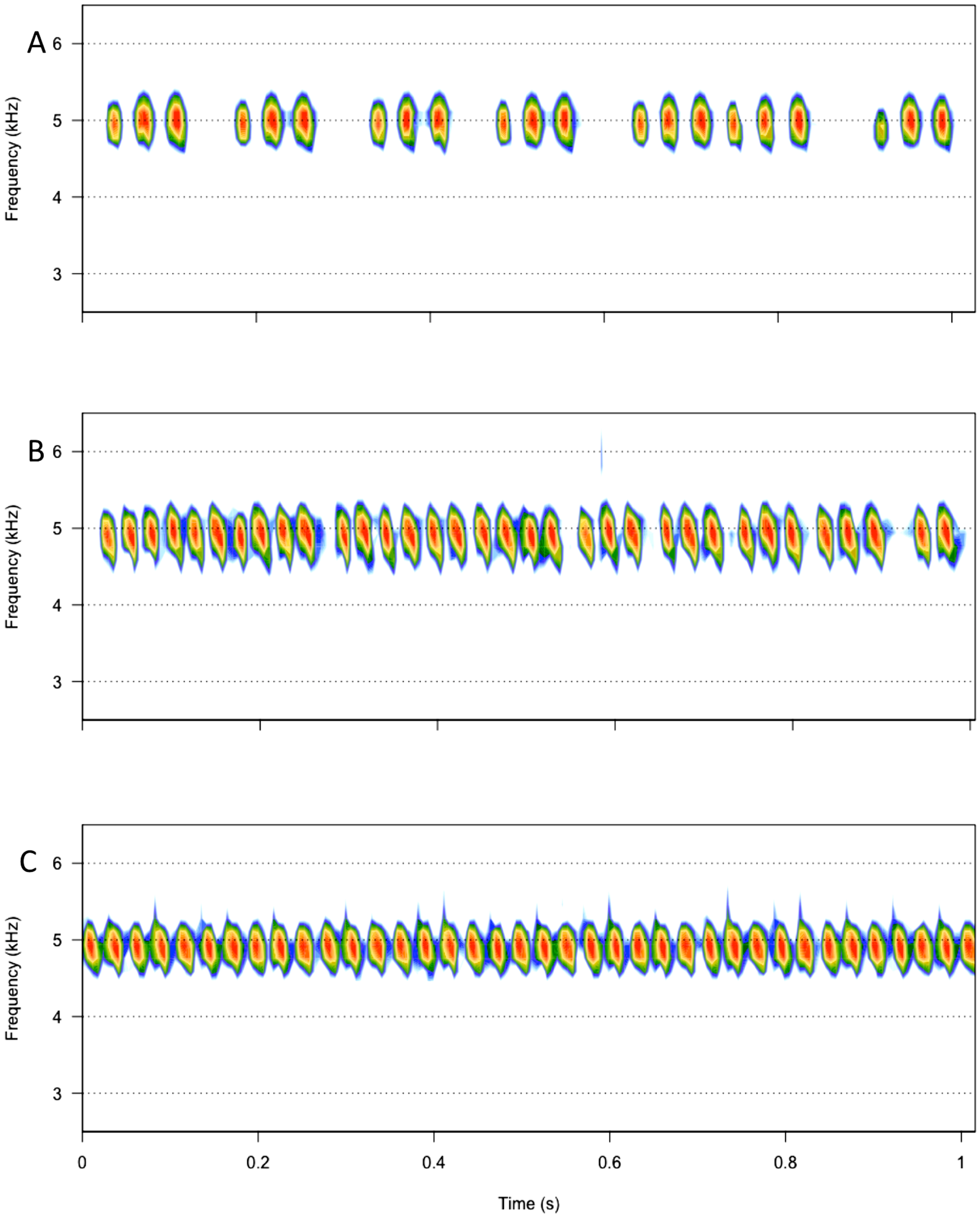

FIGURE 167. One second spectrograms of *G. cohni* showing atypical calling songs. (A) Agua Fria, AZ (2006-260), showing pulses grouped into 3s, at 22.8°C. (B) near Mazatlán, Mexico (R14-30, S14-53), showing an irregular trilling pattern, at 26°C. (C) near Mazatlán, Mexico (R14-36, S14-53), showing an almost uninterrupted trill, at 25.7°C.

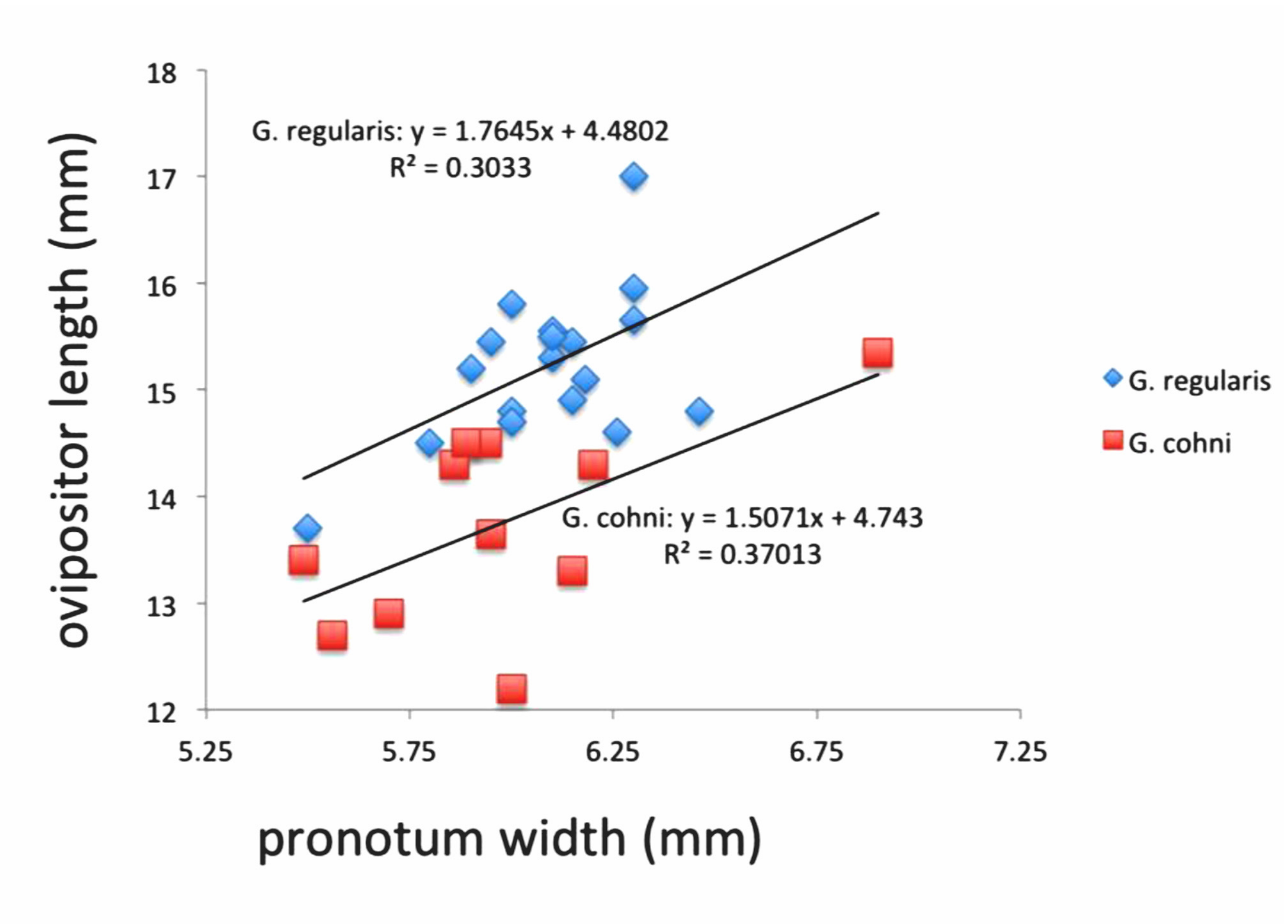

FIGURE 168. In sympatry in central Arizona, female *G. cohni* and *G. regularis* differ in relative ovipositor length, however not diagnostically so. All females are from Agua Fria National Monument, with species ID via song of lab reared sons.

Uncertain placement. **Arizona:** *Pima Co.,* Ajo, plaza area, 520m, 20-viii-1998 (S98-72) 1♂ (R98-28). This long hind winged male has 3p/c delivered evenly and probably represents *G. vocalis.* If true, this site would represent the only locality where *G. cohni* and *G. vocalis* occur microsympatrically. Hwy 86 4.4 m NW Sells, 31° 57' 25.4" -111° 56' 46.4", 12276', 29-vii-2015 (S15-108) 1♂ (R15-289, G3217). This long hind winged specimen, the only male heard here, from open Sonora Desert, sang with 3 (5) p/c. His 16S DNA mapped in the tree where *G. vocalis* and *G. cohni* are intermixed. His ITS2 gene mapped (see Fig. 157) with other *G. cohni* and separate from *G. vocalis.* Such a dry habitat is usually associated with *G. cohni* although 3 males of the more mesic associated, always long hind winged *G. multipulsator* were also collected there. Perhaps these individuals all flew here after a localized monsoon rain?

Derivation of name. This cricket was originally named in appreciation of Theodore J. Cohn.

Geographic range. Fig. 169.

Habitat. From 520-1152m. The type locality is a wooded, thickly vegetated area subject to periodic flooding, where adult males did little singing and were most easily collected by an oatmeal trail. Found in both dry (open Sonoran Desert) and wet areas of human habitation, sometimes around lawns (San Carlos Bay, S86-15), at base of planted palm trees, irrigated garden areas, etc. Also at gas stations (Mazatlán, S99-87), cracks in structures and sidewalks and in deep, dry soil cracks (the latter away from human habitation at Agua Fria).

Life cycle and seasonal occurrence. Egg diapause absent (Agua Fria). Unsure if 1 or 2 generations/year and may vary between years depending on rainfall. Adults known from late March (San Carlos Bay, S86-15) through August. Nymphs collected at Agua Fria 16-viii-2006 (2006-257 & 2006-260). We have collected the Ajo-Why area on other occasions (16-v-1999 and 17-ix-2011) besides those listed under "Specimens examined" and not heard any *G. cohni* singing. Likewise collecting the Yavapai Co. localities of Agua Fria and Cordes Junction on 18-ix-2011, 12-vi-2012, 21-viii-2012, and 31-v-2013 yielded no singing males. There appears to be some unexamined interaction between monsoon rainfall and which *Gryllus* species are present, and when, in many areas of south-central

Arizona. Despite collecting 6 *G. cohni* males, flushed with water from a grassy area, none were heard singing at 20 km S Mazatlán (S14-53) when we arrived at 11:20 PM with temperatures at 31°C.

One question stands out: how long are *Gryllus* eggs viable in the soil, especially during periods of below average summer monsoon and winter rainfall?

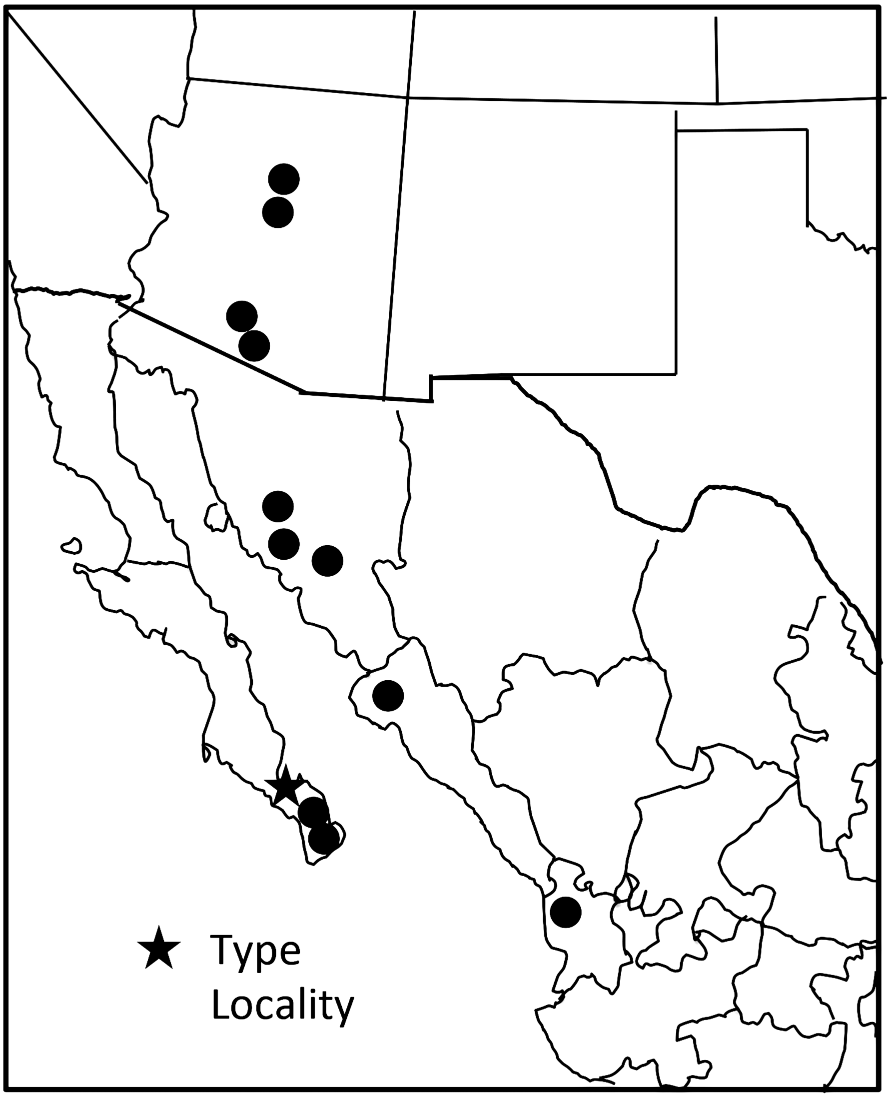

FIGURE 169. Known distribution of *G. cohni.*

Variation. **Head width:** All Mexican specimens from Playa Blanca (S85-1) and Puerto Vallarta (S83-13) with head narrower than pronotum, a condition infrequently seen in US specimens. **Hind wing length:** Of 39 individuals of *G. cohni* from Mexico, 37 have long hind wings and 2 males are dealate. In southern Arizona (Ajo and Why), all 13 collected individuals were long winged. In contrast, of the 7♂ and 8♀ from the Agua Fria National Monument area in north/central Arizona, 14 had short hind wings. **Body size:** Males from Agua Fria as small as 15.8 mm body length. In our small sample from Baja California Sur, Mexico, (Weissman *et al.* 1980), females were consistently larger than males, a characteristic also seen in those individuals from the Agua Fria area. **Song:** Number of p/c characteristically variable. Of 18 recorded males, 15 had an irregular trill with the exceptions being the single Nayarit (S11-50) specimen and 2 of 6 males from Mazatlán (S14-53). The Nayarit male was recorded twice: he had a short introductory trill and then groupings of 3-6 p/c at 27°C on 5-vii-2011, and no introductory trill with 3 or 4 p/c at 26° on 9-vii -2011. His DNA (G2074) mapped with that of other *G. cohni.* Of the 6 Mazatlán males (S14-53), 4 had an irregular trilling pattern (Fig. 167, R14-30) and 2 trilled more regularly (Fig. 167, R14-36). In southern Arizona (Ajo and Why), all 6 recorded males produced an irregular trill. Songs from Agua Fria were different from the general pattern seen in Mexico and southern Arizona in that some had significant stretches of 3p/c (Fig. 155, R15-289) in addition to periods of irregular trills. Our documentation (Weissman *et al.* 1980, Fig 10a, b) in Baja California, where calling songs at higher temperatures tended to go from discrete bursts to longer trains of trills, has not been seen in populations elsewhere.

DNA. Multilocus G101, Baja California, type locality (S95-81); G2776 Mazatlán, Mexico (S14-53); and 2016-041 Agua Fria National Monument are all sisters to 2016-036, Los Angeles Co., type locality of *G. vocalis*; G3335, Albuquerque, NM, type locality of *G. alogus;* and G3227 from Gila Bend, AZ (S15-111), locality of 'G. arizonensis' (Gray *et al.* 2019) (and see under *G. vocalis* for discussion of *G. alogus* and *'*G. arizonensis'). We caution that type locality leg G101, used in both 16S and multilocus sequencing, was removed in 2003 from a pinned specimen, eight years after collection. In both sequences, the leg mapped consistent with other *G. cohni* and sister species *G. vocalis* specimens.

Discussion. Of the US species discussed in this paper, *G. cohni* is the only one whose type locality is in Mexico. Because of its disjunct distribution (Fig. 169), we were initially uncertain if we were dealing with one taxon. But we were unable to separate, morphologically and song-wise, those from the Cape Area of Baja California Sur from those on the adjacent Mexican mainland and those from Arizona. Most importantly, 3 geographically separated samples of *G. cohni* (from Baja Sur, Sinaloa, and Arizona) map together and are well supported for both ITS2 (Fig. 157, p. 155) and in the multilocus genetic analysis (Gray *et al.* 2019). Also, 3 geographically separated, and well supported samples of *G. vocalis* (from Los Angeles, Albuquerque, and Arizona) map together (Fig. 157) and separate from sister species *G. cohni.*

We wonder if some variation on this possible historic narrative might have occurred in central Arizona to explain the complicated situation re hind wing length and songs containing 3 pulses/chirp: long hind winged (and probably able to fly), irregular trilling *G. cohni* typically is a cricket of dry habitats (before the summer monsoon rains come) and would not normally occur microsympatrically with usually short hind winged, 3p/c *G. vocalis,* since the latter prefers riparian areas in the Southwest. The spread of human habitation and the formation of cities like Ajo and Why, AZ, subsequently brought these two environments into proximity, which brought these two-sister species together and possibly facilitated hybridization and introgression. Thus, we find around central Arizona, short hind winged crickets that sing like *G. cohni* but also have periods of 3p/c in their calling songs as seen in *G. vocalis*. Consistent with this narrative is the fact that no *G. vocalis* are known along northern Sea of Cortez mainland Mexico and, hence, the widespread absence there of *G. cohni* with 3p/c song-periods. We have no data to support this scenario, but it is in principle easily testable using modern genomics.

Likewise, in this general Arizona geographical area, we find (normally rare elsewhere) long hind winged *G. vocalis* at Cottonwood Cove, NV (S81-31); Goodyear (S81-46), Buckeye (S11-102), and Gila Bend (S09-103), AZ; and Havasu Lake, CA (S83-62), although none have periods of trilling, regular or irregular song.

Given the variation in song produced by males in the same population, this species would be ideal for studies on female song preferences.

One male each from S86-15 (San Carlos Bay) and 2006-243 (Agua Fria) parasitized by tachinid *Ormia ochracea.* At the first locality, all 3 *Gryllus* species there (*multipulsator, staccato,* and *cohni*) were parasitized by this tachinid species.

The Lineaticeps Group

G. lineaticeps Stål, *G. personatus* Uhler, and *G. staccato* Weissman & Gray, n. sp.

Sister species of chirping field crickets with typically 6-9 pulses per chirp (Figs 170, 171). Separated from each other by geography (Fig. 172), song (Fig. 173), and DNA (Fig. 174).

Gryllus lineaticeps **Stål**
Variable Field Cricket
Figs 170–178, Table 1

1860 *Gryllus lineaticeps* Stål, 1861 [1860]. Kongliga Svenska fregatten Eugenies Resa omkring jorden under befäl af C.A. Virgin åren 1851–1853. Zoologi 1. p. 314.

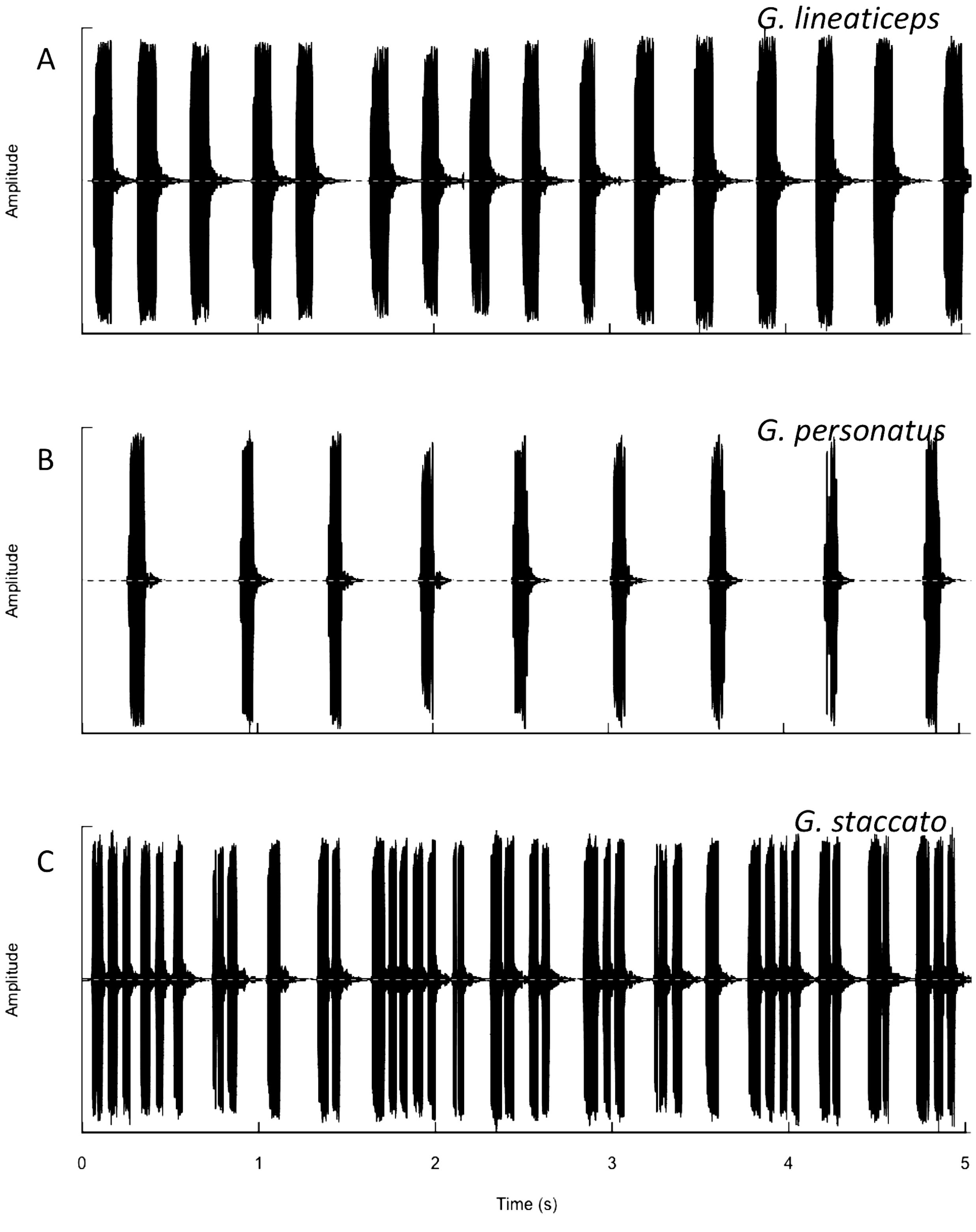

FIGURE 170. Five second waveforms of typical calling songs of (A) *G. lineaticeps*, (B) *G. personatus*, and (C) *G. staccato*. (A) *G. lineaticeps*: (R11-15) Mendocino Co., CA (S11-22), recorded at 24°C; (B) *G. personatus*: (R07-74) from Alpine, TX (S07-41), recorded at 25°C; (C) *G. staccato* (R15-291) from Gila Bend, AZ (S15-111), recorded at 25.1°C.

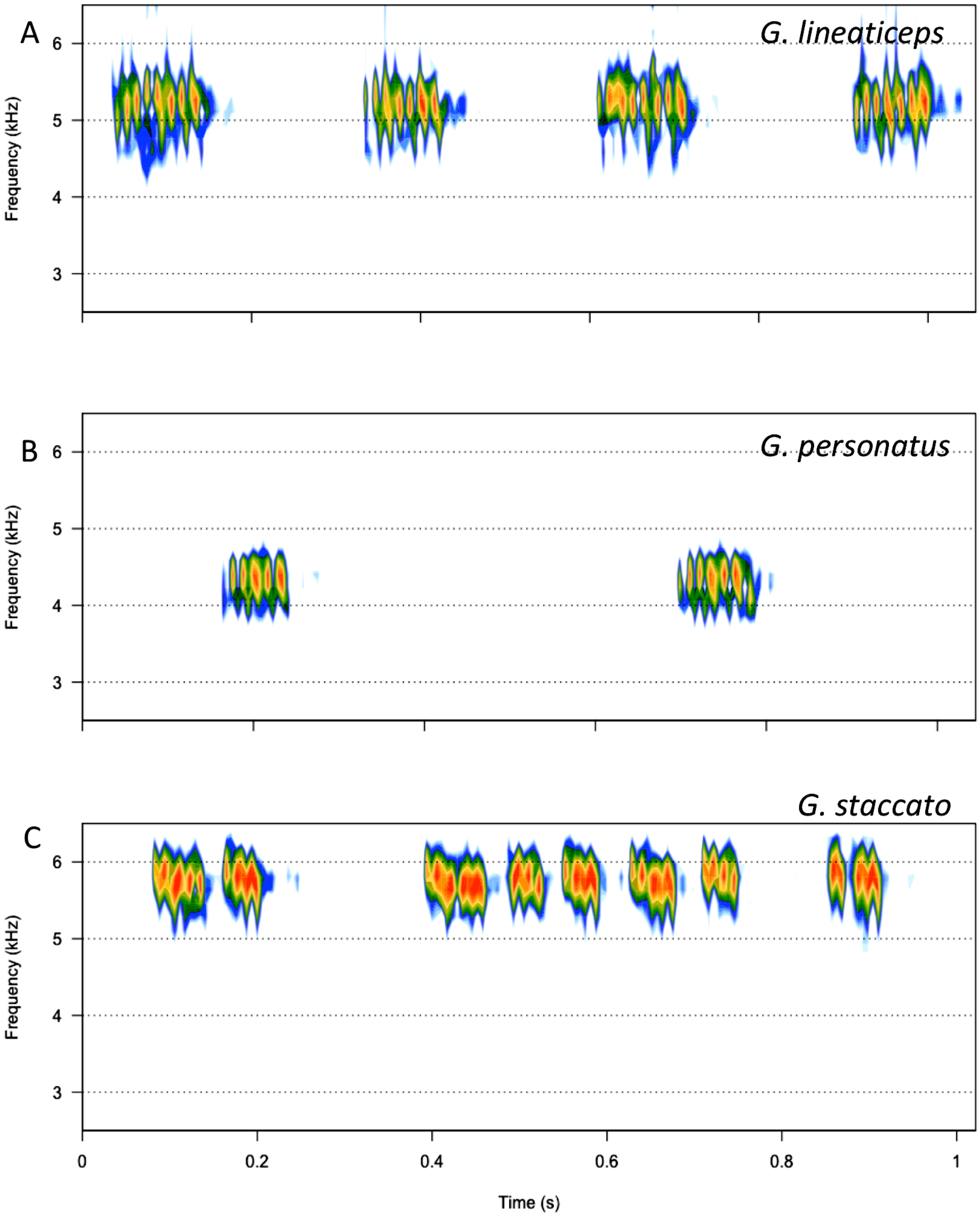

FIGURE 171. One second spectrograms of typical calling songs of (A) *G. lineaticeps*, (B) *G. personatus*, and (C) *G. staccato*, same males as in Fig. 170.

Type locality: California, San Francisco. Type female lost according to Alexander (1957). Neotype male (Fig. 175) designated by Weissman *et al*. (1980): "California, Santa Clara Co., Palo Alto, Stanford University campus, Lake Lagunita, 4-vii-1979. David B. Weissman," CAS Entomology type #13221. Body length 23.7 mm; right tegmen removed, file with 136 teeth, 3.9 mm long.

1977 'Gryllus III'. Weissman & Rentz (1977a).
1980 *Gryllus lineaticeps* Weissman *et a*l. (1980).
1981 'Gryllus III'. Rentz & Weissman (1981).
'Gryllus #3' of DBW notebooks.

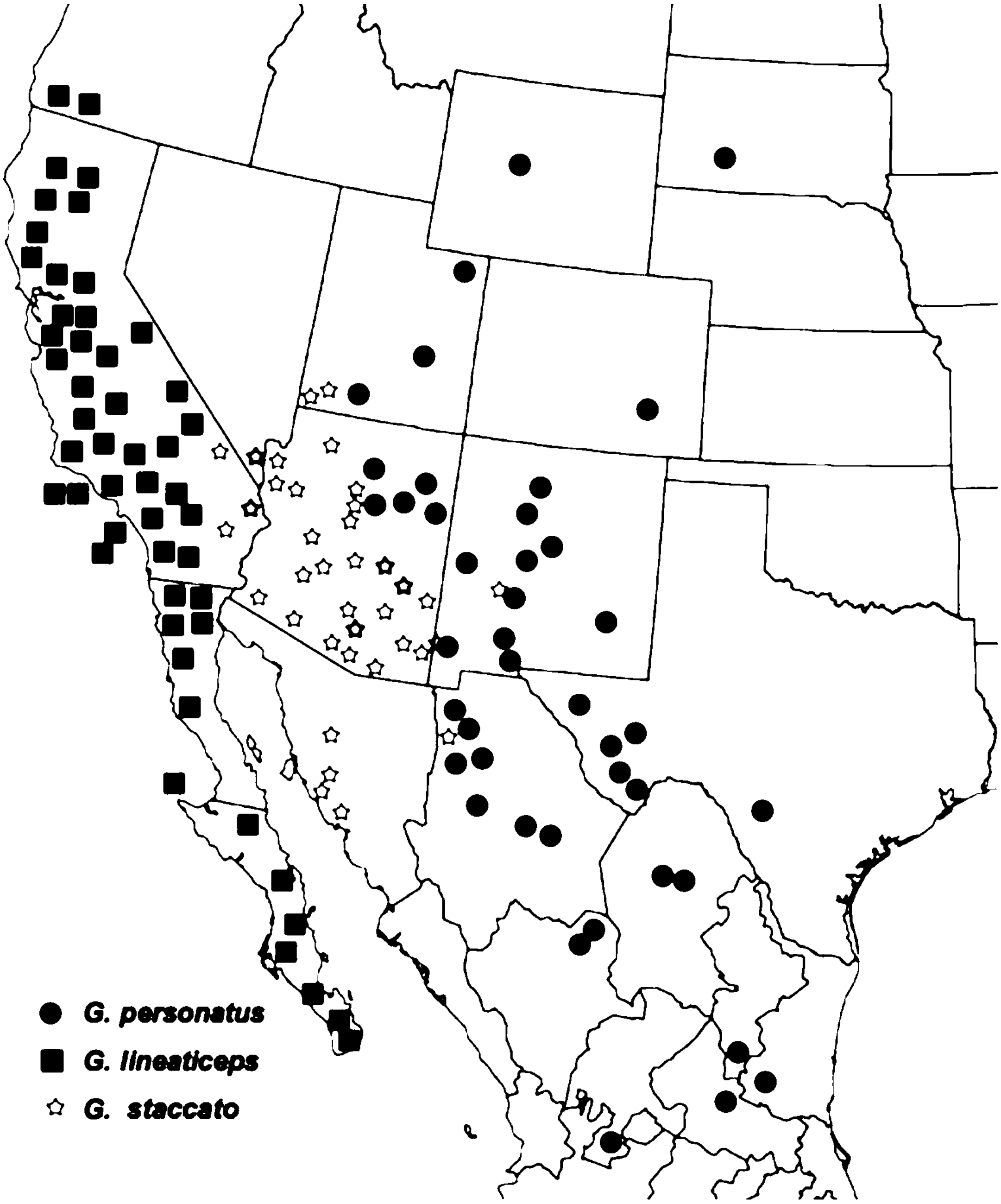

FIGURE 172. Known distribution (from Gray *et al.* 2016b) showing, basically, allopatric localities of the three Lineaticeps Group taxa.

Distribution. Restricted to southwestern Oregon, California (including all of the 8 California Channel Islands except San Miguel), and most of Baja California, Mexico.

Recognition characters and song. Medium to very large crickets (see Table 1, p. 18), widespread and ecologically diverse but prefer grassland habitats. *Song* (Fig. 176) loud, unique within its range: fast chirper, at 25°C, typically with 6 to 9 (range 5-11) pulses, frequently 150 to 250 chirps/min, pulse rate usually between 40-65 (range 32 to 83), dominant frequency 5 kHz. Two generations/year. Color variable, from red (Fig. 177) to black, within a population and between generations: first generation winter and spring adults usually darker (many black) than summer adults (many tan to reddish brown). Among western US taxa with a similar song, differs from sometimes sympatric *G. multipulsator* which has more pulses/chirp, slower chirp rate, dull (hirsute) pronotum and different microhabitat. Differs from allopatric sister species *G. personatus* which has a pale area around eye, longer ovipositor, slower chirp rate and essentially complete separation in dominant frequency (Fig. 173 and Gray *et al.* 2016b). Differs from allopatric sister species *G. staccato* which has variable pulses/chirp and faster pulse rate (Fig. 173 and Gray *et al.* 2016b).

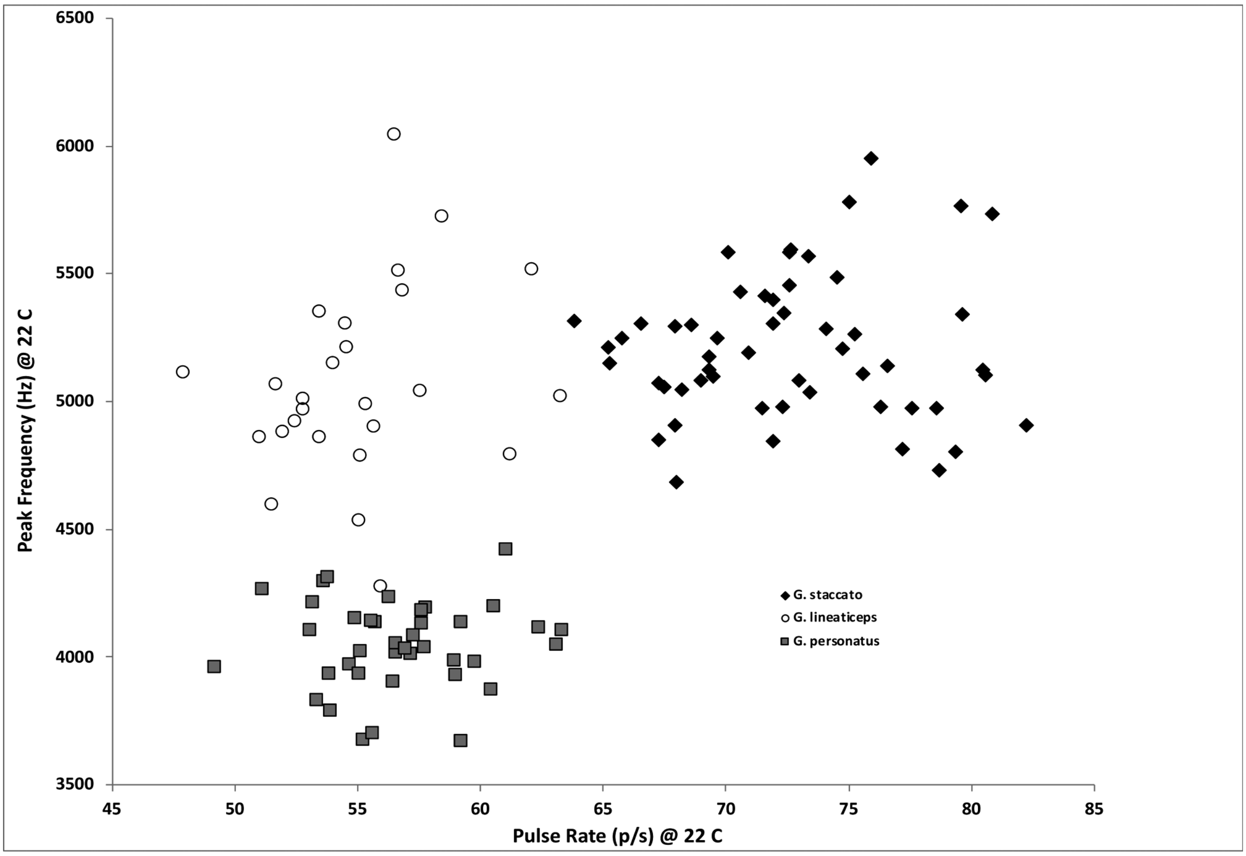

FIGURE 173. Separation of species within the Lineaticeps Group by song (from Gray *et al.* 2016b). Most points represent lab-reared individuals; therefore, it is possible that field-caught individuals (see Table 1, p. 18) would show somewhat less clear separation given known effects of developmental temperature on song in field crickets (Walker 2000).

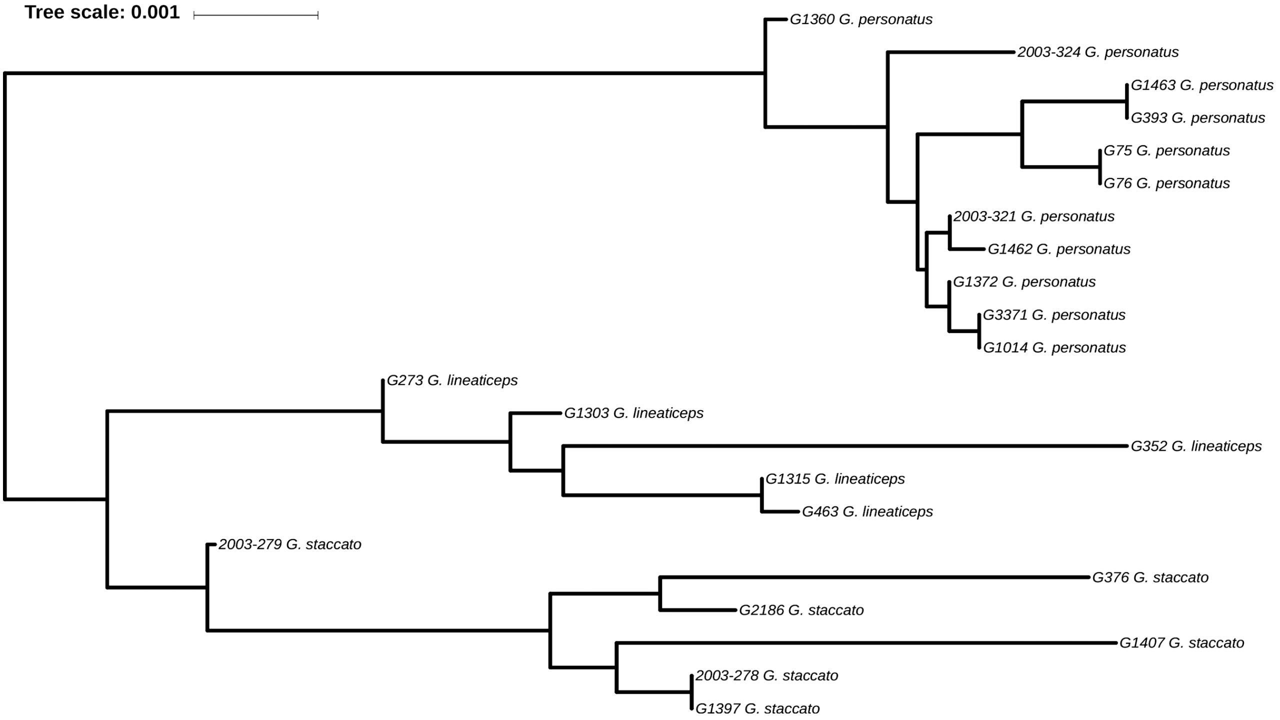

FIGURE 174. ITS2 gene tree. Collection stop numbers for ***G. lineaticeps*** samples: S00-15, Guadalupe Island, Mexico (G273); S04-64 (G352); S05-39 (G463); S09-28 (G1303); S09-37 (G1315). Collection stop numbers for ***G. personatus*** samples: S99-84, Durango, Mexico (G393); S03-127, from Coahuila, Mexico (G75, G76); S07-41 (G1014); S09-58 (G1372); S09-151, from near Janos, Mexico (G1462, G1463); S16-6 (G3371). Collection stop numbers for ***G. staccato*** samples: S04-121 (G376); S09-54 (G1397); S09-103 (G1407); S11-102 (G2186). See also Gray *et al.* (2016b).

FIGURE 175. Neotype male of *G. lineaticeps*, with labels.

Derivation of name. "line" = line; "ceps" = head or "lines on the head," indicating that perhaps the lost holotype appeared as such. Second generation specimens (including the neotype, which is from Palo Alto, CA, or some 50 km south of the type locality), especially those light-colored individuals from hot, dry locales, frequently have dark, linear stripes on the head. This condition is also commonly found in the sister taxa *G. personatus* and *G. staccato* but is not restricted to these *Gryllus* species, or even to the genus *Gryllus* in the Gryllidae.

Geographic range. See Fig. 178. Generally west of the Sierra Nevada but individuals east of the Sierra Nevada collected at Mono Lake (S78-125), Lone Pine (S78-117) and in the Mohave Desert at Barstow (S98-58 & S98-77) and the town of Mohave (S05-117). Collected on all of the 8 California Channel Islands except for San Miguel.

Habitat. Easily the most common and loudest, low elevation, California summer grassland field cricket west of the Sierra Nevada. In winter and spring, late instars and newly molted adults of the first generation found under rocks and boards. In summer, males of the second generation sing from substrate cracks in grasslands, chaparral, coastal sage, oak-woodlands and around human habitation. Usually found below 1000 m elevation, but found over 2400 m in Mexico (Weissman *et al*. 1980).

Life cycle and seasonal occurrence. No egg diapause (checked from Santa Clara Co., CA, S92-44) in either generation. Two generations/year (as least as far north as Santa Clara Co.). Overwinters as late instars with first adults in warmer parts of southern California singing during daytime as early as December. On 17-xii-1996, a few newly molted adult males and females, plus hundreds of late instars, found at California, Monterey Co., Hwy 198 at mile post 15.0 (S96-111), 411-457 m elevation. Second generation numbers larger with adult males heard starting in early summer. Unknown if a second generation occurs in northern California and southwestern Oregon localities.

Variation. **Color** (see Fig. 177): body, pronotum, head, wings, and hind femur usually variable between black to red within individuals at one locality. First generation individuals usually dark. Second generation, especially from dry, hot areas like the Central Valley, usually more reddish. Beach specimens generally light colored all over. **Pulses/chirp.** One male (San Clemente Island, R18-16, S18-24) with 11 pulses/chirp, more than seen elsewhere for this taxon. **Wing length:** Variable. Of 80 males, 16 had long hind wings. Of 60 females, 18 had long hind wings including all 10 females collected from California, Fresno Co., Coalinga (S98-86), 29-vii-1986.

Specimens of note (mostly from edges of distribution*)*. Complete locality list not given because *G. lineaticeps* is common and widely distributed wherever it occurs.—**CALIFORNIA:** *El Dorado Co.,* Finnon Reservoir, 29-iii-2005, 2340' (S05-39). *Fresno Co.,* Coalinga, 29-viii-1998 (S98-86); Jacalitos Canyon, 29-viii-1998 (S98-82 & 98-83). *Inyo Co.,* Lone Pine, 5-viii-1978 (S78-117). *Kern Co.,* Mohave, 1-ix-2005 (S05-117); Tehachapi, 28-v-2009, 3320' (S09-28). *Mendocino Co.,* 4 m E Longvale, 2-viii-1980, 1000' (S80-59). *Mono Co.,* Mono Lake, 7-viii-1978 (S78-125). *San Bernardino Co*., Barstow, 16-viii-1998, 2420' (S98-58) & 21-viii-1998 (S98-77). *San Joaquin Co.,* Tracy, 52', 10-ix-2016, RE Espinoza. *San Mateo Co.,* Stanford University's Jasper Ridge Biological Preserve, 2-v-1992 (S92-44). *Shasta Co.,* Shasta Dam, 4-viii-1980 (S80-66). *Yolo Co.,* I5 near intersection Hwy 505, 19-viii-2006, 130' (S06-77). **OREGON:** *Jackson Co.,* Emigrant Lake Recreational Area, 27-vii-1992, 1800' (S92-82). Hwy 66 ~12 m E I5, 2900', 27-vii-1992. *Josephine Co.,* Hugo, 25-vi-1978, D.C. Lightfoot.

DNA. Multilocus 2016-033 (Tracy, CA). Two sister species (Gray *et al.* 2019) are *G. personatus* (multilocus G1357 from Otero Co., Colorado) and *G. staccato* (multilocus 2016-034 from Yavapai Co., AZ). 16S and ITS2 (Fig. 174) gene trees yields nice separation from sister species *G. personatus* and *G. staccato*. In our early work, CO1 gave less clear separation between species, but also showed highly suspect signs of pseudogene amplification.

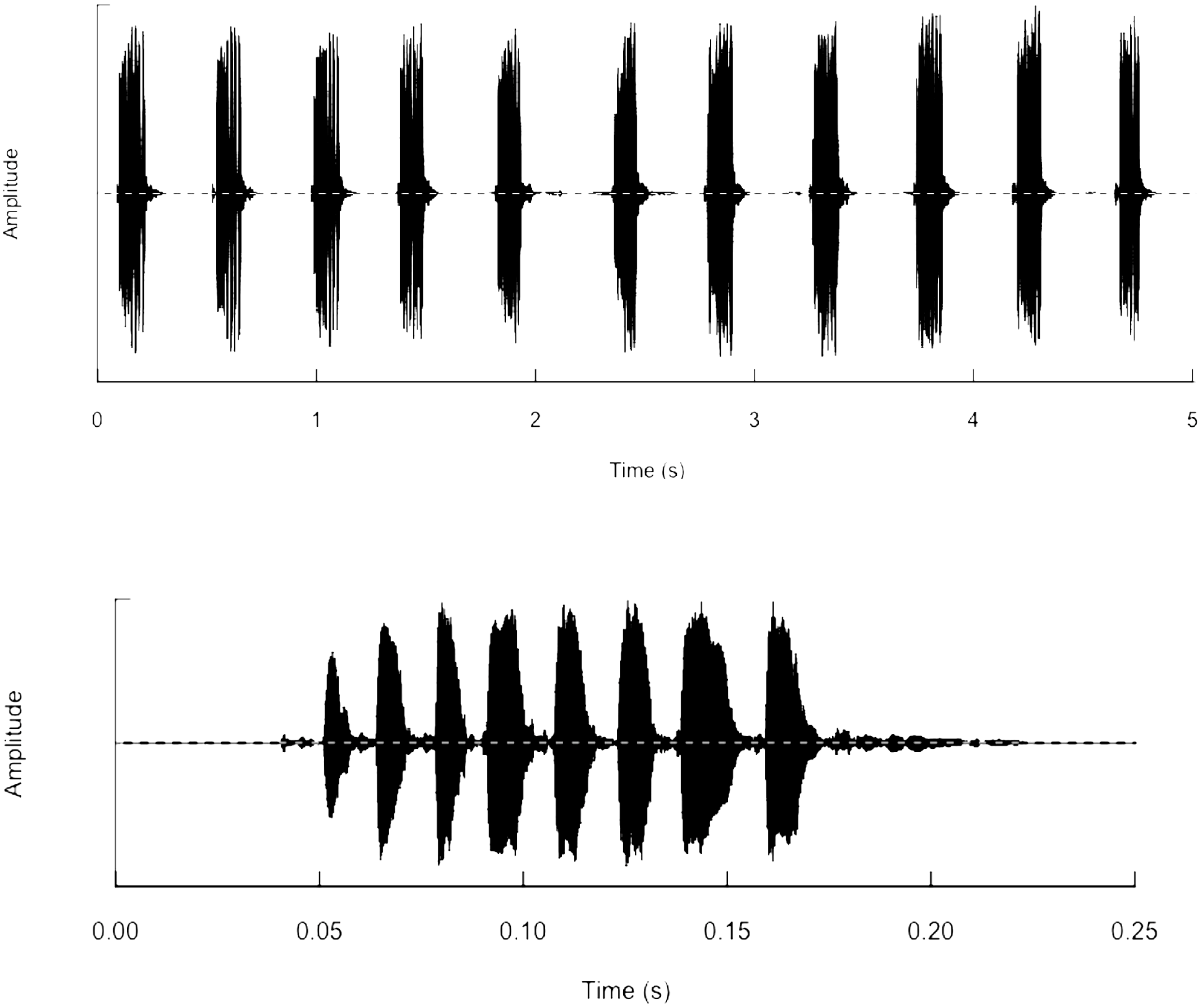

FIGURE 176. Calling song (R11-15) of *G. lineaticeps* from Mendocino Co., CA (S11-22), recorded at 25°C; lower panel shows structure of a single chirp.

Discussion. An ecologically diverse and morphologically variable species, although song, file characters and DNA consistent for one species. Responsible for periodic outbreaks in California's Central Valley with documented episodes in Coalinga as follows: 1967, R.E. Love, pers. comm.; Lindgren (1978); Caruba (1980), and DBW (unpubl.) on 28-vii-1998; where millions of macropterous, flying individuals can become a summer nuisance. This is probably the species responsible for the outbreak in Knightsen, Contra Costa Co., CA, in 2001 (https://www.sfgate.com/bayarea/article/Knightsen-crawling-with-crickets-Vacuums-2872987.php).

Those summer males singing from grassland cracks are usually impossible to flush with water given the extensive nature of the cracks. Oatmeal trails there will usually attract females and occasionally males.

FIGURE 177. Color variation in *G. lineaticeps*: Reddish male (A) and female (C) from Madera Co., CA (S15-91); black male (B) from Tuolumne Co., CA (S10-13).

Not all *Gryllus* species with long hind wings are good flyers. *G. lineaticeps* seems to be a very capable flyer as evidenced by its presence on seven of eight California Channel Islands (Weissman *et al*. 1980), and Cedros and Guadalupe Island, Mexico, the latter some 240 km west of the Pacific coast of Baja California (DBW, unpubl.), although other means of colonization are possible.

This species has been the subject of a series of studies of sexual communication, e.g. Hoback & Wagner (1997), Wagner & Harper (2003), Wagner & Basolo (2007a), and Tolle & Wagner (2011) as well as studies of tachinid fly parasitism, e.g. Gray *et al*. (2007), Wagner & Basolo (2007b), Martin & Wagner (2010), Paur & Gray (2011a), and Beckers & Wagner (2012, 2018), and female reproductive benefits (Wagner 2005).

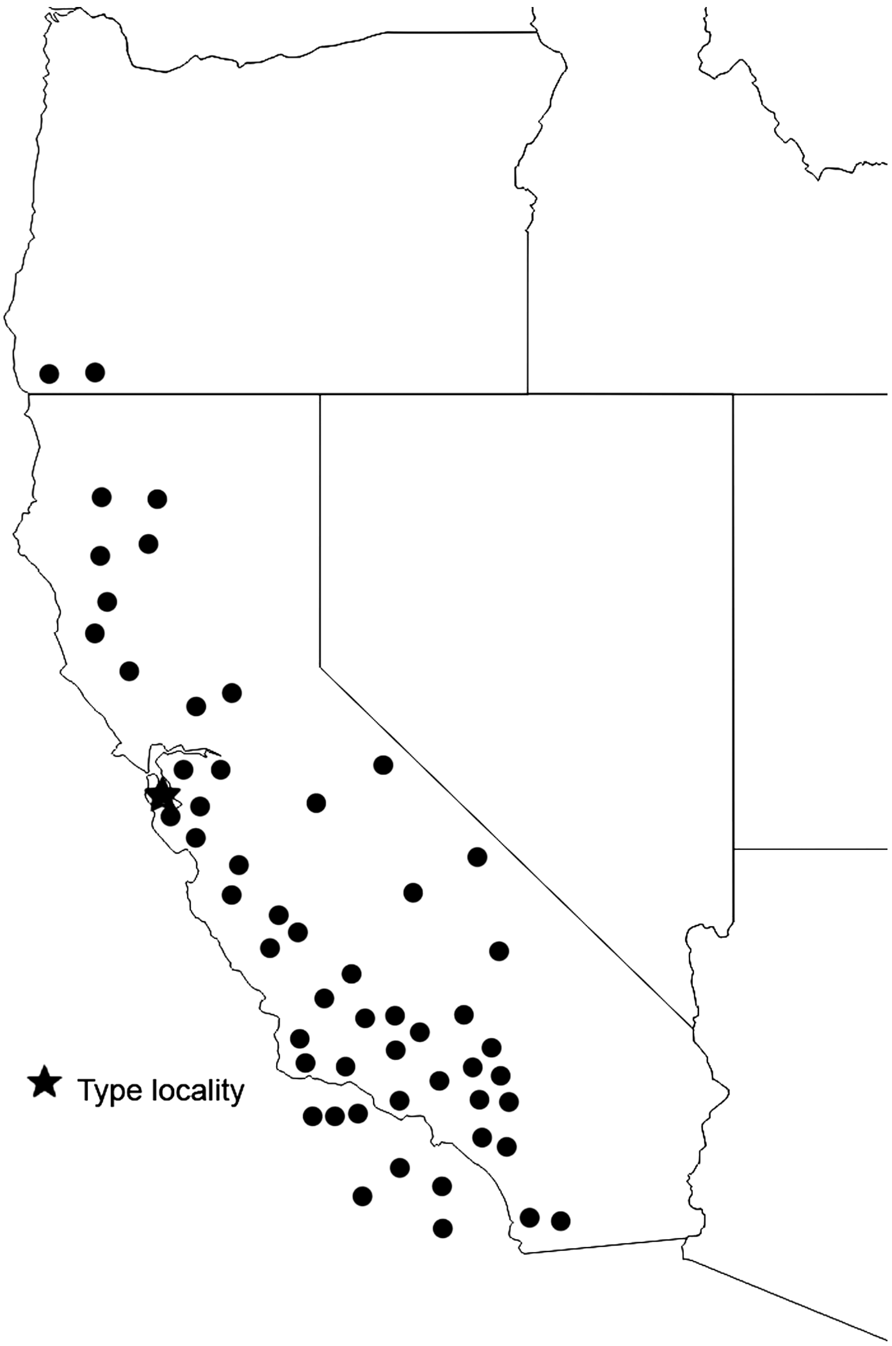

FIGURE 178. Known US distribution of *G. lineaticeps*.

Gryllus personatus Uhler

Badlands Field Cricket

Figs 170–174, 179–182, 185, Table 1

1864 *Gryllus personatus* Uhler, Proc. Ent. Soc. Philadelphia 2: p. 547. Type locality: Kansas. Holotype female (Fig. 179): "Collection of P. R. Uhler. *Gryllus personatus*_Kans. Uhler. Red type label, 14066." In addition, there is a pink circular label without writing. Deposited at ANSP. Body length 14.6 mm, hind femur length 10.3 mm, pronotum 3.5 mm long and 5.3 mm wide. Holotype is a shriveled female once preserved in alcohol but now pinned. The head and pronotum are brown, area below eye straw brown or cream, short traverse band between the eyes, fastigum of vertex with three prominent straw brown streaks, entire lateral pronotal lobe straw brown, all legs uniform straw brown. The tegmina are darker yellow brown and almost reach the tip of the abdomen. Ovipositor curved and longer than hind femur.

'Gryllus #17' of DBW notebooks.

FIGURE 179. Holotype female of *Gryllus personatus*, with labels.

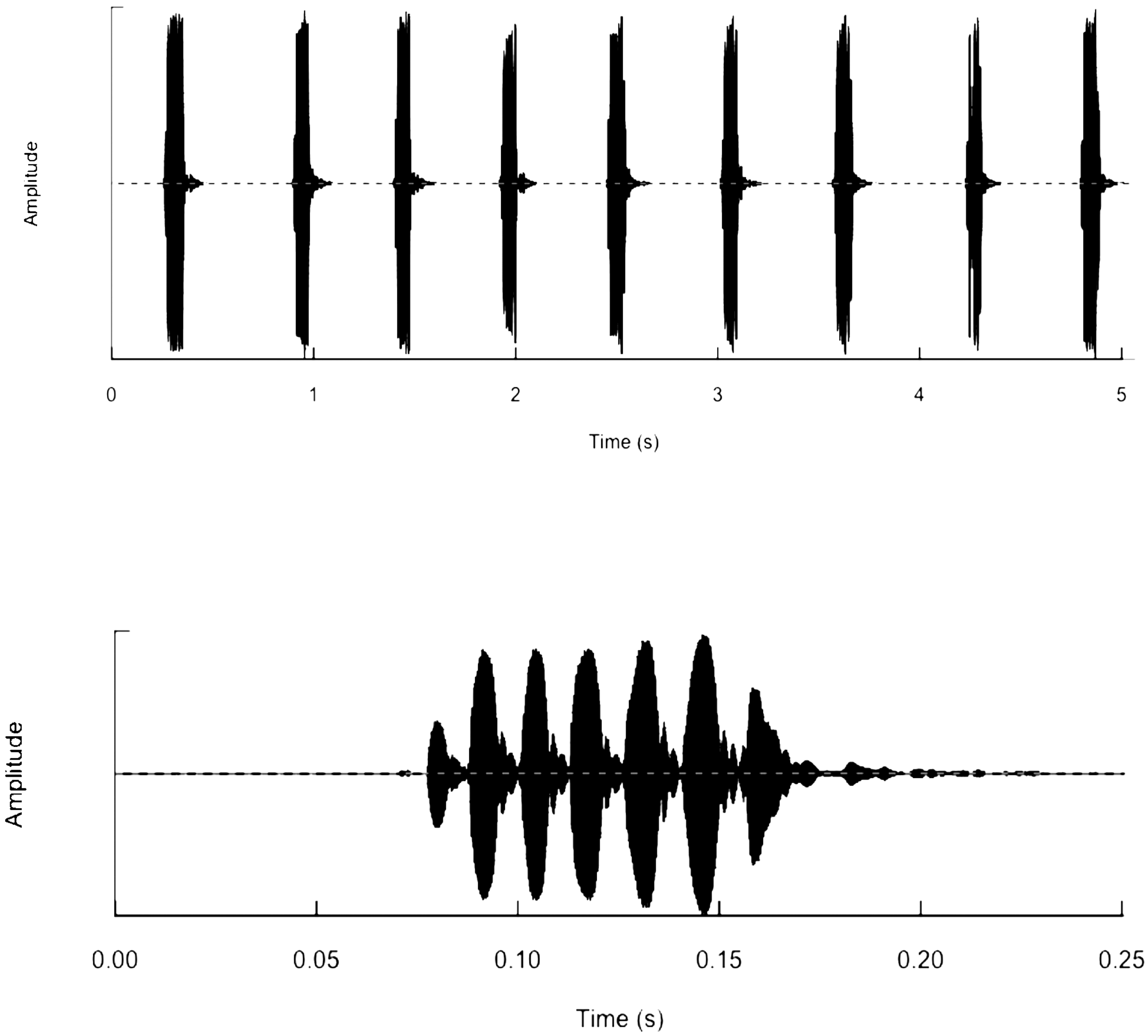

FIGURE 180. Calling song (R07-74) of *G. personatus* from Alpine, TX (S07-41), recorded at 25°C; lower panel shows structure of a single chirp.

Distribution. Known from seven western US states (see Fig. 181) and adjacent Mexico.

Recognition characters and song. Medium to very large crickets (see Table 1, p. 18). *Song* (Fig. 180, R07-74), at 25°C, unique within its range: chirps typically with 5-8 pulses, although all three males from Brackettville, TX, (S10-63), had 4 p/c. Usually from 100 to 180 c/m, pulse rate usually between 50-70 (range 48-91), dominant frequency 4 kHz. Probably two generations/year in southern distribution. Among western US taxa with similar songs, differs from sympatric (at Brackettville and Big Bend, Texas) *G. assimilis* that has a slower CR, more p/c, dull (hirsute) pronotum, inhabits moister areas such as lawns, and almost no light brown/straw colors on body. Differs from more western allopatric sister species *G. lineaticeps* which has a faster CR, higher dominant frequency (Fig. 173 and Gray *et al.* 2016b) and lacks cream colors on the head or body. Differs from usually allopatric sister species *G. staccato* that has variable p/c, a faster pulse rate and chirp rate, a higher dominant frequency (Fig. 173 and Gray *et al.* 2016b), a shorter ovipositor (Table 1, p. 18), more file teeth and teeth/mm, and occurs in hotter, dryer areas. Some male *G. staccato* can have very uniform number of pulses/chirp but can be separated from similar sounding *G. personatus* by the presence of some chirps with variable number of pulses. *G. personatus* and *G. staccato* have been found microsympatric only at the abandoned gas station at Road Forks, New Mexico (S81-38) near the southeastern Arizona border. Even there, separated by microhabitat as *G. staccato* within the confines of the abandoned gas station while *G. personatus* is in cracks in the clay-soil fields surrounding the gas station. Both taxa can have linear head stripes, cream colored areas completely around the eyes frequently extending onto the lower, adjacent half of pronotum, and speckles on face between eyes. *G. personatus* usually at higher elevations.

Derivation of name. “persona” = mask; “tus” = having the nature of, which nicely describes the similarity seen in the holotype and many of our specimens that have facial and pronotum markings as seen in Fig. 179.

Geographic range. Fig. 181. Known from east and west of the Rockies from 335–2005m. Despite much collecting effort in the type locality of “Kansas,” we have not found this species there. It does occur near the western Kansas border at La Junta, Colorado (S09-82). Given the amount of land usage change in Kansas in the 150 years since the type was described, its absence in that state is not surprising. Fortunately, the distinctive coloration and color pattern of the holotype female leave us confident that this ID is correct. While we document 6 species of *Gryllus* in Kansas, none look like the holotype of *G. personatus*.

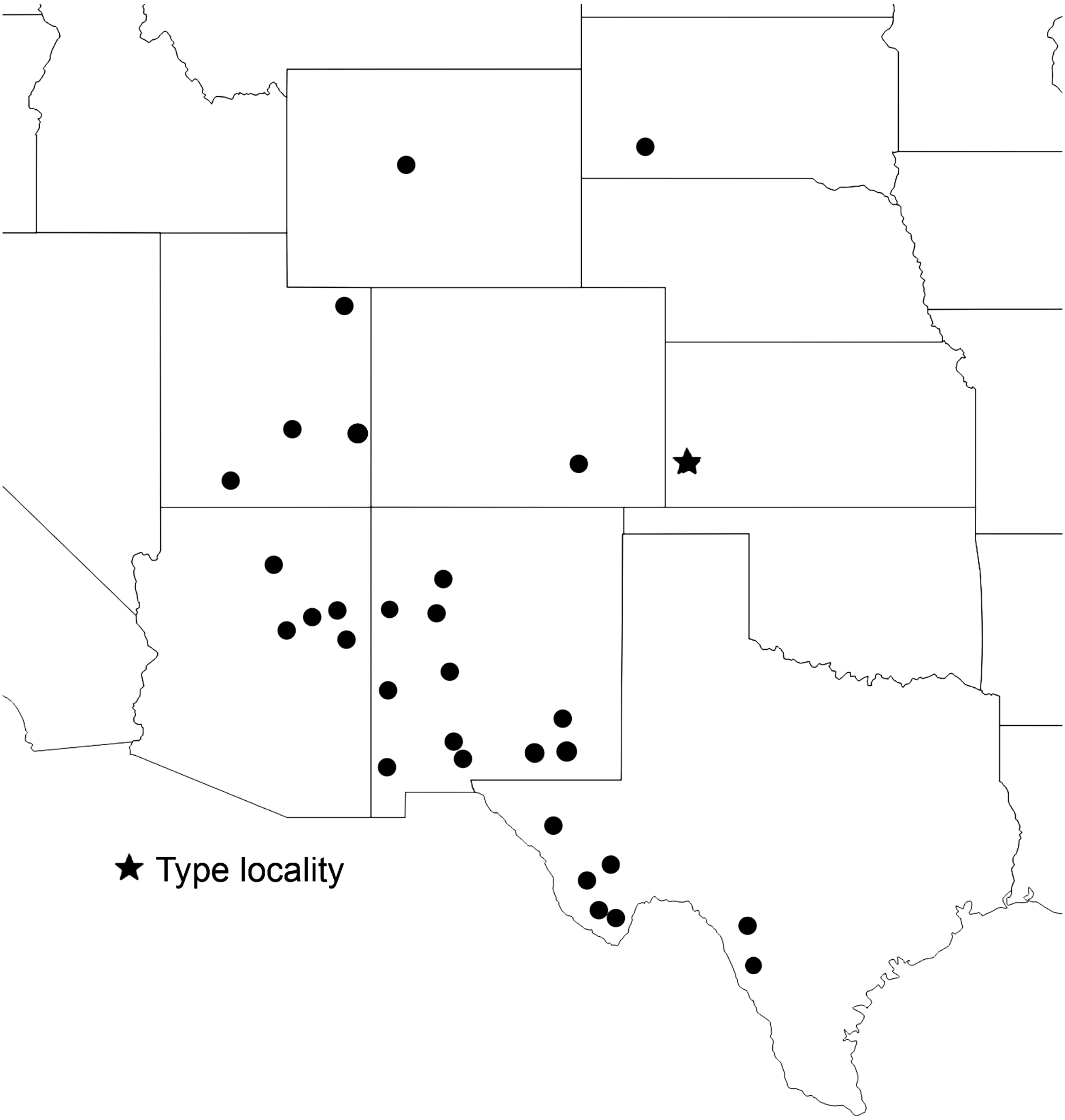

FIGURE 181. Known US distribution of *G. personatus.*

Habitat. When far from human habitation, this cricket frequently associated with clay-type badlands (Road Forks, NM, S81-38; near Dinosaur National Monument, CO, S99-128; and Badlands National Park, SD, S09-89), usually living in deep cracks and the only *Gryllus* resident there, except at Badlands where it occurs with *G. mak-*

hosica. Found within ~100 meters of *G. saxatilis* in San Juan Co., UT (38.399167, -109.401148, on 26-v-2017), but separated by microhabitat (clay soils v. rocky slope). Also occurs around human structures in towns away from clay soils.

Life cycle and seasonal occurrence. No egg diapause (checked from Las Cruces, NM, S83-103; and Tom Green Co., TX, S88-31). Probably 2 generations/year in southern distribution (e.g. Big Bend, Texas [S85-39]), but undoubtedly one generation in Badlands National Park, South Dakota. Adults known from mid-March into September but we have not collected areas where it could occur outside of this time period.

Variation. **Color**: Variable from light colored bodies, frequently with linear head stripes (Fig. 182) similar to those seen in *G. staccato,* to individuals almost pure black except for a light-colored patch below the eyes (Fig. 182) as seen in one male from Badlands National Park, SD, S93-53 and one female from Alpine, TX, S07-41). Females can have a light tegminal stripe along the fore wing angle (Fig. 182). **Pulses/chirp:** see "Discussion". **Wing length:** Of 155 individuals of both sexes, 56 had long hind wings.

FIGURE 182. Color variation in *G. personatus*, moving left to right: Navajo Co., AZ (S91-86); Navajo Co., AZ (S91-88); Navajo Co., AZ (S91-86); Tom Green Co., TX (S88-31); Alpine, TX (S07-41).

Specimens examined. **Arizona.** *Coconino Co.,* 3.1 m SE Yuba City, 4800', 6-viii-1991 (S91-82), 1♀. Hwy 99 6.85 road m NW intersection US 40, 4900', 8-viii-1991 (S91-89) 1♀. *Navajo Co.,* Holbrook, 5080' 8-ix-1999 (S99-116) 1♂. Winslow, 4852', 10-viii-2003, 10♂ 9♀; 10-viii-2010, 4♂ 9♀; 27-vii-2012, 6♀. Hwy 77 0-12 m N US40, 5400', 7-viii-1991 (S91-86) 5♂ 5♀. Hwy 180 1 m S entrance Petrified Forest National Park, 5400', 8-viii-1991 (S91-88) 1♂; 8-ix-1999 (S99-114) 1♀. **Colorado.** *Crowley Co.,* Manzanola, 4200', 26-viii-1989 (S89-65) 1♂ 3♀. *Huerfano Co.,* 10 m E Walsenburg, 5800' 22-vi-1987 (S87-64) 1♂ 1♀. *Otero Co.,* La Junta 4100', 2-vii-2009 (S09-82) 2♂ 6♀. *Pueblo Co.,* Hwy 96 between Fowler and Hwy 50, 4300-4600', 26-viii-1989 (S89-64) 1♂. **New Mexico.** *Chaves Co.,* Roswell, 28-vi-2009 (S09-58) 2♂. *Cibola Co.,* Grants, 6340' 1-vii-1994 (S94-43) 2♂. *Dona Ana Co.,* Las Cruces, 26-vi-1983 (S83-103) 5♂ 2♀; Las Cruces, University New Mexico, 23-viii-1982 (S82-99) 2♂. *Eddy Co.,* Artesia, 3428', 30-vi-2015 (S15-58) 1♂ 1♀. Hope, 4095' 30-vi-2015 (S15-57) 1♂ 1♀. *Hidalgo Co.,* Road Forks, 4000', 29-vii-1981 (S81-38) 2♂. *McKinley Co.,* Gallup, 2005m, 27-vii-2003, 35° 31' 56.9" -108° 39' 57.8 (DAG2003-31) 1♂. *Sandoval Co.,* San Ysidro, 5600' 6-vi-1985 (S85-51) 1♂. *Socorro Co.,* Socorro 4460' 13-vi-2007 (S07-50) 3♂ 2♀; 29-vi-2015 (S15-54) 1♂ 1♀. **South Dakota.** *Jackson Co.,* Badlands National Park, Big Badlands Overlook, 3100', 22-vi-1993 (S93-53) 12♂ 3♀; 30-vii-1997 (S97-90) 1♂. Cedar Pass, 2700' 29-viii-1989 (S89-75) 1♂; 3-vii-2009 (S09-89) 4♀. **Utah.** *San Juan Co.,* Blackridge, 3.1 m E Hwy 191, 5849', 38.399167, -109.401148, 26-v-2017, 1♀. *Uintah Co.,* Hwy 149 1 m S entrance Dinosaur National Monument, 5000' 10-ix-1999 (S99-128) 1♂. *Washington Co.,* W border of Zion National Park, 4060' 10-vi-1996 (S96-55) 1♂ 1♀. *Wayne Co.,* Hanksville, 4500' 1-viii-1992 (S92-109) 1♂. **Texas.** *Brewster Co.,* Alpine, 4200', 5-vi-1991 (S91-44) 1♂ 3♀; 12-vi-2007 (S07-41) 6♂ 4♀. Big Bend National Park, Rio Grande Village, 2100' 11-iii-1985 (S85-39) 4♂ 4♀; 9-vi-1985 (S85-56) 4♂ 2♀; 5-vi-1991 (S91-43) 2♂ 2♀; 28-v-2016 (S16-12) 5♂ 6♀. 12 m SW Marfa, 19-viii-1984 (S84-53) 1♂. Hwy 118 near Terlingua, 2566' 2-vii-2015 (S15-71) 5♂ 2♀. *Culberson Co.,* Van Horn, 4100' 6-vi-1991 (S91-48) 5♂ 2♀. *Dimmit Co.,* 19-viii-1964, TJ Walker, 2♂. *Kinney Co.,* Brackettville, 1160' 7 and 8-ix-2010 (S10-63) 4♂ 6♀. *Presidio Co.,* Presidio, 2400' 26-vi-1986 (S86-46) 1♂; 27-v-2016 (S16-5, 6) 2♂ 2♀. *Tom Green Co.,* near junction Hwy 277 and 67, 1900' 11-vi-1988 (S88-31) 2♂ 1♀. **Wyoming.** *Fremont Co.,* Shoshoni, 4849', 18-vii-2011 (S11-72) 1♂.

DNA. Multilocus G1357, La Junta, CO, S09-82. Two sister species are *G. lineaticeps* (multilocus 2016-033) and *G. staccato* (multilocus 2016-034) (Gray *et al.* 2019). 16S DNA groups all 3 species together (also see Gray *et al.* 2016b).

Discussion. G. personatus typically has between 5-8 p/c, except for the 3 collected males from Brackettville, Texas (S10-63), its most eastern locality, where each had 4 p/c. *G. assimilis* has similarly spaced chirps but with 6-9 p/c, and it is generally separated ecologically from the former. We initially wondered if calling-song character displacement might be operative in reducing the p/c in this Brackettville *G. personatus* population? We subsequently discovered both species also sympatric at Rio Grande Village (S16-12) in Big Bend National Park, TX, where *G. assimilis* sang its typical song and the 5 recorded males of *G. personatus* had 6-7 (range 5-8) p/c.

G. personatus has been used in several recent investigations: Gray *et al.* 2016b, Gabel *et al.* 2016, Hennig *et al.* 2016, Blankers *et al.* 2016.

Gryllus staccato **Weissman & Gray, n. sp.**

Stutter-Chirping Field Cricket
Figs 170–174, 183–188, Table 1

'Gryllus #15' in DBW notebooks.
'G15' and irregular chirping cricket in Sakaguchi & Gray 2011, Blankers *et al.* 2016.
'G. staccato' in Gray *et al*. 2016b, Gabel *et al.* 2016, Hennig *et al.* 2016.

Distribution. Arizona and adjacent deserts of California, Nevada, Utah, and New Mexico.

Recognition characters and song. Most variable calling song of any US *Gryllus.* A medium to large sized cricket with a shiny pronotum generally at low elevations in some of the hottest, driest desert areas of the southwestern US, including most of Arizona (except for the northeast corner). *Song* loud, unique for New World *Gryllus*: many individuals produce a highly irregular "stuttered" series of chirps (Fig. 183, R15-291) with high variability in inter-chirp interval. Chirps at 25°C with variable p/c (typically 3-9; range 1 to 10), variable CR (typically 120-240; range 100-720) depending on p/c and inter-chirp interval, pulse rate 70-110, dominant frequency 5.25 kHz. Within most populations, 10 to 60% of males sing with a more or less constant number of p/c and uniform inter-chirp interval (Fig. 184A, R11-124) with some males (see Fig 184B, R09-147) singing both regular and irregular segments. Color usually light (Fig. 186) but dark individuals (Fig. 187) known even in summer. If male singing irregular stutter-chirp song, then can be confused with no other US *Gryllus*. If singing with constant p/c and uniform inter-chirp intervals in the Southwestern US, then only has to be distinguished from *G. lineaticeps, G. personatus*, and *G. multipulsator.* From allopatric sister species *G. lineaticeps,* no overlap in distribution (Fig. 172), DNA (Fig. 174), and pulse rate (Fig. 173). From allopatric sister species *G. personatus*, which it most closely resembles morphologically and which it geographically broadly overlaps in only north-central Arizona and SW New Mexico (but has been only found microsympatric with *G. personatus* at Road Forks [S81-38 and S12-104] and Socorro [S07-50], New Mexico), *G. staccato* is distinguished by a combination of characters (Table 1, p. 18): more file teeth and more teeth/mm on average, shorter ovipositor relative to body size (Fig. 185), microhabitat different (dirt substrate vs. clay substrate), although both can occur at gas stations that have bright night lights, no overlap in dominant frequency (Fig. 173), irregular pulses/chirp, faster PR and CR, and differences in DNA. Both taxa can have linear head stripes, cream colored areas completely around the eyes frequently extending onto the lower, adjacent half of pronotum, and speckles on face between eyes. *G. personatus* usually at higher elevations. From *G. multipulsator*, which it overlaps in distribution in southeastern CA, southern NV, and west-central AZ, the latter has more p/c, slower CR and a hirsute (dull) pronotum and general absence of linear lines on the head.

*Holotype***.** Male (Fig. 186). USA. Arizona, Pima Co., Ajo. 1-viii-2009. 520m. D.B. Weissman. S09-102, R09-149, DNA sample G1410. 16S ribosomal RNA gene GenBank accession # MN136664. Body 25.3, HF 12.88, LC 13.09. Right tegmen removed: 149 teeth, file length 3.45, TL 14.8, TW 4.6. Type deposited in CAS, Entomology Type #19271.

Paratypes. (Total: 132♂ 109♀) **Arizona.** *Cochise Co.,* Benson, 1240m, 27-vi-2009 (S09-54) 1♂. Wilcox Playa, 4155', 29-vii-2015 (S15-104) 32° 11' 55.5" -109° 52' 42.4", 2♂ 1♀. *Coconino Co.,* Sedona, 4400', 25-vi-1980 (S80-45) 4♂; 15-vi-1990 (S90-49) 1♂; 30-vi-1994 (S94-35) 1♂; 12-vi-1996 (S96-61, at airport) 1♀; 15-vi, 2007 (S07-61) 1♂ 5♀. *Gila Co.,* Coolidge Dam, 2400', 30-vii-1981 (S81-43) 2♂. Globe, 3548', 30-vii-1981 (S81-44)

3♂. *Graham Co.,* Safford, 2920': 16-vi-1990 (S90-51) 6♂ 1♀; 28-vii-2015 (S15-103) 1♂ 2♀. 4.5m S Safford, 3180', 10-vi-2012 (S12-20) 1♀. Hwy 366 near intersection with Hwy 191, 3333', 28-vii-2015 (S15-102) 4♂ 2♀. *La Paz Co.,* Wenden, 550m, 14-ix-2011 (S11-87) 2♂ 2♀. *Maricopa Co.,* Aguila 2100' 23-vii-1990 (S90-71) 2♂ 2♀. Buckeye, 260m, 18-ix-2011 (S11-102) 5♂ 6♀. Gila Bend, 220m: 31-vii-1981 (S81-47) 1♂ 4♀; i-viii-2009 (S09-103) 2♂ 2♀; 18-ix-2011 (S11-101) 2♂; 30-vii-2015 (S15-111) 28♂ 23♀. Goodyear, 31-vii-1981 (S81-46) 1♂. Phoenix, 30-vii-2015 (S15-113) 1♂ 1♀. *Mohave Co.,* Hwy 68 2m E California border, 1000', 24-vi-1980 (S80-38) 1♂. Kingman, 3700', 2-viii-1992 (S92-113) 3♂ 2♀; 16-vi-2007 (S07-68) 1♂. 3 m SE Kingman on road to Hualapai Mt. Park, 3950', 3-viii-1991 (S91-67) 5♂ 2♀. *Pima Co.,* Ajo, 540m, 20-viii-1998 (S98-72 & 74) 7♂ 3♀; 15-v-1999 (S99-26) 1♂; 17-ix-2011 (S11-99) 2♂ 1♀; 29-vii-2015 (S15-109) 1♂ 2♀. Catalina, 2940', 18-viii-1998 (S98-65) 2♂ 10♀. Robles Junction, 29-vii-2015 (S15-106) 1♀. Hwy 286 6.3 m S Robles Junction, 1100m, 17-ix-2011 (S11-95) 2♂ 1♀. Hwy 86 10.5 m W Hwy 286, 850m, 17-ix-2011 (S11-97) 3♂ 1♀. Sells, 29-vii-2015 (S15-107) 1♂ 2♀. Tucson, 930m, 27-vi-2009 (S09-53) 5♂ 2♀. Saguaro Rd into Tucson, 2200-2900', 28-vii-1981 (S81-35) 8♂ 3♀. Why, 1740', 20-viii-1998 (S98-71) 4♀. *Pinal Co.,* Picacho Peak State Park, 1780', 18-viii-1998 (S98-66) 1♂. *Yavapai Co.,* Agua Fria Nat. Monument, 1130m, 19-ix, 2011 (S11-105) 1♂ 8♀; 12-vi-2012 (S12-24) 1♀. Camp Verde, 22-viii-2012, (S12-107) 1♀. Cordes Junction, 1100m, 18-ix-2011 (S11-103) 2♂. *Yuma Co.,* Telegraph Pass, 210m, 15-ix-2011, (S11-92) 1♂. Yuma, Arizona Western College, 200', 18-vi-1990 (S90-54) 1♂ 1♀. **California.** *San Bernardino Co.,* Essex, 5.1 m W, 1500', 21-viii-1998 (S98-76) 1♀. Havasu Lake, 140': 6-vi-1983 (S83-62) 1♂ heard; 13-xi-2011 (S11-84) 3♂. **Nevada.** *Clark Co.,* Cottonwood Cove: 750', 24-vi-1980 (S80-36) 1♀; 26-vii-1981 (S81-31) 1♂. **New Mexico.** *Hidalgo Co*., Road Forks, 4195', 29-vii-1981 (S81-38) 1♂; 21-viii-2012 (S12-104) 5♂ 9♀. **Utah.** *Washington Co.,* Hurricane, 1040m, 20-iv-1999 (S99-12) 1♂. La Verkin, 1040m, 11-ix-2004 (S04-121) 3♂.

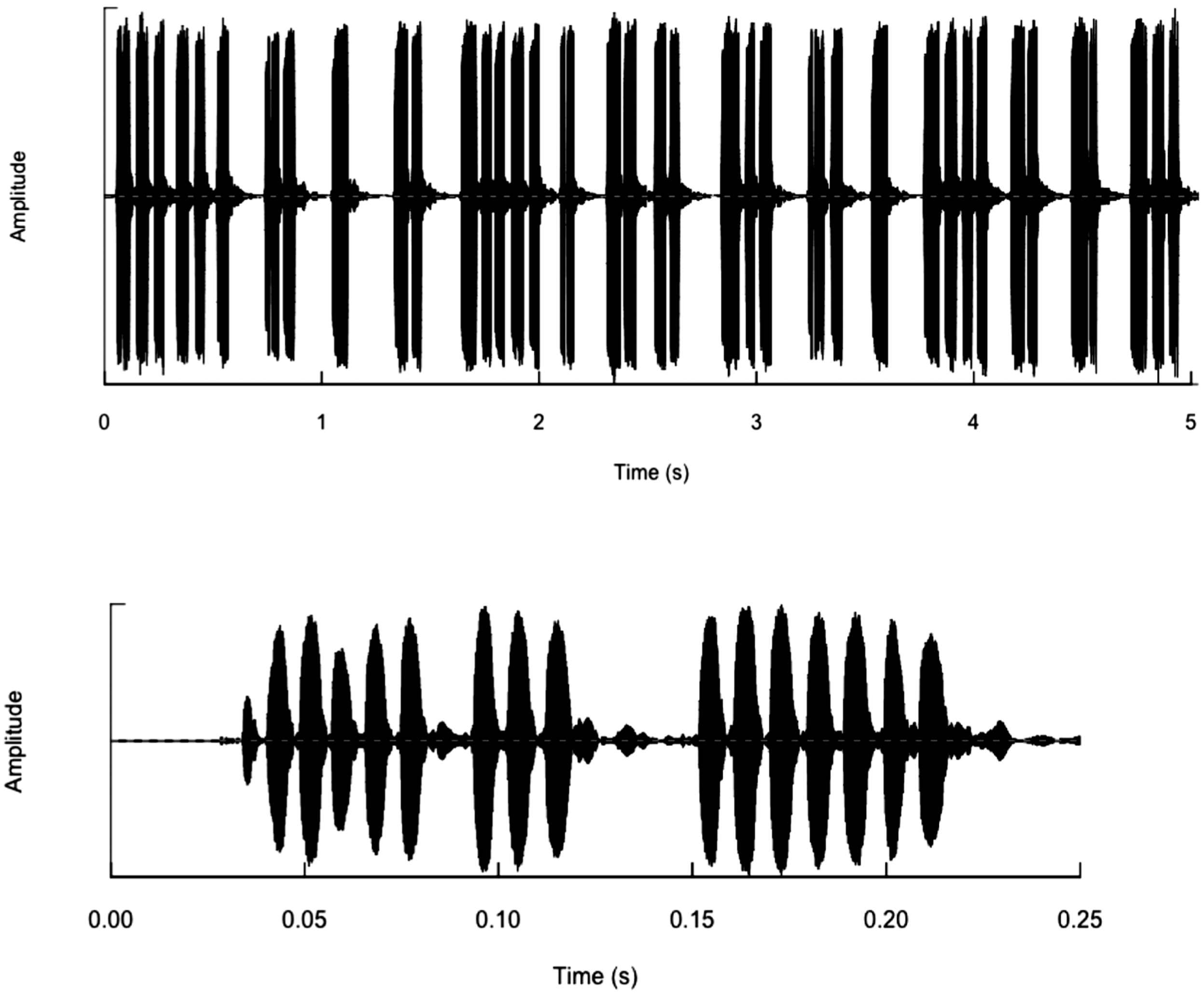

FIGURE 183. Typical (upper panel), irregular calling song (R15-291) of *G. staccato* from Gila Bend, AZ (S15-111), recorded at 25.1°C. Lower panel shows more detailed structure of the 'stutter-chirp'.

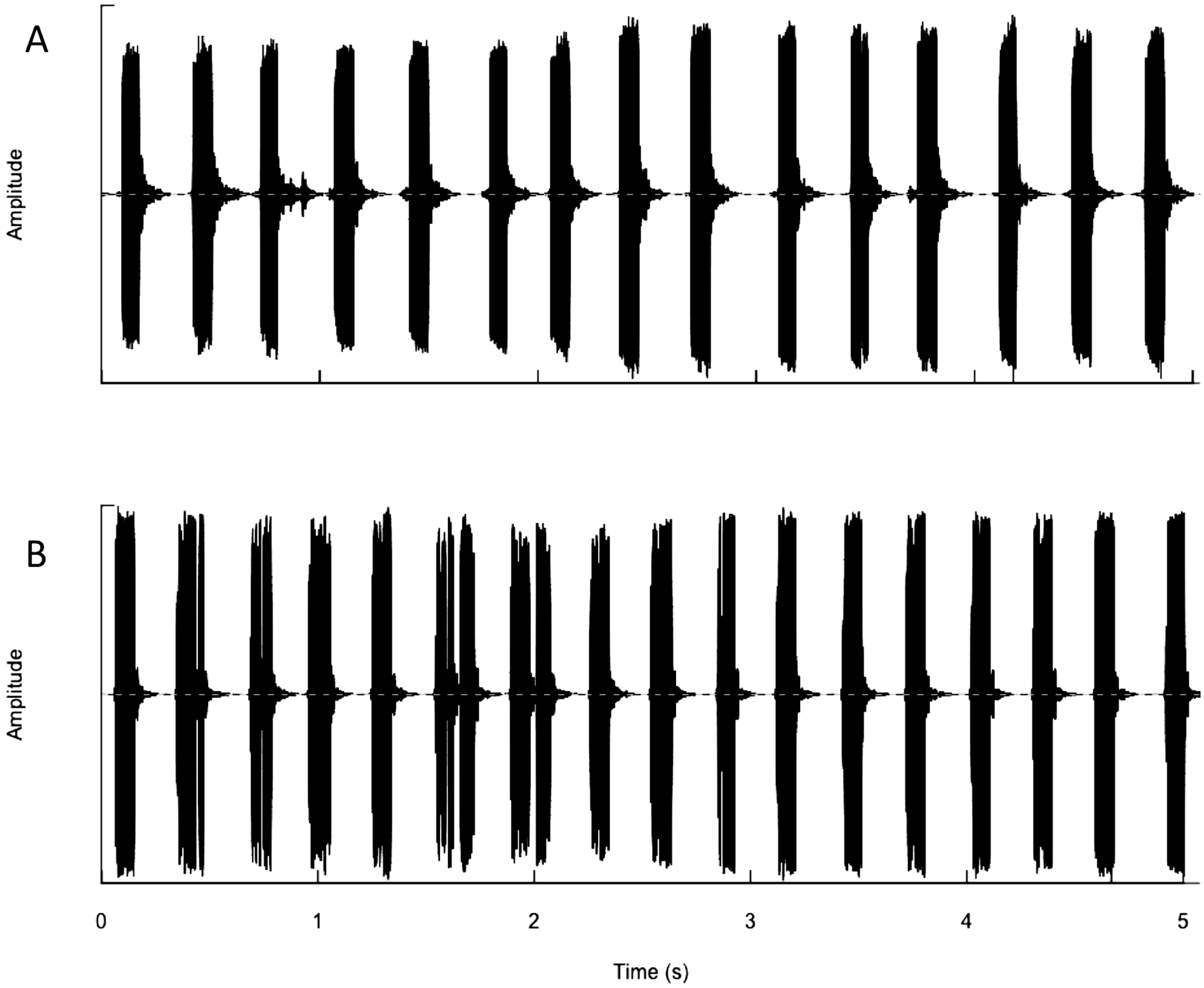

FIGURE 184. (A). Regularly spaced calling song (R11-124) of *G. staccato* from Buckeye, AZ (S11-102), recorded at 26°C. (B) Calling song (R09-147) of *G. staccato* from Tucson, AZ (S09-53), recorded at 27.5°C showing both regular and irregular spacing of chirps within the same individual.

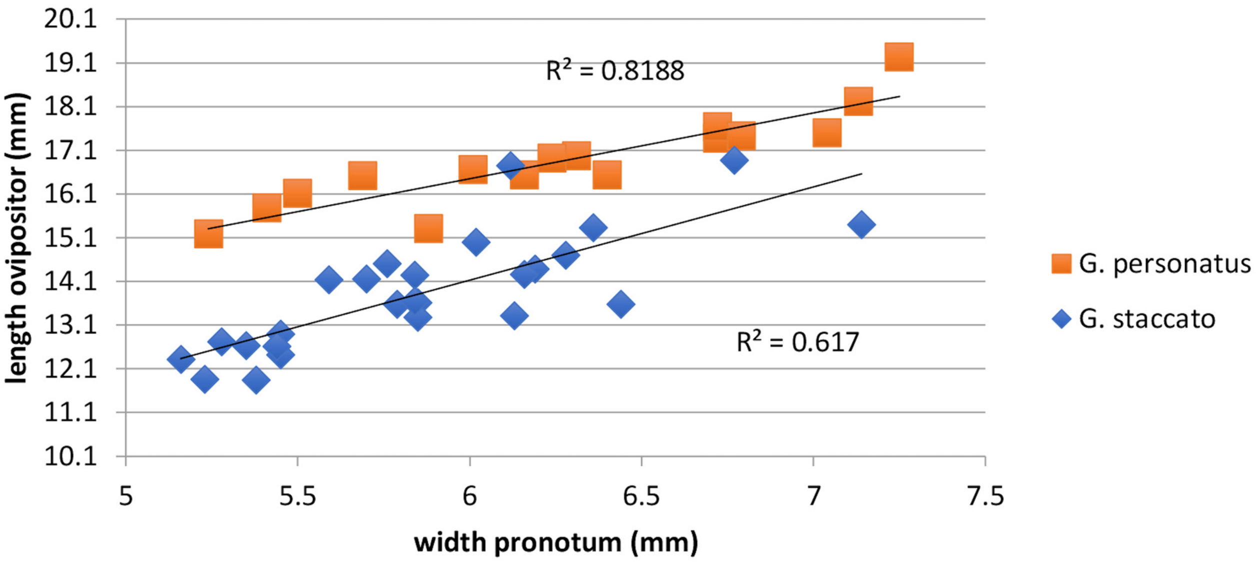

FIGURE 185. Regression of width pronotum vs. length ovipositor in *G. staccato* vs. *G. personatus.*

FIGURE 186. Holotype male (upper) of *G. staccato*. Female (lower) from Pima Co., AZ (S11-95). Note cream colored area, below eye, on male.

Song records only. (only one male heard at each locality)*:* **Arizona**, Coconino Co., Flagstaff, 6900', 21-viii-1982 (S82-86); **California**, Inyo Co., Death Valley Nat. Park, Furnace Creek, -52m, 23-vi-1980 (S80-32). **New Mexico**, Socorro Co., Socorro, 4460', 13-vi-2007 (S07-50).

Derivation of name. Staccato means "something that is abruptly discontinuous or disjointed in quality or character," which describes the calling song of most males.

Geographic range. (Fig. 188). Also, south into the Mexican states of Sonora, Chihuahua, and Sinaloa.

FIGURE 187. Dark color variation in *G. staccato* from Colonia Juarez, Chihuahua, Mexico (S01-71).

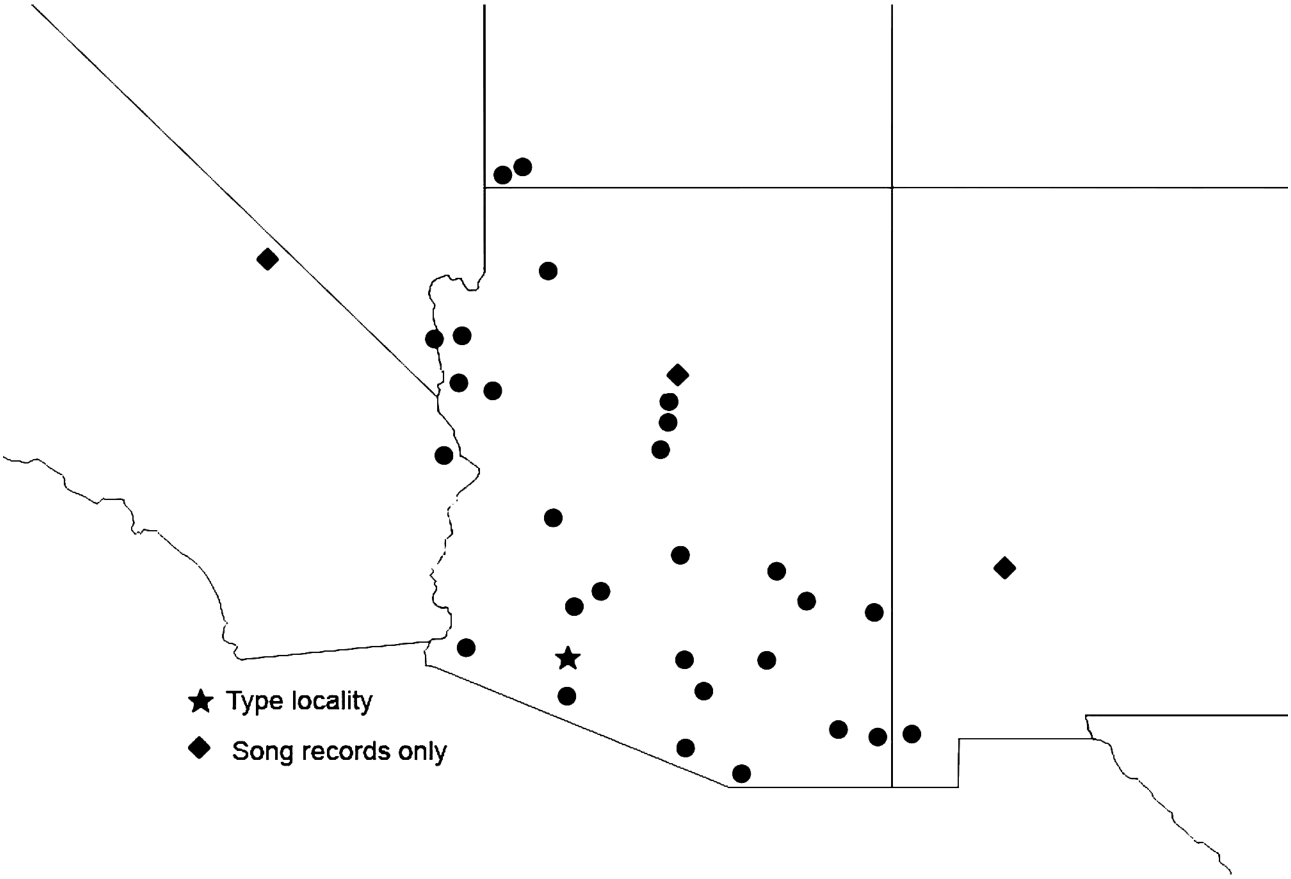

FIGURE 188. Known US distribution of *G. staccato*.

Habitat. Primarily open desert grassland/scrubland below 1220m but occasionally at higher elevations, e.g. mixed oak/ juniper/pine woodland at 2026m (Schnebly Hill, ~5 m E Sedona, AZ, 7-vii-2003 [DAG 2003-305]) and 2103m within the town of Flagstaff, AZ (S82-86). Flies well and frequents lighted areas around human structures, especially gas stations with all night florescent lights. Can sing in the open or from cracks in the ground. Large population in rock garden area at McDonald's in Gila Bend (S15-111). Wilcox Playa, AZ, (S15-104) males sang in daytime 1 meter above ground, along with *G. lightfooti,* from within *Yucca elata* plants.

Life cycle and seasonal occurrence. No egg diapause in Arizona localities: Ajo (S11-99), Yuma (S90-54), and Safford (90-51). Probably 2 generations/year although may depend upon rainfall. Adults known from April to October, but months outside of these have not been checked. Breeds continuously under laboratory conditions.

Variation. See Table 1 (p. 18) for measurements. **Color:** Varies from light tan to almost solid black (Fig. 187), although face always with some areas of tan or cream. Most light-colored individuals with three longitudinal stripes on top of head, middle stripe sometimes broken. In very dark individuals, stripes not visible. **Hind wing length:** Variable in both sexes, with about 80% of all adults with long hind wings. Yet even in individuals whose hind wings don't extend beyond the tip of the abdomen, the hind wings present are longer than those in taxa that always have short hind wings. Of 62 individuals from Gila Bend (S81-47, S09-103, S11-101, S15-111), 60 had long hind wings and 2 had shed their hind wings. **Song:** *Chirp rate*—Within a population, both regular and irregular chirp rate songs are commonly heard. We found mixed song populations at several Arizona localities: Kingman (S91-67), Ajo (S98-74), Tucson (S09-53), Sedona (S94-35), Buckeye (S11-102), Gila Bend (S11-101) and Robles Junction (S11-95); and at Road Forks, New Mexico (S12-104). We have recorded a number of individuals that produce both regular and irregular songs (e.g. DAG 2004-006, Wickenburg, Maricopa Co., AZ, 4-iv-2004; DAG 2004-084, Organ Pipe Cactus National Monument, Pima Co., AZ, 8-iv-2004). DNA from individuals of *G. staccato* with both regular and irregular songs confirms that one species is involved (Fig. 174). ***Pulse rate***—Since we measured pulse rate between the last two pulses in a chirp, the pulse rate decreases as the number of pulses increases. This phenomenon was illustrated in *G. multipulsator* (Fig. 69, p. 81, and Fig. 2B in Weissman *et al*. 2009) where a pulse-by-pulse analysis showed that the pulse period increases for each sequential pulse in a chirp, due to increasing pulse duration. Extrapolating this general finding (Weissman unpubl.) to *G. staccato* males with songs with 7-9 p/c and comparing their PR (calculated between the last two pulses in a chirp) to irregular songs with 2-8 p/c, shows a similar phenomenon: the PR in a chirp with 3 pulses is higher than the PR in a chirp with 8 pulses. Even so, the PR in *G. staccato* is higher than *G. personatus* chirps with the same number of pulses. Thus, an irregular-song *G. staccato* male with 3 p/c can have a PR of 111 at 25°C. This same male, in a chirp of eight pulses, can have a PR of 83 at the same temperature. For comparison, a *G. personatus* with 8 p/c would have a PR around 65 at 25°C.

DNA. Multilocus 2016-034 from Yavapai Co., AZ. Two sister species *G. lineaticeps* 2016-033 (Tracy, CA) and *G. personatus* G1357 (Otero Co., CO) (Gray *et al.* 2019).

Discussion. There were unusual sex ratios at some Arizona and New Mexico gas station collections: Catalina (S98-65), Why (S98-71), and Road Forks (S12-104). At these localities, night collecting mostly yielded adult females, possibly from two causes: (1) males were in better hiding places, especially if singing or (2) males were already dead because parasitized by tachinids. At Agua Fria National Monument (S11-105), on 19-ix-2011, only one male *G. staccato* heard but unable to collect since singing from deep soil crack. That same night we collected one male and eight females at oatmeal trails. This one collected male sang with 7-8 p/c with a variable CR. We wonder if this male survived the tachinid onslaught because he was taciturn or his song was not attractive to the fly parasitoids (see Sakaguchi & Gray 2011, for discussion).

Singing males are easy to approach. They should make excellent material for female choice studies given the variability in the calling song.

G. staccato and *G. personatus* can hybridize and backcross in the laboratory (DAG, unpublished) but different microhabitats, and geographic allopatry, probably prevent such events in nature, although they can be "brought together" at bright lights in gas stations (e.g. Road Forks, NM, S81-38).

Male *G. staccato* parasitized by tachinid *Ormia ochracea* were collected from the following Arizona localities: Catalina (S98-65); Wenden (S11-87); 6 m S Robles Junction (S11-95); Cordes Junction (S11-103), and Agua Fria (Sakaguchi & Gray 2011).

The Chisosensis Group

G. chisosensis Weissman & Gray, n. sp. and *G. veletisoides* Weissman & Gray, n. sp.

Geographically distant but genetically closely related 4-5 pulse chirping species (Figs 189, 190), separated by pulse rate, geography, and DNA (Fig. 191); closely related to *G. montis* genetic Clades 2 and 3 which are geographically intermediate.

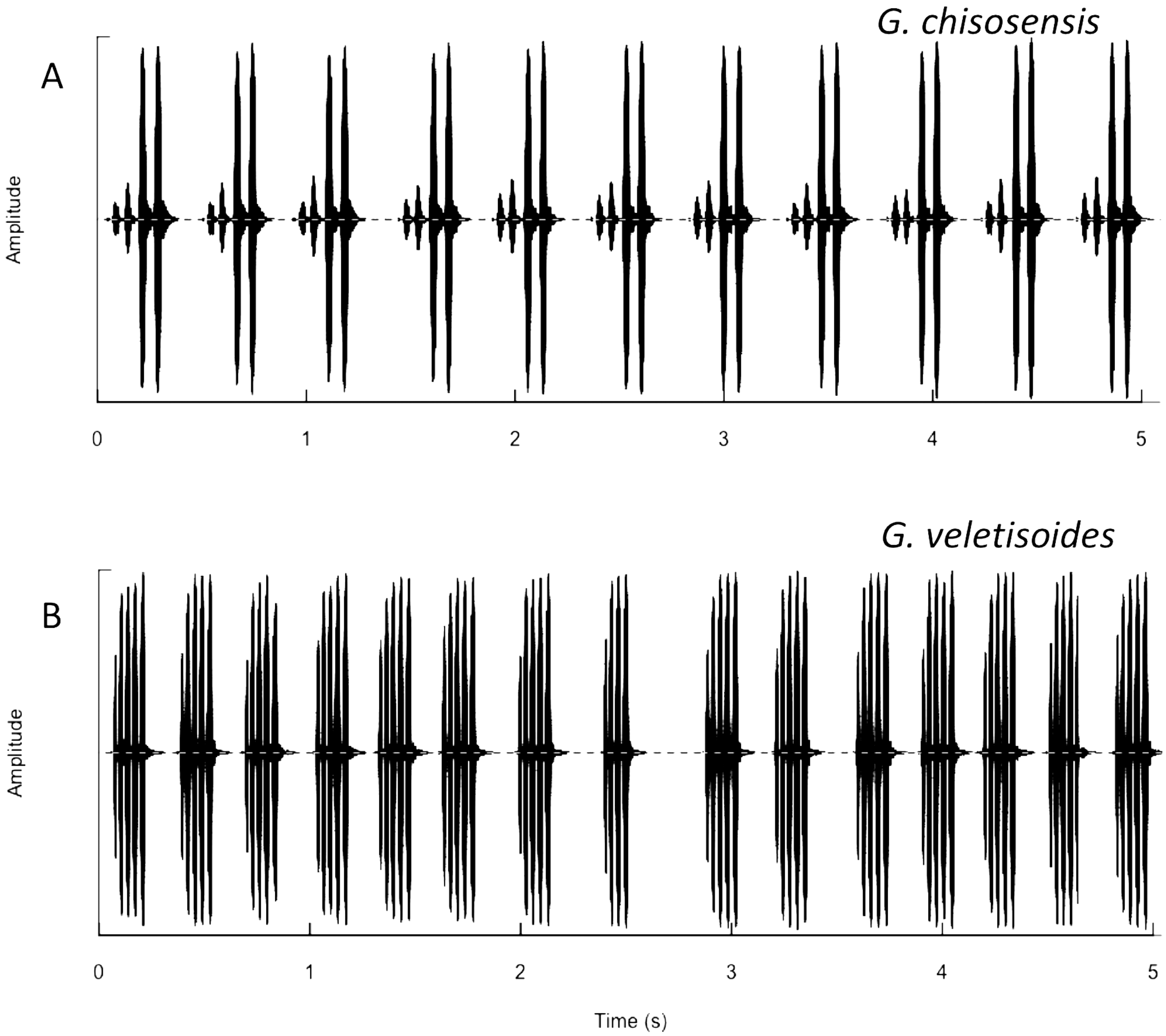

FIGURE 189. Five second waveforms of calling songs of (A) *G. chisosensis* and (B) *G. veletisoides*. (A) *G. chisosensis*: holotype male, at 24°C; (B) *G. veletisoides*: (R06-21) type locality (S06-30), at 25°C.

Gryllus chisosensis **Weissman and Gray, n. sp.**

Chisos Mountains Field Cricket
Figs 189–194, Table 1

Distribution. Known only from the Chisos Mountains in Big Bend National Park, Texas.

Recognition characters and song. A sky island, rock associated, completely black except for inside of hind femur (Fig. 192), long cerci probably always longer than ovipositor in situ, always short hind winged cricket. *Song* (Fig. 193, R07-116) a chirp of 4-5 p/c, 90-150 c/m, PR 14-17 at 25°C. Separated from morphologically similar *G.*

longicercus, whose nearest populations are in the Chianti Mountains, just south Shafter, Presidio Co., (or ~116 air km NW of the type locality) by the following: while both taxa have long cerci, > 168 teeth, and associated with rocky habitats, *G. longicercus* generally has more teeth/mm and is not usually found in pinyon-juniper oak woodlands but in open, rocky Sonoran and Chihuahuan desert scrub habitats. The pulse rate in all western *G. longicercus* is typically <14 at 25°C while it is >14 in *G. chisosensis*. This higher pulse rate is approached by some Mt. Lemmon (R90-180, R90-235, R94-76, R09-132, R12-48), and Tucson (R90-240), Arizona, *G. longicercus* but not quite equaled. Even a male *G. longicercus* from Mountainair, New Mexico (S15-52, R15-341), with only 155 file teeth, fewer teeth than any of the 5 males of *G. chisosensis,* sang with a PR of 10.8. But, perhaps most importantly for these isolated crickets, is that their 16S, ITS2, and multilocus DNA profiles are significantly different from that seen in all populations of *G. longicercus.* Also, morphologically similar to sympatric, and more widespread and common, *G. transpecos* but separated (Table 1, p. 18) by no overlap in number of teeth and PR and minor overlap in teeth/mm and cerci length. The latter two taxa are also separated by microhabitat in that *G. chisosensis* prefers deep piles of rocks while *G. transpecos,* while preferring rocky habitats like rocky road cuts, is not associated with deep rock piles. The difference in pulse rate is apparent, in the field, between these three taxa, with *G. chisosensis* somewhat in between the PR of *G. longicercus* and *G. transpecos.*

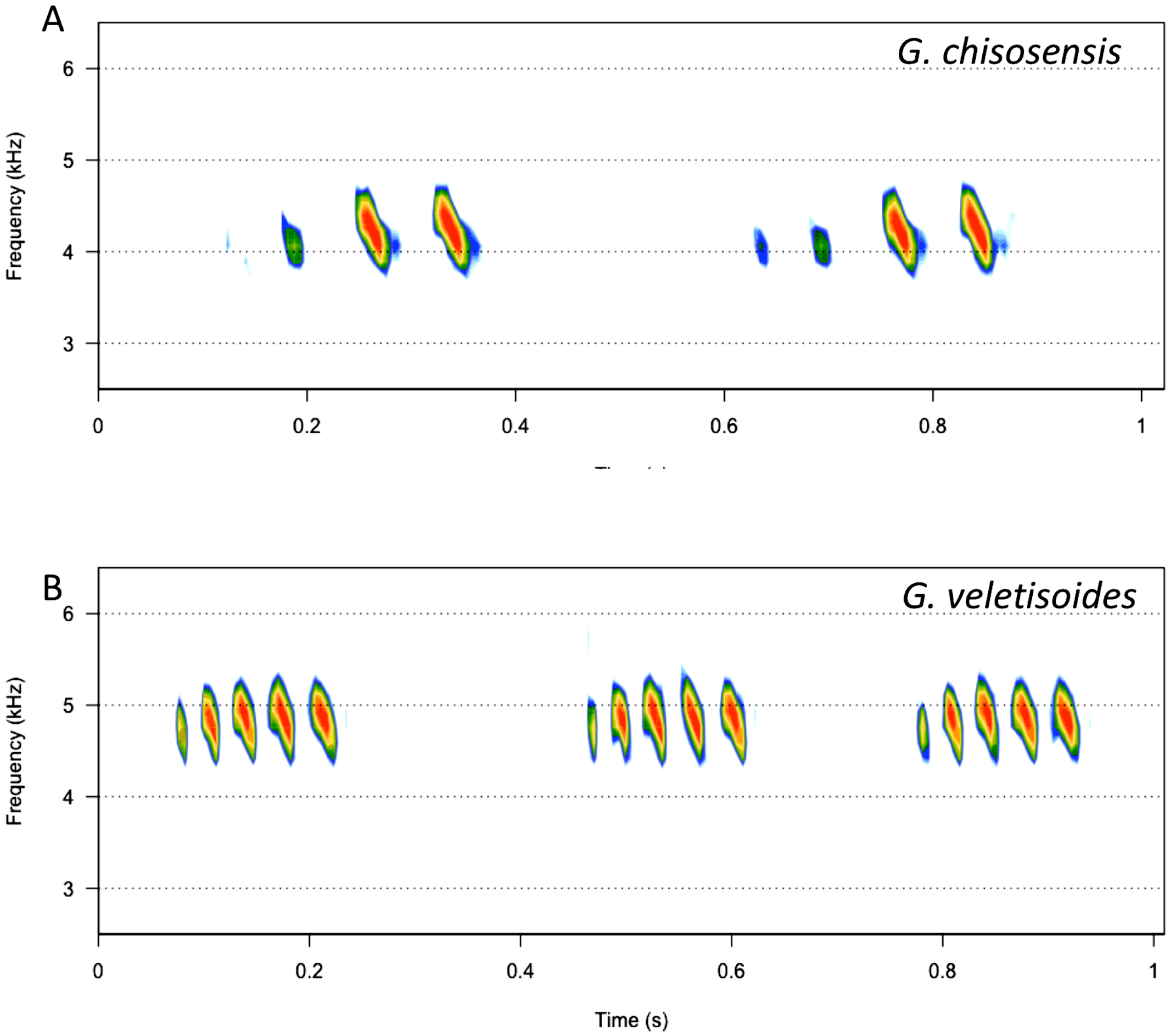

FIGURE 190. One second spectrograms of calling songs of (A) *G. chisosensis* and (B) *G. veletisoides*, same males as in Fig. 189.

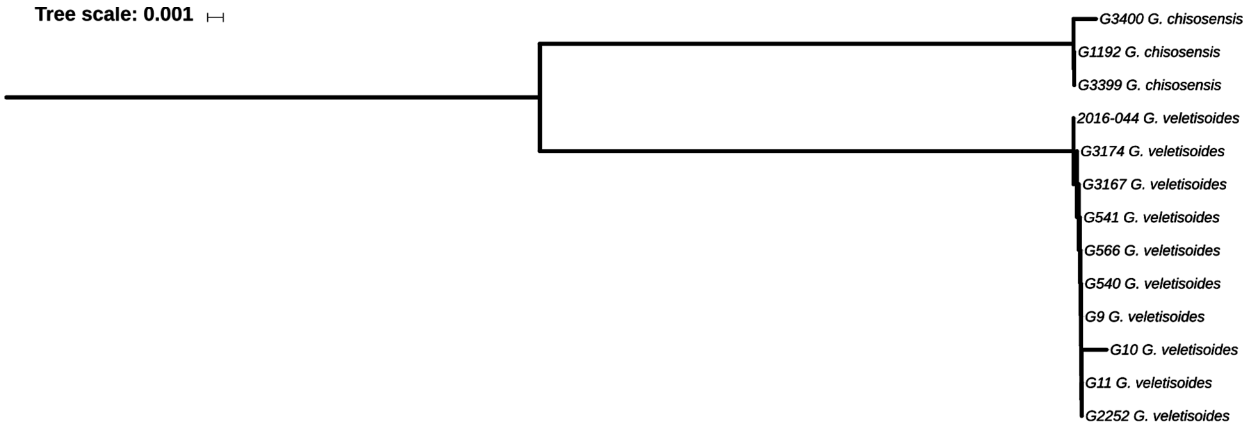

FIGURE 191. ITS2 gene tree. Collection stop numbers for ***G. chisosensis***: S07-36 (G1192); S16-13 (G3399, G3400). Collection stop numbers for ***G. veletisoides***: S03-21 (G9, G10); S03-23 (G11); S06-30 (G540, G541, G566); S12-41 (G2252); S15-81 (G3167, G3174, 2016-044).

FIGURE 192. Holotype male (left) of *G. chisosensis.* Female (right) from near type locality in Big Bend National Park (S16-13).

Holotype. Male (Fig. 192). USA. Texas. *Brewster Co.,* Big Bend National Park, Basin Junction Road, near Lost Mine Trail, 12-vi-2007, 5460’, 29° 16.471’ -103° 17.211’, S07-36, R07-116, G1192, right tegmen removed, 192 teeth, BL 18.32, HF 11.81, left cercus 17.71. Deposited at CAS, Entomology type # 19225. GenBank accession numbers: 16S = MK446451; ITS2 = MK441857.

Paratypes. (4♂ 1♀) **Texas.** *Brewster Co.,* Big Bend National Park, tunnel 18.7 m SE Panther Junction, 9-vi-1985, 2057’ 29° 12’ 08.04” -102° 58’ 38.87” (S85-57) 1♂; 5-vi-1991 (S91-42) 2♂. Basin Junction Road, 28-v-2016, 5555’, 29° 16’ 37.68” -103° 16’ 59.95” (S16-13) 1♂, 1 last instar female (molt to adult 6-vi-2016).

Song records only. Type locality, 5-vi-1991 (S91-41) 1♂.

Derivation of name. Named after the Chisos Mountains, a sky-island mountain range that is the only known locality.

Geographic range. (Fig. 194). Restricted to the Chisos Mountains in the Big Bend region of Texas.

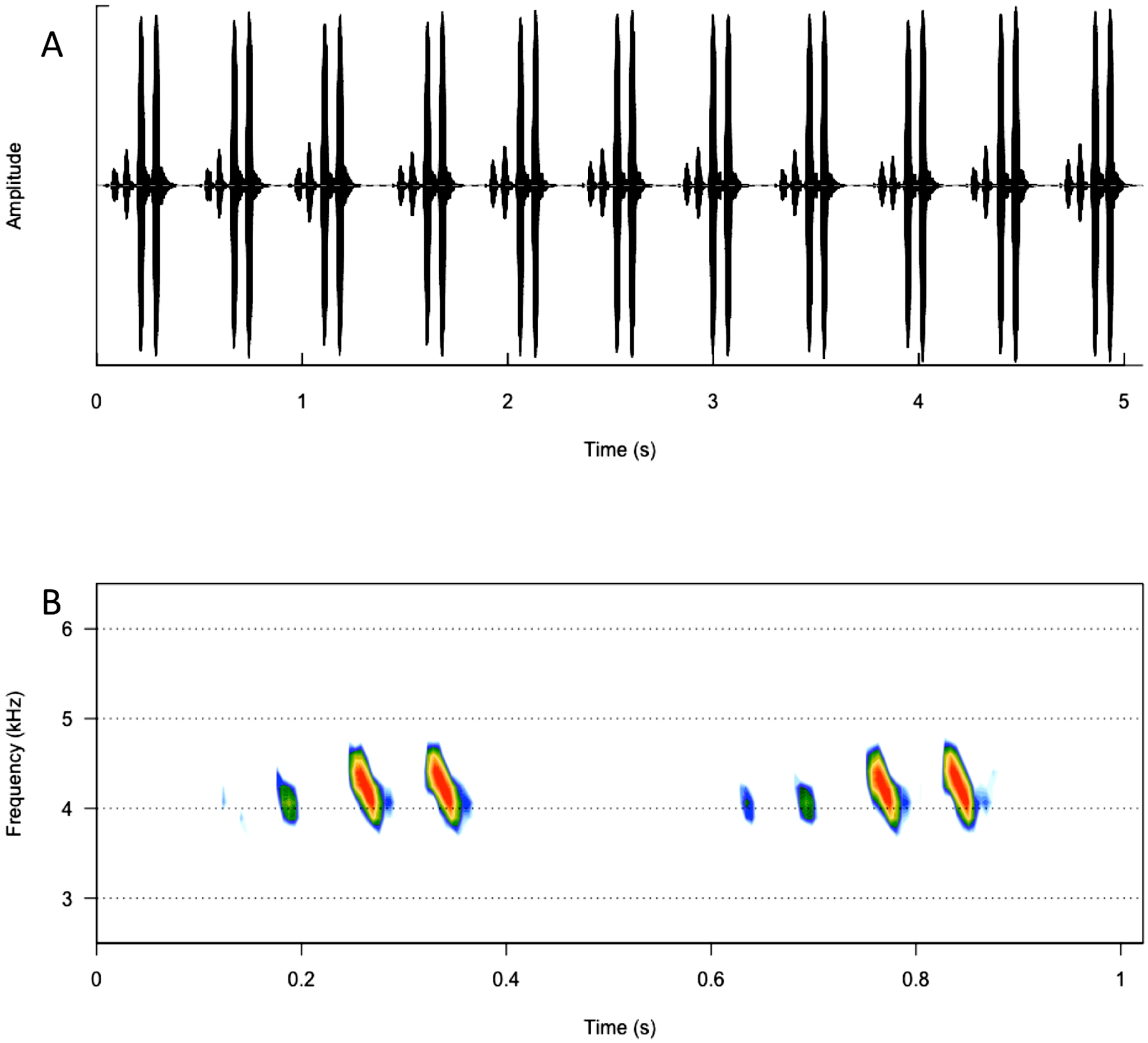

FIGURE 193. Calling song (R07-116) of holotype *G. chisosensis,* recorded at 24°C. Top: 5 s waveform; Bottom: 1 s spectrogram. Note that in this recording, the first two pulses are much quieter than the last two pulses. The four additional recordings that we have of *G. chisosensis* males also show a similar pattern (R85-134 [S85-57]; R91-71 & R91-129 [S91-42], R16-27 [S16-13]). It is fairly common in *Gryllus* for the first few pulses to be of lower amplitude than the last pulses, so we caution that, even if typical for this species, this is not a diagnostic feature.

Habitat. Pinyon-Juniper oak woodland, usually in extensive rock piles on talus slopes. The immediate area around the tunnel on the road to Rio Grande Village is not tree associated, or with talus slopes, but the pulse rate in the 3 males collected there agrees with that from around the type locality. Unfortunately, given the age of the material, no DNA was available for comparison.

Life cycle and seasonal occurrence. Egg diapause not checked but we assume not present. Probably one generation/year. Singing adults only known from May 28th until June 12th as collecting limited. Our only collected female was a last instar on 28-v-2016. No males heard at the tunnel 30 km SE Panther Junction on 28-v-2016 nor attracted to oatmeal.

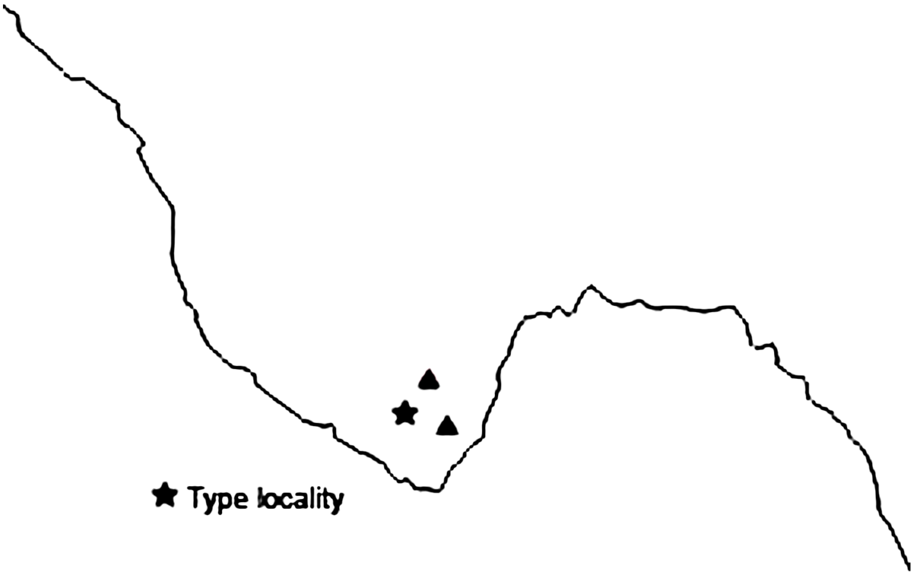

FIGURE 194. Known distribution of *G. chisosensis*.

Variation. Nothing of note in the small series collected by us.

DNA. Multilocus G3400 maps by itself (Gray *et al.* 2019) but associated with the Lineaticeps Group and *G. veletisoides*. ITS2 (Fig. 191) also places *G. chisosensis* near *G. veletisoides*. Despite phenotypic, ecological, and song similarity, *G. chisosensis* and *G. longicercus* are not especially closely related: genetic similarity using Tamura-Nei distances for ITS2 was 98.8 ± 1.02 within *G. chisosensis* (n = 3), and 98.9 ± 0.69 within *G. longicercus* (n = 16), but only 85.3 ± 0.28 between species [Note: ITS2 distances are heavily influenced by repeat regions and gaps; 85% similarity in ITS2 is not equivalent to 15% sequence divergence in coding DNA].

Discussion. In the field, the pulse rate of *G. chisosensis* never sounded slow enough for *G. longicercus*, despite the appropriate rocky habitat, long cerci, and high number of file teeth. Only after uncovering initial significant differences in 16S (ca. 3.4% sequence divergence) and ITS2, with later agreement from multilocus analysis (Gray *et al.* 2019), coupled with its sky island habitat, did we decide to call this a species endemic to the Chisos Mountains. The slower pulse rate could also be distinguished from sympatric *G. transpecos* when both found together at the type locality and at the northwest end of the tunnel 30 km SE Panther Junction (S85-57 and S91-42). This cricket is never common and where found, is difficult to collect since it retreats into the deep rock piles from whence it may continue to sing while rocks are being moved, a behavior seen in other rock-chirping species.

The Chisos Mountains are home to at least two other described endemic orthopteroids: the walking stick *Diapheromera torquata* Hebard and the katydid *Paracyrtophyllus excelsus* (Rehn and Hebard).

Gryllus veletisoides **Weissman & Gray, n. sp.**

West Coast Spring Field Cricket
Figs 137, 138, 189–191, 195–200, Table 1

‘G. VII’ of Weissman & Rentz 1977a.
G. veletis of Weissman *et al.* 1980.
G. veletis and ‘G. western veletis’ of DBW notebooks.

Distribution. California and Oregon west of the Sierra Nevada and Cascade Mountain Ranges.

Recognition characters and song. Medium sized, cerci short (usually <10 mm) and never as long as ovipositor in situ, black except for occasional red area on inside hind femur (Fig. 195), almost always short hind winged, wide pronotum, spring and summer species usually associated with grassy, frequently moist areas. Song a slow, usually irregular chirp (Fig. 196, R06-21)) with 4-5 (range 3-6) p/c and a PR generally from 21 to 30 at 25°C. There are only three *Gryllus* species with overlapping distributions and similar slow chirp songs: *G. brevicaudus* has a shorter ovipositor, slightly longer cerci, and a unique (especially in males) yellow-orange tinged area on the lateral tegmina field; *G. pennsylvanicus* overlaps in distribution only in west-central Oregon and differs (Table 1, p. 18) from *G. veletisoides* by having more file teeth, a slower PR, and an egg diapause that results in summer, and not spring adults; and *G. saxatilis* which differs in habitat (usually much drier and with rocks), longer cerci, and more teeth in file.

FIGURE 195. Right: Holotype male of *G. veletisoides*. Left: Female of G. *veletisoides*, also from type locality (S06-30).

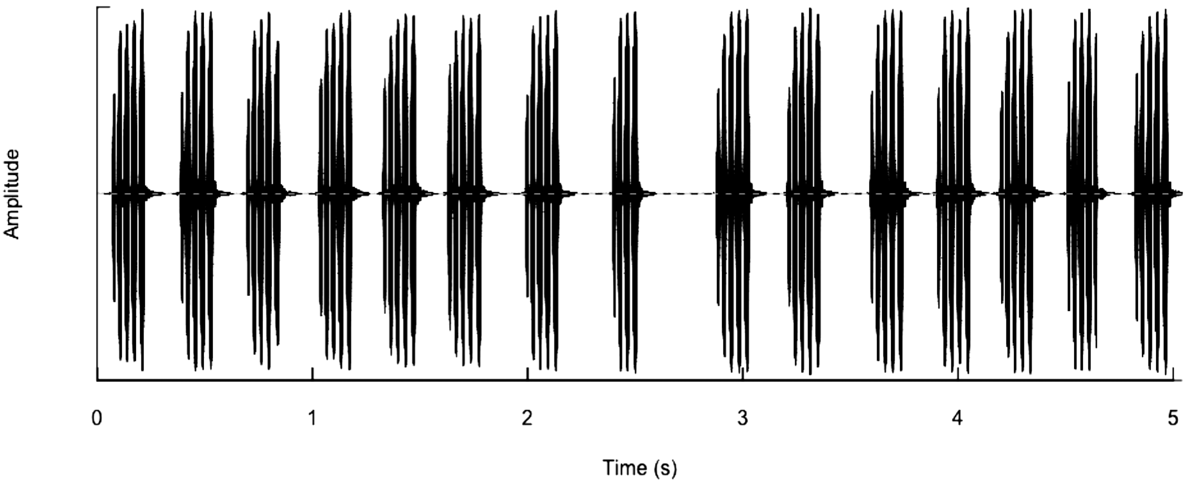

FIGURE 196. Calling song (R06-21) of *G. veletisoides* from type locality (S06-30), recorded at 25°C.

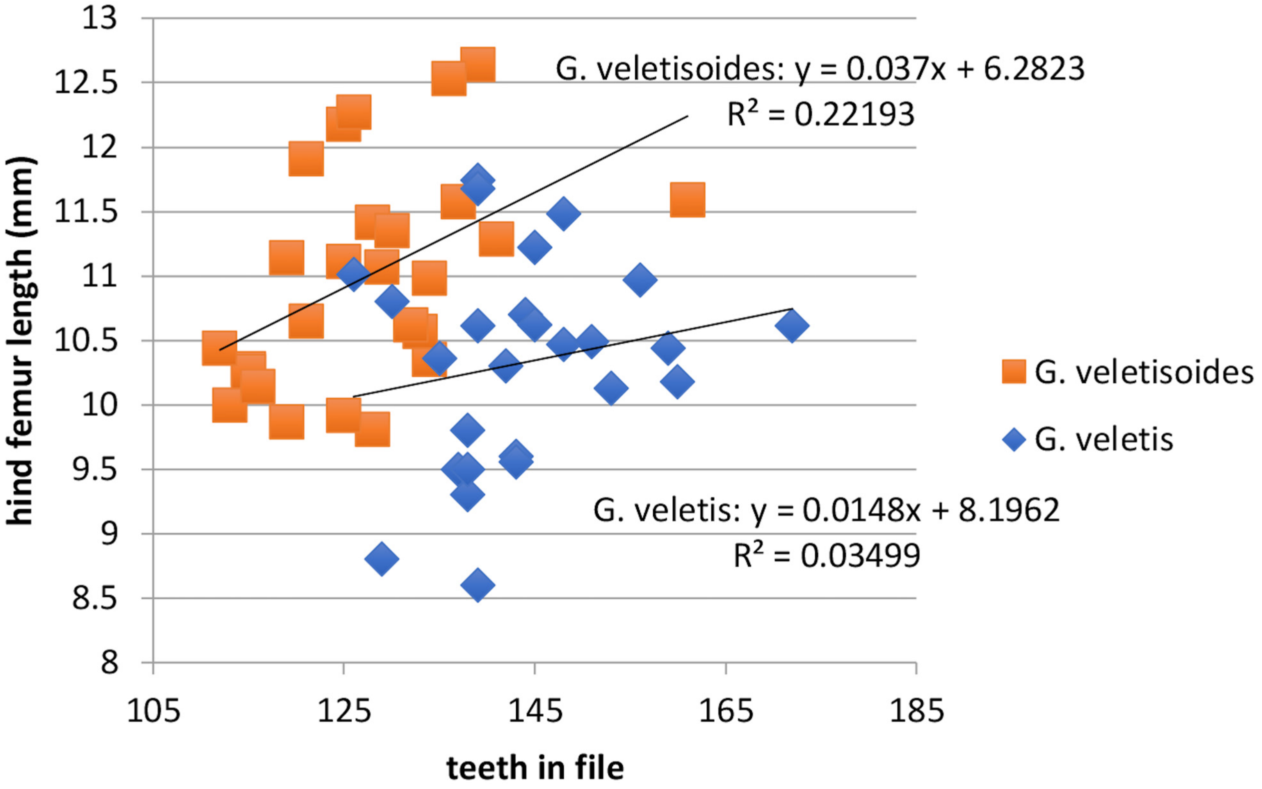

FIGURE 197. Regression file teeth number vs. hind femur length in *G. veletisoides* vs. *G. veletis.*

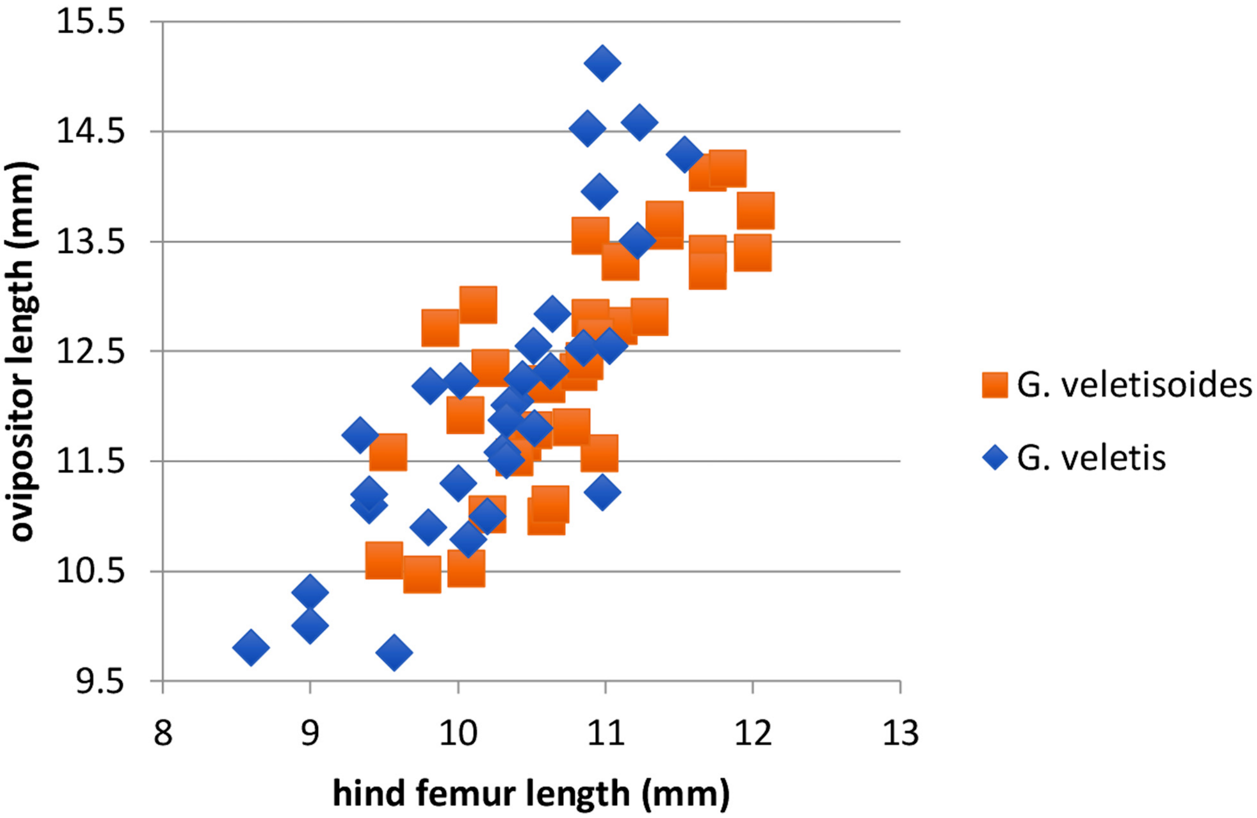

FIGURE 198. Regression hind femur length vs. ovipositor length in *G. veletisoides* vs. *G. veletis.*

Differs from morphologically similar, always allopatric *G. veletis* by geography (latter always east of the Sierra Nevada and Cascade Mountain Ranges), relatively fewer teeth in the file (Fig. 197), and different DNA (Fig. 6, p. 28). They are not separated by ovipositor length (Fig. 198). The two taxa are some 120 km apart between the nearest California localities of Acton (S09-26) and Barstow (S03-73).

Holotype. Male (Fig. 195). USA, California, Santa Clara Co., Los Gatos, Los Gatos Creek at Lark Ave., 10-v-2006, 82m, 37° 15' 09.41" -121° 57' 47.52. D.B. Weissman. S06-30, R06-22, G566. BL 20.84, HF 11.08, RC 8.48. GenBank accession numbers: 16S = MN136662; ITS2 = MN136861. Right tegmen removed 132 teeth, file length 2.9, TL 9.4, TW 3.9. Type deposited in CAS, Entomology Type #19276.

Paratypes. (Total 134♂ 82♀). **California.** *Calaveras Co.,* Lake Comanche Recreational Area near Valley Springs, 15-vi-2013, 74m, 38° 13' 28.18" -120° 55' 27.46" (S13-37) 5♂ 5♀. *Colusa Co.,* Colusa Sacramento River SRA, 18-vii-2015, 96' (S15-81) 39° 13' 12.3" -122° 00' 56.1, 4♂ 8♀. Willows, 29-viii-2003, 120' (S03-87) 2♂ 1♀. *El Dorado Co.,* Finnon Reservoir, 29-iii-2005, 2340' (S05-39) 1♂ 1♀. *Fresno Co.,* Fresno, 6-vi-1980, 2♂. Jacalitos Canyon, 18-viii-2001, 840-1020' (S01-97) 2♂; 4-v-2003 (S03-31 & 32) 3♂. Kingsburg, 18-iv-2003, 340' (S03-21) 3♂; 4-v-2003, (S03-25) 14♂ 5♀. *Kern Co.,* Bakersfield, Kern River bed dry wash at Cal State Bakersfield, 5-viii-1980, 372' (S80-70) 3♂ 2♀; 18-vi-2012 (S12-43) 1♂. Sand Ridge 4 m N Edison, 22-xii-1983, 1000', (S83-163) 1♂. *Los Angeles Co.,* Acton, 29-vi-2003, 2800' (S03-75) 1♂ 1♀; 17-vi-2012 (S12-41) 1♂ 1♀. Santa Clara River bed near Acton, 28-v-2009 (S09-26) 1♂ 1♀. *Marin Co.,* San Rafael, 21-vii-2007 (S07-75) 1♂. *Mariposa Co.,* El Portal, El Portal Middle School, 25-iv-2010, 1700' (S10-12) 5♂. *Merced Co.,* 4 m E Dos Palos, 29-viii-1981 (S81-75) 2♂ 4♀. *Monterey Co.,* King City, 7-viii-1980 (S80-77) 2♂. *San Benito Co.,* Pinnacles National Monument, Chalone Campground, 22-iv-2006, 1070' (S06-14) 2♂. Hwy. 25 1.2 m S Paicines, 1-viii-1980, 1000' (S80-53) 3♂. Hwy. 25 4.5 m N Paicines, 1-viii-1980 (S80-54) 1♂. Road to Fremont Peak State Park 4.7 m S Hwy. 156, 21-iii-2003, 600' (S03-6) 3♂ 3♀. *San Luis Obispo Co.,* 3 m S Nipomo, 15-iii-1985, 200' (S85-35) 1♂ 2♀. Santa Margarita, 23-vi-1992, 800' (S92-55) 3♂. *Santa Barbara Co.,* Guadalupe, 15-iii-1985 (S85-33) 2♀. Hwy. 166 0.7 m W Santa Maria, 23-vi-1992, 0' (S92-56) 7♂ 4♀. *Santa Clara Co.,* Campbell, 3-viii-2005, 250' (S05-71) 2♂. Los Gatos, 3-iv-1990 (S90-27) 2♀; 20-ii-1995 (S95-17) 1♂; early July (S03-77) 1♂. Type locality, 6-iii-1995 (S95-2A) 1♂; 2-x-1995 (S95-103) 1♂; 14-viii-1997 (S97-119) 7♂ 7♀; 12-ix-2000 (S00-45) 1♂; 22-iv-2002 (S02-4) 1♂ 1♀; 5-vii-2003 (S03-82) 1♂; 10-v-2006 (S06-30) 12♂ 11♀. Palo Alto, 14-iv-1984 (S84-16) 2♂ 1♀. Mt. View, 9-vi-1982 (S82-20) 1♂. San Jose, 15-viii-1980 (S80-78) 2♂; 16-v-1987 (S87-28) 3♂ 3♀. Stanford University, Lake Lagunita, 26-viii-1983 (S83-113) 1♂; 2-v-1992 (S92-45), song record only. *Santa Cruz Co.,* Ben Lomond, near E Zayante Fire Station, 31-iii-1995, 300' (S95-26) 3♂ 1♀; 20-iv-1996 (S96-24) 3♂ 2♀; 23-iv-2003, (S03-23) 4♂ 1♀. Santa Cruz, 1113 Laurent St., 13-ix-2015 (S15-120) 1♂. *Siskiyou Co*., Yreka (S83-35) 2♂. *Solano Co*., Lake Solano County Park, 5-viii-2014, 168' (S14-60) 1♂. *Stanislaus Co*., Road J9 2m N junction with J17, 5-viii-1980 (S80-69) 1♂. 14.5 m E Gilroy, 29-viii-1981 (S81-78) 2♂. *Sutter Co.,* Sutter Buttes, 14-iii-2015 (S15-2) 1♀. *Tulare Co.,* 1.2–3 m E Springvale, 4-v-2003, 1200' (S03-26 & 30) 4♂. *Ventura Co.,* Los Padres National Forest, Reyes Creek, 3735', 8-v-2005, 34.67920 -119.30810 (DAG 2005-058) 1♂. **Oregon.** *Benton Co.,* Corvallis, 25-v-1983 (S83-38) 3♂ 1♀. *Jackson Co.,* Phoenix, 24-ix-2004, 1500' (S04-132) 1♂. Rogue River, 30-v-1983, 1100' (S83-34) 5♂ 5♀. *Josephine Co.,* Selma, 30-v-1983 (S83-37) 1♂. *Lane Co.,* Eugene, 200', 18-viii-2005 (S05-78) 1♂; 16-vi-2006, (S06-33) 4♂ 4♀.

Song records only. **California.** *Los Angeles Co.,* California State University Northridge, Botanic Garden area, 8-v-2003, 812' (S03-47), at least 3 males heard; most southern known locality.

Derivation of name. Named in reference to its being morphologically and song-wise almost indistinguishable from *G. veletis*.

Geographic range. (Fig. 199). Includes California's Central Valley and the western foothills of the Sierras (El Portal, S10-12), and up to 1138m in Ventura Co.

Habitat and behavior. Usually areas with increased moisture like open meadows, along streams, and watered gardens but also in vegetation in dry river beds (Acton, S12-41) and canyons (Jacalitos Canyon, S03-31 & 32) all usually at elevations below 850m. At Ben Lomond, Santa Cruz Co., CA, on sandy substrate. Many males sing from under cover of vegetation. Several adult females can be found together under rocks and boards; such associations also seen, but rarely, in adult males (e.g. El Portal, S10-12). Such social behavior is in contrast to the more solitary nature described for eastern *G. veletis* (Alexander & Bigelow 1960), but consistent with *G. veletis* in the west (see discussion under *G. veletis*, p. 145).

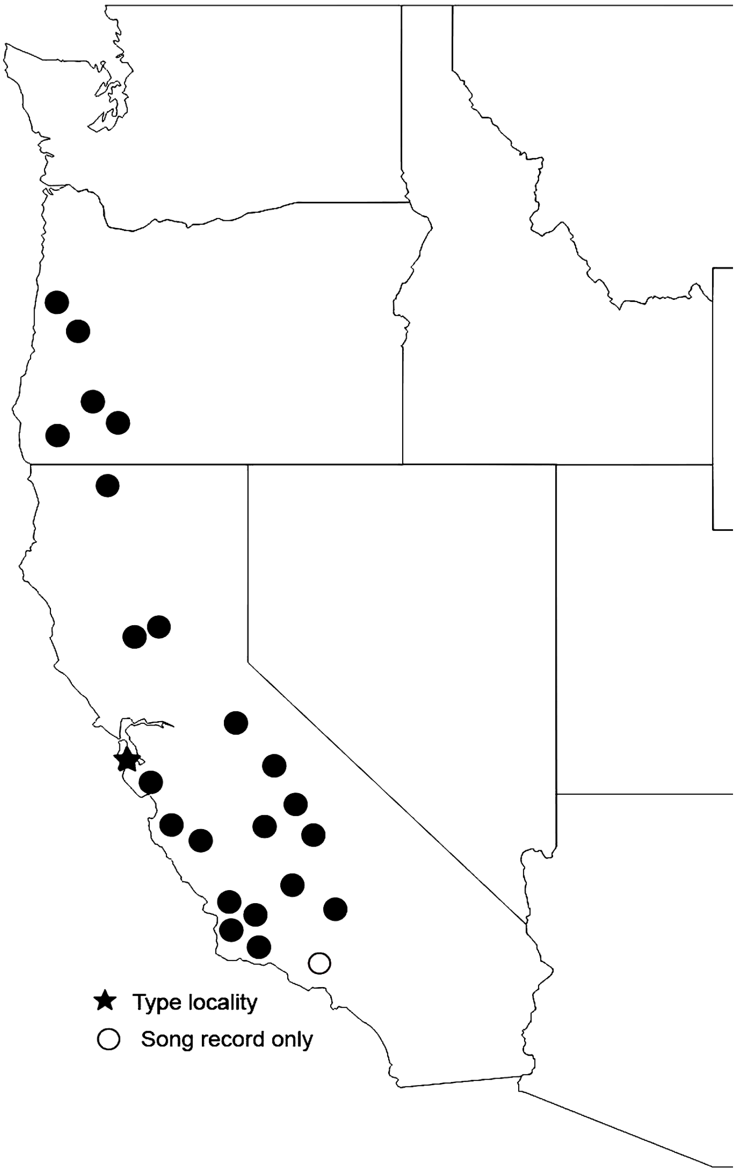

FIGURE 199. Known distribution of *G. veletisoides.*

Life cycle and seasonal characteristics. No egg diapause. Most areas with one generation/year but in selective California populations (e.g. Merced Co., S81-75, and probably other Central Valley localities; Santa Cruz, S15-120; Los Gatos, S97-119 & S00-45; and Campbell, S05-71), in certain, but not every year, one finds DNA confirmed (see G3334 under "DNA" below) second generation adults, although never as common or as widely distributed as first-generation adults. There is an almost 6-week period (mid-June to end of July) during which no males of *G. veletisoides* are heard singing in Santa Clara Co., CA. Eggs from these second-generation females also without an egg diapause (Los Gatos, CA, S97-119) but the hatching nymphs appear to be inconsequential for future generations because they do not become late instars (at which time they can overwinter) before the onset of winter and apparently die off as early instars. Two alternative interpretations for these "second generation" adults are possible: (1) Most eggs laid by first generation females hatch without a diapause but a low percentage have a delay of a few months and nymphs from those latter eggs do not mature until late summer (see Walker 1980 for a discussion of different egg hatching rates in *G. firmus).* (2) These "second generation" adults could be the adults of those "second generation" adults from the previous year, and they overwinter as very early instars or as eggs in diapause. We have not done the careful analysis needed to examine (1). We doubt (2) because even eggs or early instars that overwinter should molt to adult before August. By way of comparison, *G. pennsylvanicus* has diapausing eggs that overwinter yet next year's adults start singing in early August (Alexander & Meral 1967). Adults of *G. veletisoides* are known from Los Gatos, CA, from 20-ii (S95-17) to 2-x (S95-103) and also from 22-xii-1983 (Sand Ridge, CA, S83-163). The latter 1983 male might be either a second generation 1983 adult or a first generation 1984 adult. We suspect that more late summer collecting within the study area would uncover more of these second-generation populations. On the other hand, the only male heard and collected from Phoenix, OR (S04-132) on 24-ix-2004, is undoubtedly a late surviving first generation male since the weather is probably too cool in coastal southern Oregon to enable maturation of a second generation.

Variation. **Hind femur color:** Usually solid black (Fig. 200) although some with majority of inner aspect reddish. **Hind wing length:** Only one male (Kingsburg, Fresno Co., S03-25) with long hind wings from more than 200 adults. **Tegmina color:** Most black with few brown. All 5 females from Calaveras Co. (S13-37) with tegminal bars. **Cerci length:** Only 1 male (Fresno Co., S03-25) and 1 female (Calaveras Co., S13-37) with cerci longer than 10mm. Cerci are so short that usually intact even late in the season.

FIGURE 200. More typical dark color, this male *G. veletisoides* from Fresno Co., CA (S03-21).

DNA. Multilocus G568 first generation Los Gatos, S06-30 (type locality, collected 10-v-2006); and G3334 second generation Santa Cruz, S15-120 (collected 13-ix-2015) map (Gray *et al.* 2019) nearest to *G. chisosensis* and Clades 2 and 3 of *G. montis*, and distant from *G. veletis*. Despite their similarity, *G. veletis* and *G. veletisoides* are not close relatives within the North American *Gryllus*. Genetic similarity using Tamura-Nei distances for ITS2 was 96.7 ± 2.66 within *G. veletis* (n = 25 from across both *G. veletis* ITS2 clades, see *G. veletis* description and Discussion), and 99.9 ± 0.08 within *G. veletisoides* (n = 10), but only 88.9 ± 0.27 between species.

Discussion. Along with *G. brevicaudus* and *G. lineaticeps*, the earliest singing field cricket in the San Francisco Bay area. Populations of *G. veletisoides* can have high densities.

Preliminary hybridization studies conducted in 2003 between California virgin *G. veletisoides* and virgin *G. veletis* from the Midwestern US, before we had genetic data, produced the following results: 3 females from Indiana crossed with Fresno, CA, males—two females had documented matings (with visible passed spermatophores) but only one of these two female laid eggs. The third female also laid eggs. No eggs from any female hatched. One female from Illinois mated with a Fresno, CA, male and laid eggs but none hatched. One female from Iowa matched with a male from Los Gatos, CA, laid eggs (never saw a passed spermatophore) but none hatched. Thus, from eggs laid by four Midwestern females, no eggs hatched. As controls, an Indiana female mated with a North Dakota male produced lots of eggs that hatched while a North Dakota female that mated with an Illinois male produced eggs that didn't hatch.

The Montis Group

G. montis Weissman & Gray, n. sp.

An almost certainly polyphyletic grouping of four genetic clades of chirping crickets which are all found under tree cover in mountainous regions of the Southwestern US (Fig. 201). They remain indistinguishable to us except by DNA, which is why we have lumped them together as a single "Group." We discuss the characteristics and distributions of all four DNA Clades here, but we note that DNA Clade 4 is phylogenetically a stand-alone entry related to the Saxatilis Group. The relationships among DNA Clades 1-3 are not consistently resolved by 16S and ITS2, and also vary based on which analysis is applied to the multilocus data (Gray *et al*. 2019). In all cases, song is typically a slow chirp with four-pulses per chirp (Fig. 202).

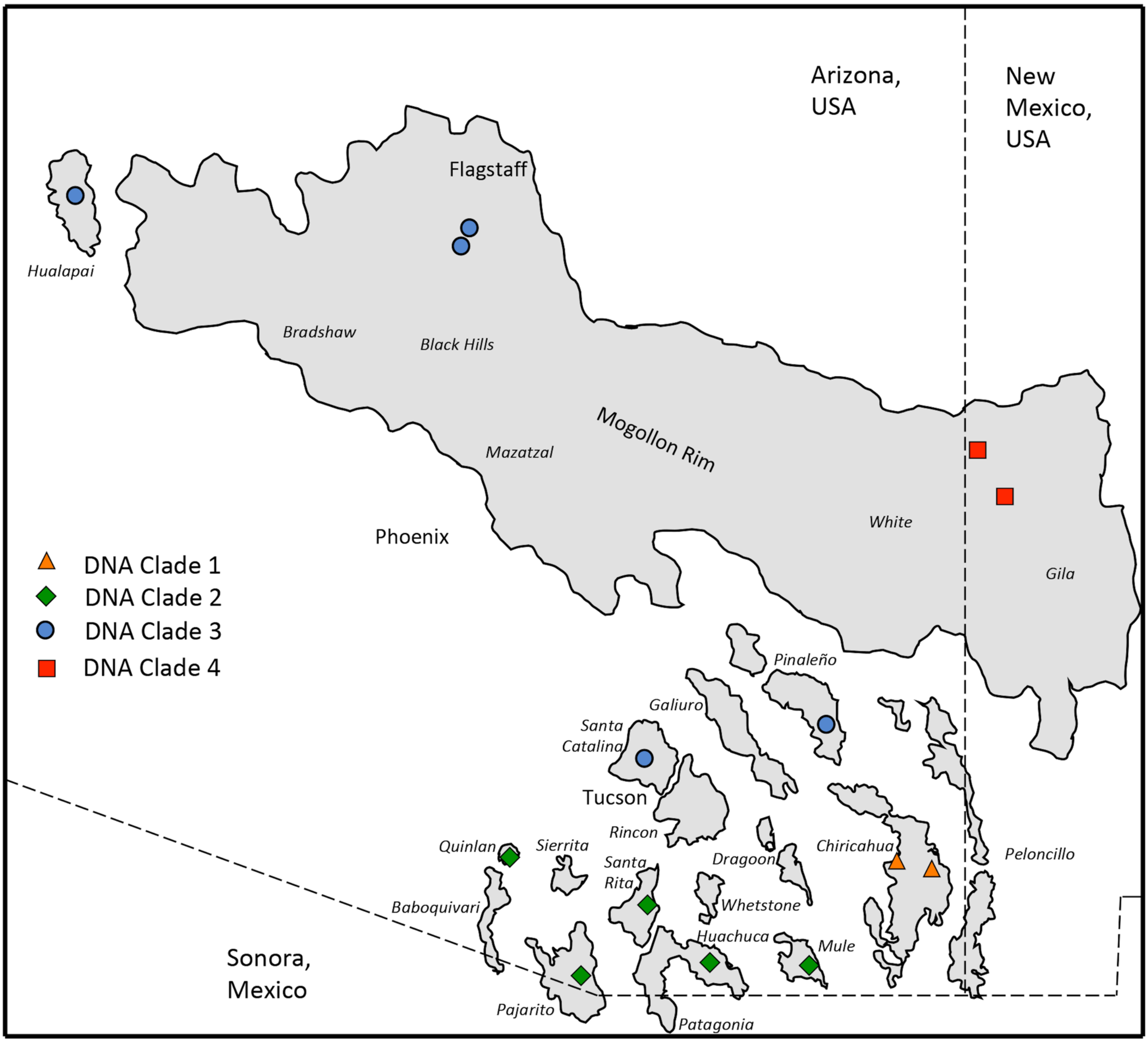

FIGURE 201. Known distribution of *G. montis*, with locality coding based on multilocus DNA Clade.

Gryllus montis Weissman & Gray, n. sp.

Mountain Wood Cricket
Figs 132, 201–206, Table 1

'G. #25, #31', 'mountain Gryllus' and 'red legged Gryllus' of DBW notebooks.

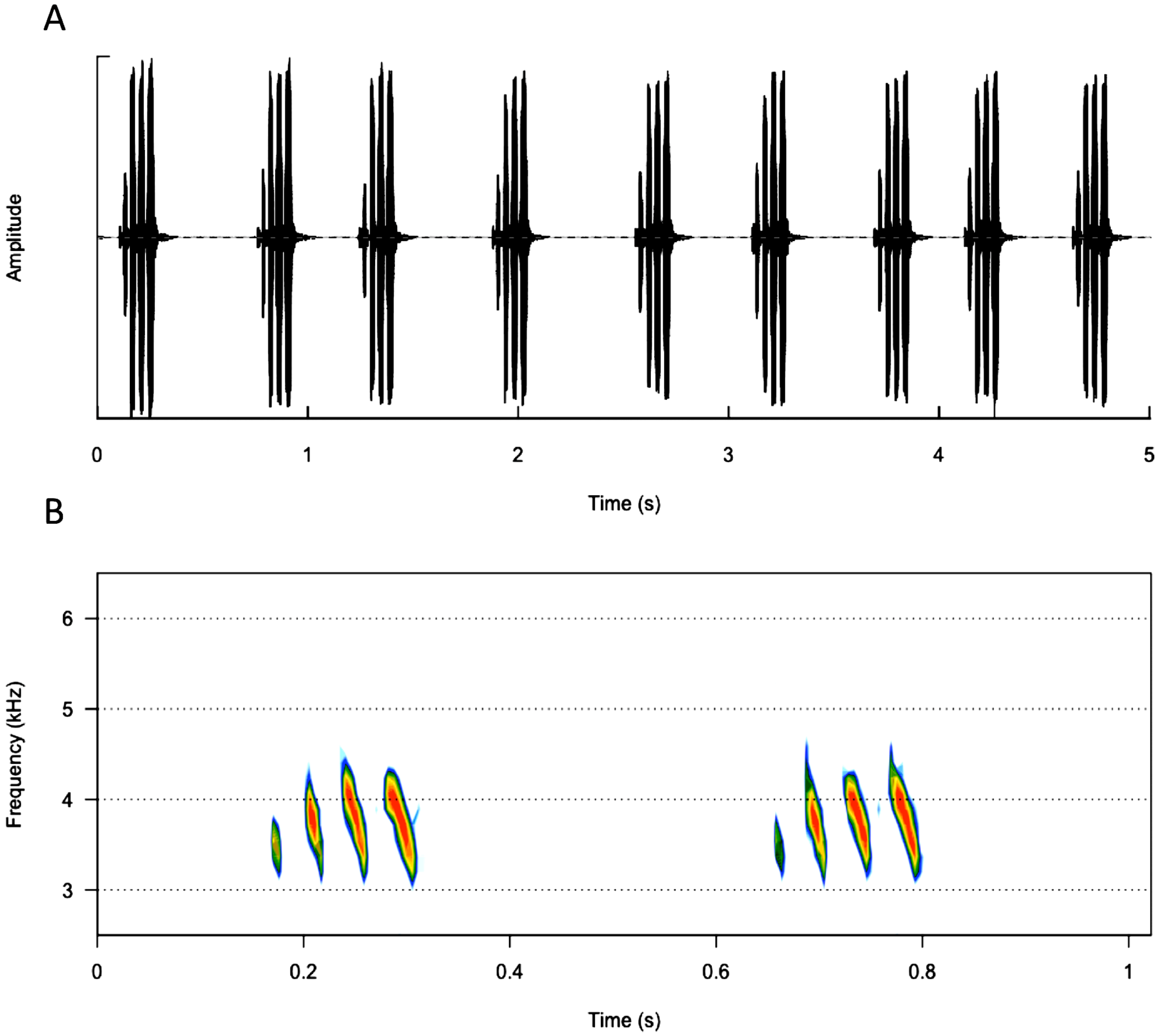

FIGURE 202. A. Typical calling song of *G. montis* (R13-71) from the type locality (S13-17), recorded at 25.5°C. B. One second spectrogram of typical calling song of *G. montis,* same male as in A.

Distribution. Arizona and western New Mexico.

Recognition characters and song. A polyphyletic complex of sky island taxa, with variable and geographically structured DNA, that we treat here as one "species" because of absence of clearly distinguishing morphological, song, or ecological characters to separate what appears to be up to 4 clades (see Discussion below). A small to medium sized, narrow body, short tegmina, early maturing, generally with black head and pronotum, leaf litter inhabiting, slow chirping cricket found in mountainous, wooded terrain from 1280–2560m, almost always with a tree canopy overhead. Cerci medium length, never longer than ovipositor in situ. Tegmina in both sexes black but can have a tegminal bar, especially in females with reddish hind legs. Hind legs usually black except for reddish inner aspect of hind femur, although most individuals in populations from western New Mexico and Ramsey Canyon, Arizona, have entire rear leg reddish. Frequently the only *Gryllus* at a site and populations, with few males singing, can be dense. *Song* (Fig. 202, R13-71) 3–5 p/c (range 3–6), 90–150 c/m, PR at 25°C 18–25 (range 17.5–27.8).

G. montis can be separated from other slow chirping western US taxa, as follows: DNA Clade 2 individuals from type locality (Ramsey Canyon, AZ) and DNA Clade 3 individuals most genetically similar to Mohave Desert-separated, and allopatric *G. veletisoides* but distinguished by cerci 2–4 mm shorter in *G. veletisoides* which is only found at low elevations and not associated with mountain top woodlands. From Organ Mts., New Mexico, endemic *G. sotol* (nearest populations are ~265 km apart), separated by later maturing, generally more teeth/mm in *G. sotol* which is associated with open Chihuahuan Desert as opposed to under mountain top tree covered habitats. From ecologically, morphologically and DNA Clade 1 genetically similar but allopatric (nearest populations are ~510 km apart on opposite sides of the Rocky Mts.) Davis Mts., Texas, endemic *G. planeta,* by *G. montis* having a slower pulse rate (Table 1, p. 18), slightly longer cerci, and longer ovipositor. From morphologically and similar song *G. lightfooti*, distinguished by microhabitat: under tree canopy for *G. montis* vs. more open, adjacent shrub-grasslands, frequently with *Yucca elata*, for *G. lightfooti*. *G. montis*, despite being at higher, cooler elevations, can become adult a full month before *G. lightfooti*. Cerci in *G. montis* never longer than ovipositor in situ while some 50% of *G. lightfooti* females are. Adult female *G. lightfooti* typically have distinctive tegminal bars while few females of *G. montis* do. Chirp rate is more rapid in *G. lightfooti*. Also, morphologically similar to *G. veletis* but distinguished by cerci 2–4 mm longer in *G. montis* and the latter's preference for tree cover. *G. montis* DNA Clade 4 and *G. veletis* are microsympatric at NM, Catron Co., just southwest of Reserve (S01-39) and 3.5 km south of Reserve (S07-53), and separable there by longer cerci length in faster chirping *G. montis* with entire hind leg reddish, as opposed to almost solid black hind legs of *G. veletis*. Separated from allopatric (nearest populations are 480 km apart on opposite sides of the Continental Divide) *G. transpecos* by ITS2 genetics, habitat, shorter ovipositor and longer cerci in the latter. Compared to occasionally sympatric (Kitt Peak, S13-36; road to Hualapai Mt Park, S90-56; Bog Springs, Madera Canyon) *G. longicercus*, cerci shorter than ovipositor tip in *G. montis* with less file teeth and a faster pulse rate (Table 1, p. 18). Similar to slow chirping *G. saxatilis* but *G. montis* has shorter cerci, a non-rocky habitat, and earlier maturation when individuals from similar elevations compared.

Holotype. Male (Fig. 203): Arizona, Cochise Co., Ramsey Canyon Reserve near Sierra Vista, 1-vi-2013, 5233', 31° 27' 34.7" -110° 17' 44.6". S13-17, R13-67, G2475. 16S GenBank accession # MK446561; ITS2 GenBank accession # MK441899. BL21.46, HF 11.4, LC 10.93. Right tegmen removed: 128 teeth, FL 3.35, TL 10.8, TW 4.55. Type deposited in CAS, Entomology #19266.

FIGURE 203. Holotype male (left) and type locality female (right) of *G. montis.*

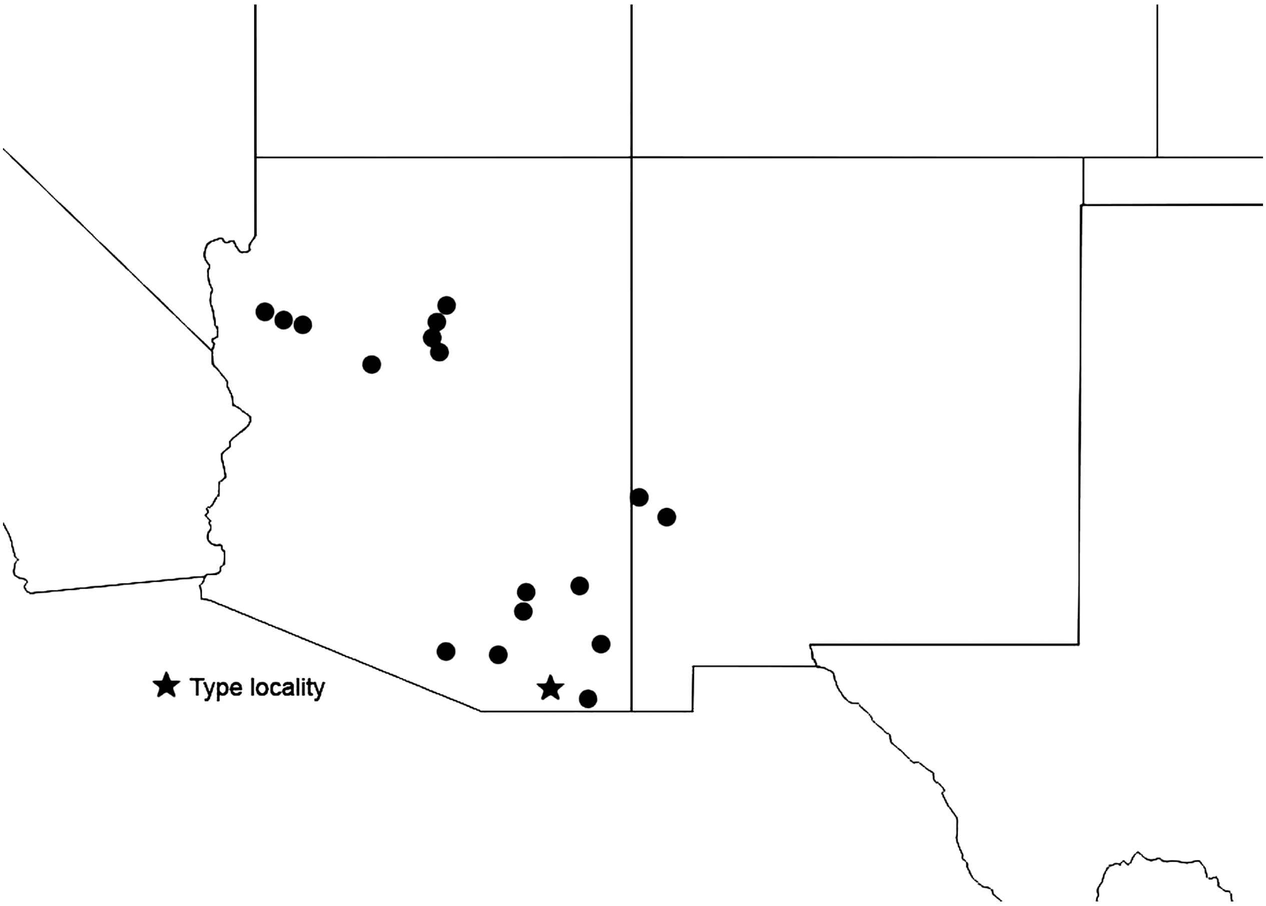

FIGURE 204. Known distribution of *G. montis.*

Paratypes. (267♂ 189♀). **Arizona**: **Clade 1:** Chiricahua National Monument, Visitor's Center, 5348', 2-vi-2013 (S13-21) 15♂ 10♀. Portal, Southwestern Research Station, 20-viii-2012, 5400' (S12-103) 1♂ 4♀. Chiricahua Mts., Herb Martyr Dam Campground, 5620', 22-vi-2008 (S08-51) 3♂ 1♀, DC Lightfoot. Cave Creek Canyon, Sunny Flat Campground, 5107', 21-vi-2008 (S08-50) 6♂ 3♀, DC Lightfoot. **Clade 2:** *Cochise Co.,* Bisbee, 5500', 1-vi-2013 (S13-18) 7♂ 6♀. Coronado National Forest, Reef Campsite, 29-ix-2012, 7150', 31.42873° -110.28987° (S12-123) 5♂ 2♀, all collected as nymphs. Huachuca Mts., Parker Canyon Lake, 7-iv-2004, 5400' 4♂. Ramsey Canyon Preserve, 1-vi-2013 (S13-17) 15♂ 18♀. *Pima Co.,* Kitt Peak, 17-vi-1990 (S90-52) 3♂ 4♀; picnic area at mile 10.5, 6277', 8-vi-2013 (S13-36) 9♂ 5♀. *Santa Cruz Co.,* Madera Canyon Rec Area, 4900', 26-vii-1990, (S90-79) 14♂ 12♀; 5-vii-1994 (S94-57) 7♂ 5♀; 11-ix-2010, as nymphs, 5887', 2010-082 1♂. Pajarito Mts., Sycamore Canyon, 4017', 8-iv-2004, 31.4303° -111.1895°, 1♂, as nymph. **Clade 3:** *Coconino Co.,* Sedona, 4680', 25-vi-1980 (S80-44) 2♂; 16-v-1995 (S95-37) 1♂; 12-vi-1996 (S96-62) 1♂. Hwy 89A 4 m N Sedona, 4900', 25-vi-1980 (S80-43) 1♂; 12-vi-1996 (S96-63) 3♂ 3♀; 15-vi-2007 (S07-60) 4♂ 8♀. Hwy 89A 6 m N Sedona, 5350', 15-vi-2007 (S07-59) 3♂. Hwy 89A 8.9 m N Sedona, 15-vi-2007 (S07-58) 2♂ 1♀. 9 m S Flagstaff on Hwy 89A, MP 390, 6500' 5-viii-1991 (S91-76) 10♂ 6♀. 15 m S Flagstaff on Hwy 89A, 6000', 25-vi-1980 (S80-42) 12♂ 13♀. *Graham Co.,* Pinaleño Mts., Hwy 366, Mt. Graham, 5000-8400', 4-vii-1994 (S94-53) 10♂ 3♀; 10-vi-2012, 7900' (S12-18) 11♂ 4♀. *Mohave Co.,* Hualapai Mt. Park, 6700', 19-vi, 1990 (S90-55) 11♂ 11♀; 3-viii-1991 (S91-62) 1♂ 2♀; 16-vi-2007 (S07-62, 63) 6♂ 1♀. Road between Hualapai Mt. Park and Kingman: 12.7 m SE Kingman, 6000', 3-viii-1991 (S91-63) 4♂ 5♀; 13-vi-2012 (S12-30) 15♂ 10♀. 11 m SE Kingman, 5700', 3-viii-1991 (S91-64) 2♂; 16-vi-2007 (S07-65) 2♂. 8.7 m SE Kingman, 5400', 19-vi-1990 (S90-56) 4♂; 3-viii-1991 (S91-65) 9♂ 8♀; 13-vi-2012 (S12-31) 3♂ 2♀. Mt. Lemmon Recreational Area, Mile 13, 5900', 27-vii-1990 (S90-81) 6♂ 1♀; 7-vii-1994 (S94-60) 8♂ 6♀; Mile 11.7, 5800', 27-vi-2009 (S09-50) 3♂ 4♀; Mile 11.3, 5840', 11-vi-2012 (S12-22) 8♂ 18♀. Oracle, 4260', 18-viii-1998 (S98-64) 4♀. *Yavapai Co.,* Prescott National Forest, Hwy 89A 25 m NE Prescott, 6820', 30-vi-1994 (S94-38) 7♂. Sedona Airport, 12-vi-1996, 5060' (S96-61) 2♂; 15-vi-2007 (S07-61) 1♂. **New Mexico: Clade 4:** *Catron Co.,* Reserve, 5870' 20-v-2001 (S01-39) 3♂. Hwy 12 2.2 m SW Reserve, 6020', 3-vii-1994 (S94-51) 10♂ 1♀

(female collected as last instar); 20-v-2001 (S01-40) 2♂ 1♀; 14-vi-2007 (S07-53) 2♂ 5♀. Hwy 180 1 m E AZ—NM border, 7880', 20-v-2001 (S01-41) 4♂, 1 male nymph; 14-vi-2007 (S07-54) 4♂ 3♀.

Derivation of name. "montis" meaning of the mountains to reflect where this complex is found.

Geographic range. Fig. 204.

Habitat. Straminicolous (living in leaf litter), highest known inhabiting US *Gryllus* and, along with geographically restricted *G. planeta*, only obligate forest *Gryllus* west of Texas. Found in most (every?) sky island woodlands above 1250m of western New Mexico and Arizona. Associated with oaks, pines and occasional junipers and living in leaf litter on forest floor. Also in riparian situations with ash and sycamores (AZ, 6 m N Sedona, S07-59). Rarely in open dirt area at 2408m surrounded by pines (AZ, Mt. Graham, S12-18). After sunset, individuals of both sexes walk around on top of leaf litter with males rarely singing. Nevertheless, some males (e.g. S07-54, near AZ-NM border) sing well into the night at low temperatures that suppress singing in males of most other species.

Life cycle and seasonal occurrence. One generation/year. No egg diapause S91-76 (14.5 km S Flagstaff), S07-54 (near AZ-NM border), S12-18 (Mt. Graham), S12-103 (Southwest Research Station), S13-17 (Ramsey Canyon). Even in late spring/early summer on Mt Graham, at 2573m (S94-53, 4-vii-1994) and 2408m (S12-18, 10-vi-2012), most of population apparently adult for a while since many with damaged cerci. Yet at the lower type locality (Ramsey Canyon, S13-17), only ~30% of population adult on 1-vi-2013. Both sexes readily attracted to oatmeal trails.

We collected a number of late instar nymphs from AZ, Cochise Co., Reef Campsite (S12-123, 2180m), on 29-ix-2012, and initially kept them at 27C° on 12L/12D. By 29-xi-2012, 5♂ and 2♀ had molted to adult. Subsequently, all individuals exposed to outdoor photoperiod and temperatures between 12-22°C. Males first started singing in April. If this behavior reflects natural life cycle, then *G. montis* at Reef Campsite may overwinter as either adults or late instars.

Variation. **File tooth number:** Individuals on Mt. Lemmon with higher tooth numbers (range 143-171) than elsewhere (Table 1, p. 18). **Hind femur color**: The entire rear leg of most individuals from western New Mexico and the type locality of Ramsey Canyon are reddish. Females in such populations more likely to have tegminal bars. **Ovipositor length:** Longest known ovipositor (19.8 mm) is from a female from Reef Campsite, Cochise Co., AZ (S12-123), at 2180m, that was raised to adult in the laboratory.

DNA. This complex appears likely to be polyphyletic (Gray *et al.* 2019, and see Discussion below) with affinities to other mid to high elevation Southwestern species (e.g. *G. sotol*, *G. planeta*, and *G. transpecos*) as well as to west coast *G. veletisoides*.

Discussion. The Madrean Sky Islands of Arizona, Sonora, Chihuahua, and New Mexico are a set of some 60 high elevation mountains rising out of lowland valleys and surrounded by Sonoran and Chihuahuan Deserts (Warshall 1995). As such, populations of flightless crickets located on such mountain peaks are probably genetically isolated. We are unsure about the relationships of these populations of *G. montis* as different genes, and the multilocus species' tree analysis, segregate into different clades. Thus, we summarize these genetic relationships here but leave decisions as to species' boundaries for future investigations. Should any of these clades have at least one distinguishing morphological character, then species' status for that clade would be appropriate.

Sequencing ~500 genes with the multilocus technique yields support for 4 clades (Fig. 201, and Gray *et al.* 2019): Clade 1 is found in far southeastern Arizona and includes 2 localities in the Chiricahua Mts.: Chiricahua National Monument (G2464, S13-21) and at the Southwestern Research Station (G2416, S12-103). Clade 2 is found distributed across other southern Arizona sky islands, and includes populations from Huachuca Mts. (G2475, S13-17, type locality of Ramsey Canyon); Quinlan Mts. (G2491, S13-36, Kitt Peak); Pajarito Mts. (2004-073, Sycamore Canyon); Santa Rita Mts. (2005-012, Madera Canyon); and the Mule Mts. (G2471, S13-18, Bisbee). Clade 3 is distributed across the remainder of our Arizona mountain localities: Santa Catalina Mts. (G1353, S09-50, Mt. Lemmon); Pinaleno Mts. (G2241, S12-18, Mt. Graham); Hualapai Mts. (G1151, S07-62, Hualapai Mt. Park); and around Sedona (G1097, S07-60) and to the north towards Flagstaff (G1126, S07-59; and G1051, S07-58). Clade 4 includes two New Mexico localities along the border with Arizona (G1123, S07-54) and around the town of Reserve (G1048, S07-53).

If we apply the four clade names from the multilocus analysis to additional samples with sequenced 16S mtDNA (Fig. 205) or ITS2 nDNA (Fig. 206) based on geography, we get additional support for the distinctness of some clades, although with variable consistency. The distinctness of Clade 4 from Clades 1-3 is supported by all analyses; however, we note that inclusion of the Clade 4 samples as *G. montis* appears to make *G. montis* polyphyletic. The 16S gene sequences yield a much messier picture: Clade 1 (Chiricahua Mts.) shares haplotypes with *G. veletis*; Clade 4 (NM/AZ border, Continental Divide region) shares haplotypes with *G. lightfooti*; Clade 3 individuals from the same population, tend to cluster together, but not necessarily especially close to other Clade 3 localities. For example, Kingman, AZ, Clade 3 samples are well clustered but somewhat separate from Sedona, AZ, Clade 3 samples. The nuclear ITS2 gene sequences demonstrate that *G. montis* Clade 1 is distinct from *G. veletis* despite their 16S DNA being the same. *G. montis* Clade 4 is likewise distinct from *G. lightfooti* in ITS2 despite their 16S DNA being the same (Tamura-Nei ITS2 distances: within *G. montis* Clade 4 0.0097 ± 0.0052; within *G. lightfooti* 0.0073 ± 0.0050; between *G. montis* Clade 4 and *G. lightfooti* 0.0307 ± 0.0040). Both Clade 2 and Clade 3 ITS2 sequences do cluster generally together, but with a few anomalous Clade 2 sequences and two groups of Clade 3 sequences, some apparently close to *G. longicercus* ITS2.

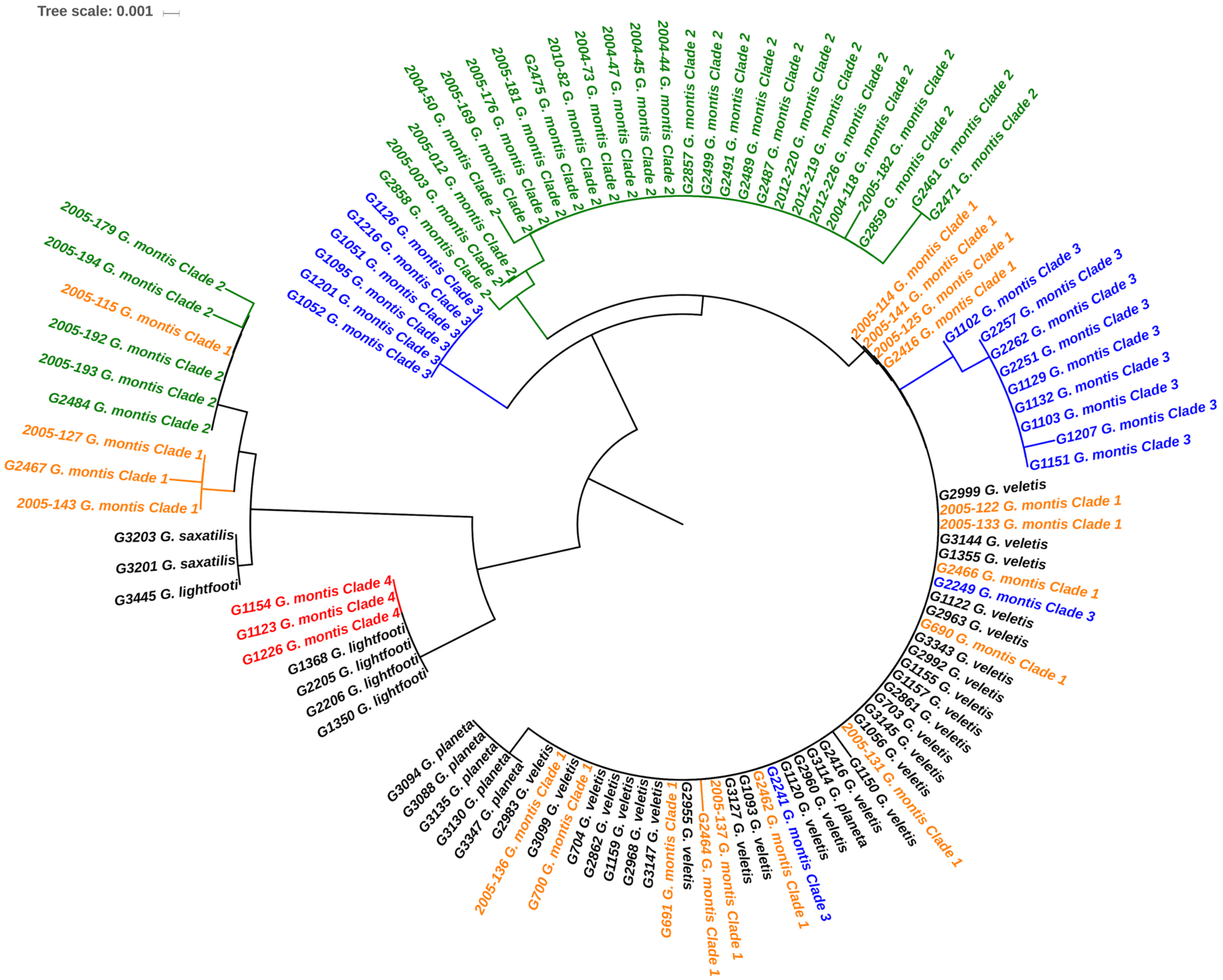

FIGURE 205. 16S gene tree, indicating multilocus DNA clade based on locality. *G. montis* **Clade 1** samples (orange) mostly have 16S DNA like *G. veletis*, as do two *G. montis* **Clade 3** samples (blue, both from Mt. Graham). *G. montis* **Clade 2** samples (green) fall into two groups. *G. montis* Clade 3 samples mostly fall into two geographically separated groups (Hualapai Mtn. near Kingman, AZ, and Sedona, AZ area). *G. montis* **Clade 4** samples have 16S DNA like *G. lightfooti*. Collection stop numbers: ***G. montis*** samples: S07-45 (G1194); S07-54 (G1123, G1154, G1226); S07-58 (G1051, G1216); S07-59 (G1095, G1126); S07-60 (G1052, G1201); S07-62 (G1102, G1151); S07-63 (G1129, G1207); S07-65 (G1103, G1132); S08-50 (G690, G691); S08-51 (G700); S12-18 (G2241, G2249); S12-30 (G2251, G2257); S12-31 (G2262); S12-103 (G2416); S13-17 (G2475, G2857, G2859); S13-18 (G2461, G 2471); S13-21 (G2462, G2464, G2466); S13-36 (G2487, G2489, G2491, G2499); Parker Canyon Lake, Cochise Co., AZ (2004-44, 45, 47, 50, 73); Madera Canyon, Bog Springs, Santa Cruz Co., AZ (2004-118, 2005-003, 012); Madera Canyon, Mt. Wrightson picnic area, Santa Cruz Co., AZ (2010-082); Cave Creek Canyon, Chiricahua Mts., Cochise Co., AZ (2005-115, 122, 127, 131, 133, 136, 137, 143); Miller Canyon, Huachuca Mts., Cochise Co., AZ (2005-169, 176, 179, 181, 192, 193, 194); Reef Camp, Huachuca Mts., Cochise Co., AZ (2012-219, 220, 226). ***G. veletis*** samples: S04-107 (G2861, G2862); S07-51 (G1155, G1159); S07-53 (G1120, G1122, G1157); S07-57 (G1056, G1093); S07-72 (G1150); S08-53 (G703, G704); S09-63 (G1355); S15-19 (G2892, G2960, G2999); S15-25 (G2955, G2963, G2968, G2983, G2992); S15-51 (G3099, G3127); S15-53 (G3343); S15-67 (G3144); S15-78 (G3145, G3147). ***G. lightfooti*** samples: S09-51 (G1368); S09-59 (G1350); S11-86 (G2205); S11-88 (G2206). ***G. saxatilis*** samples: S15-89 (G3201, G3203). ***G. planeta*** samples: S15-61 (G3088, G3094, G3114, G3135, G3347); S15-63 (G3130).

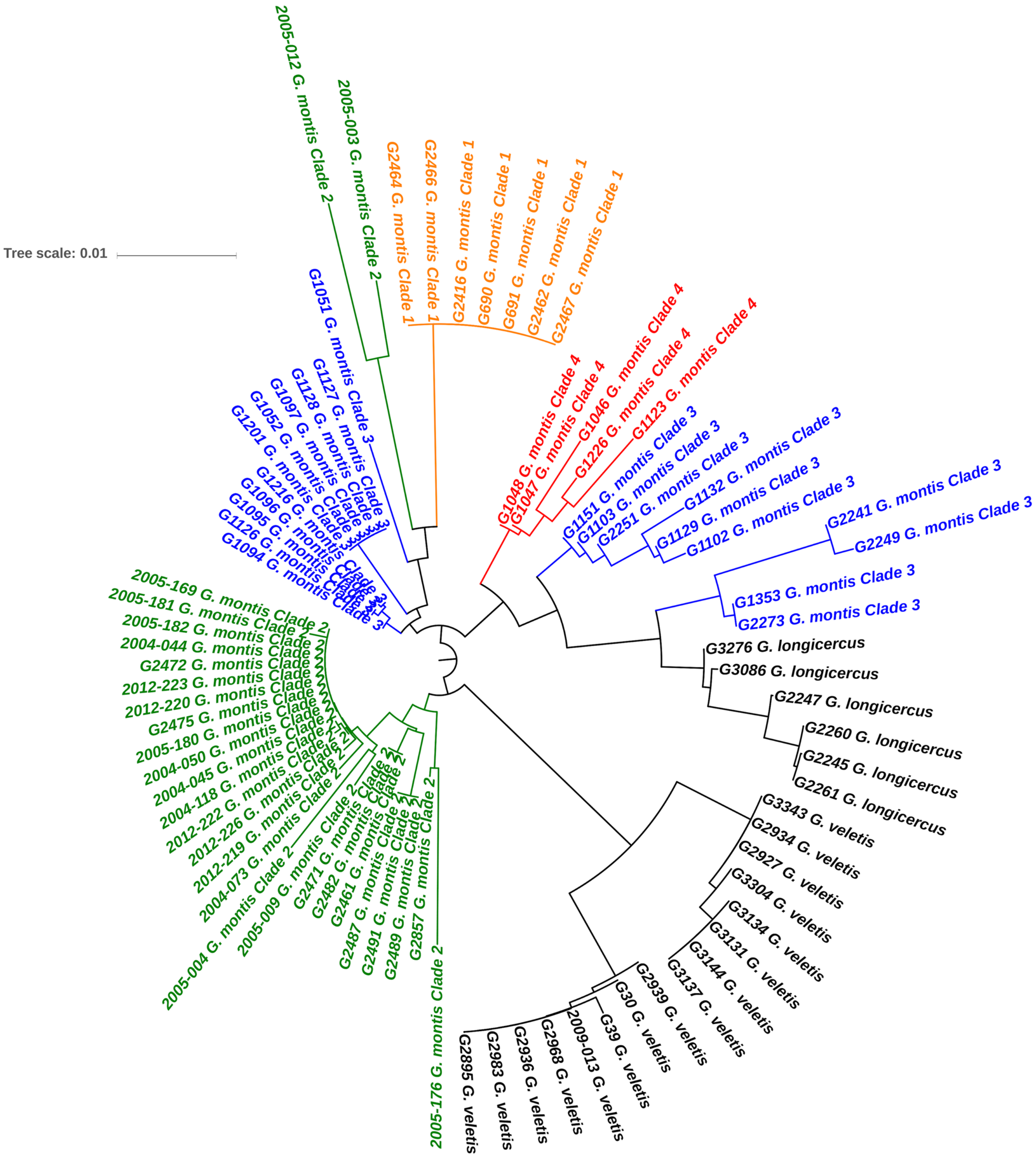

FIGURE 206. ITS2 gene tree, indicating multilocus DNA clade based on locality. ***G. veletis*** samples: S03-58 (G39); S03-60 (G30); S15-9 (G2939); S15-16 (G2927, G2934); S15-21 (G2895); S15-24 (G2936); S15-25 (G2968, G2983); S15-53 (G3343); S15-62 (G3131, G3134, G3304); S15-67 (G3137, G3144). ***G. montis*** samples: S07-53 (G1046, G1047, G1048); S07-54 (G1123, G1226); S07-58 (G1051, G1094, G1216); S07-59 (G1095, G1096, G1126); S07-60 (G1052, G1097, G1127, G1128, G1201); S07-62 (G1102, G1151); S07-63 (G1129); S07-65 (G1103, G1132); S08-50 (G690, G691); S09-50 (G1353); S12-18 (G2241, G2249); S12-22 (G2273); S12-30 (G2251); S12-103 (G2416); S13-17 (G2472, G2475, G2857); S13-18 (G2461, G2471, G2482; S13-21 (G2462, G2464, G2466, G2467); S13-36 (G2487, G2489, G2491); Parker Canyon Lake, Cochise Co., AZ (2004-44, 45, 50, 73); Madera Canyon, Bog Springs, Santa Cruz Co., AZ (2004-118, 2005-003, 004, 009, 012); Miller Canyon, Huachuca Mts., Cochise Co., AZ (2005-169, 176, 180, 181, 182); Reef Camp, Huachuca Mts., Cochise Co., AZ (2012-219, 220, 222, 223, 226). ***G. longicercus*** samples: S12-23 (G2245, G2247, G2260, G2261); S15-52 (G3086, G3276).

The multilocus analysis also varies in placement of *G. montis* Clade 1 depending upon analysis method: concatenated analysis places *G. montis* Clade 1 within the Veletis Group, whereas Astral analysis places *G. montis* Clade 1 with *G. montis* Clade 2. Given the apparent capture of *G. veletis* mtDNA by *G. montis* Clade 1 and *G. lightfooti* mtDNA by *G. montis* Clade 4, and the inconsistency between the concatenated and the Astral analyses, we predict that further more detailed genetic data, e.g. RAD-seq, will reveal a history of hybridization among the southwestern montane species of *Gryllus*.

During altitudinal transects in Arizona, starting in high elevation trees, one hears *G. montis* seamlessly transition to lower elevation, more open grassland *G. lightfooti* on Kitt Peak, Mt. Lemmon, Mt. Graham, Madera Canyon, and the Sedona area, with no or a very narrow zone of overlap. Also, *G. montis* can be narrowly sympatric, during such transects, with the lower elevation slow chirper *G. longicercus* (Kingman, Bisbee, Kitt Peak, Mt. Lemmon). *G. montis* microsympatric with both *G. lightfooti* and *G. longicercus* at 8.4 km SE Hualapai Mt. Park (S90-56) at 1524m, and in the town of Bisbee (S13-18). All 3 sympatric slow chirpers are acoustically distinguishable as follows: *G. longicercus* with individual pulses countable, both *G. montis* and *G. lightfooti* with pulses not countable but chirp rate some 50% slower in former compared to latter.

Hualapai Mt. Park, Mohave Co., AZ, is at 1829m, in good forest, and *G. montis* is common there. As one drives down Hualapai Mt. Road toward Kingman, female field crickets are occasionally observed wandering on the road. We can thus easily see the transition from almost all black *G. montis,* without tegminal bars, while under the tree canopy, to *G. lightfooti,* with tegminal bars, once into more open shrub-grassland. This shift is also seen while driving out of Madera Canyon in the Santa Rita Mountains. For example, at Bog Springs campground area under tree cover at 1527 m elevation, *G. montis* and *G. longicercus* found microsympatric (19-viii-2004); within 2.2 km linear distance into Sonoran grassland on Proctor Road at 1333 m elevation, both species completely replaced by *G. lightfooti* (10-ix-2010). The same situation occurs as one loses elevation going east from the Southwestern Research Station, near Portal, toward New Mexico.

Even surprising for a cricket species that lives at high elevations, repeated attempts to kill adults from Herb Martyr Dam, Chiricahua Mts. (S08-51), by placing them in a home freezer (-15°C) for 1-2 hours duration, all failed. Such treatment normally kills adult *Gryllus* of all species. On the fourth try, freezing them overnight succeeded.

Parasitized by tachinid *Exoristoides johnsoni* at both 40 km NE Prescott (S94-38, 2 males: one with 2 and second with 3 larvae); and 3.5 km SW Reserve (S94-51, 2 males: one with 1 and second with 2 larvae). Parasitized by mermithids: 1 female Ramsey Canyon (S13-17). One of seven males collected 26-vii-2005 at Miller Canyon, Huachuca Mountains (31.42620°, -110.25816°) parasitized by tachinid *Ormia ochracea* (1 larvae).

The Lightfooti Group

G. lightfooti Weissman & Gray, n. sp.; *G. sotol* Weissman & Gray, n. sp.; *G. transpecos* Weissman & Gray, n. sp.

Sister species of chirping field crickets found primarily in Sonoran and Chihuahuan Desert scrub grasslands (*G. lightfooti*); the Organ Mountains of southern New Mexico (*G. sotol*); and in western Texas (*G. transpecos*). Songs similar, typically 3-5 pulse chirps (Figs 207, 208); best separated from each other by combination of distribution, habitat, morphology, and DNA (Gray *et al.* 2019, Fig. 209).

Gryllus lightfooti **Weissman & Gray, n. sp.**

Arboreal Desert Field Cricket
Figs 205, 207–212, Table 1

‘G. #23’, ‘yucca Gryllus’ in DBW notebooks.

Distribution. Southeastern California through central and southern Arizona and New Mexico, into western Texas.

Recognition characters and song. A frequently arboreal, locally common field cricket that ranges from southeastern California through central and southern Arizona and New Mexico, into western Texas. Typically, a desert grassland species, extending into desert scrub and upper desert grassland/oak conifer zones. They can also colonize

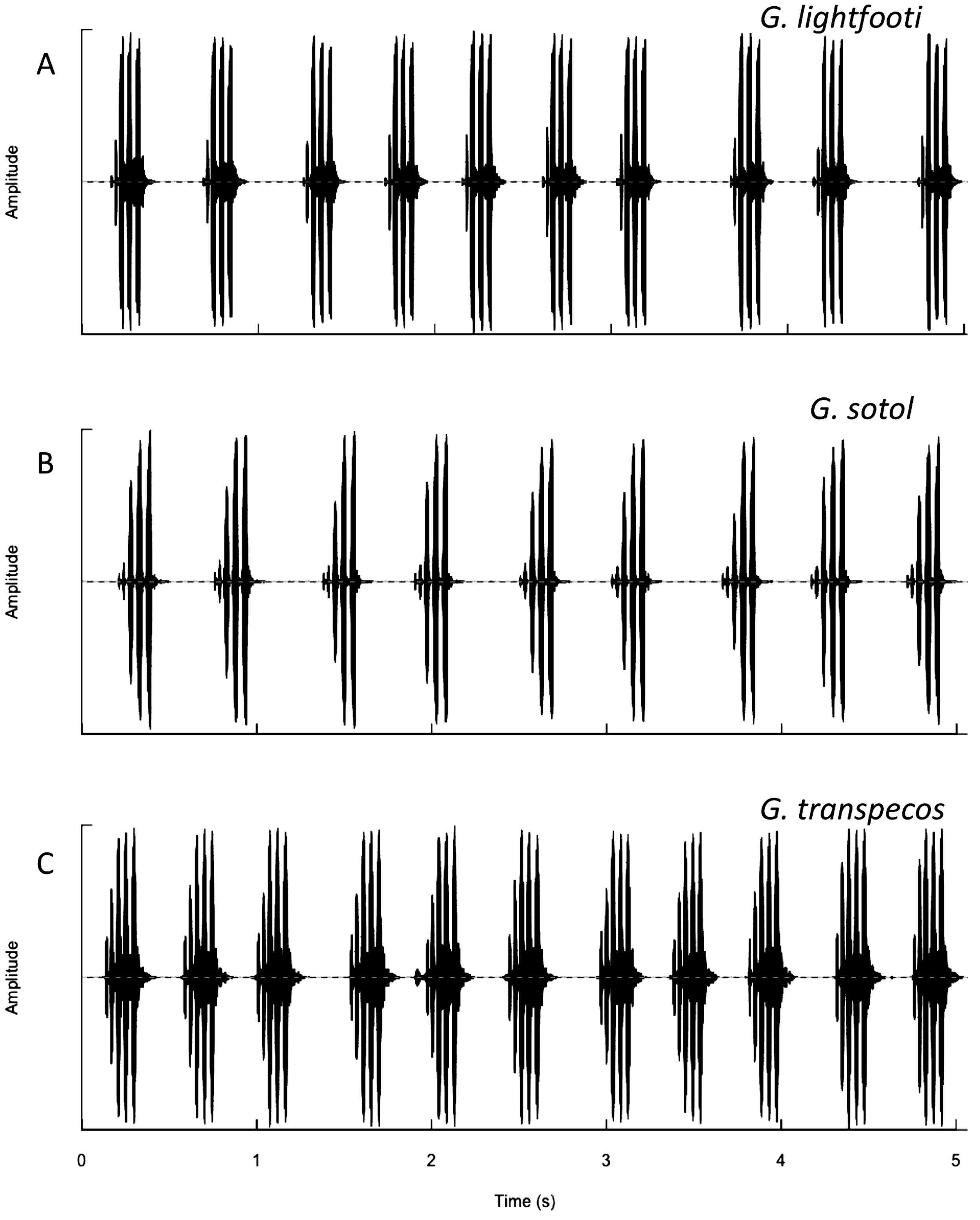

FIGURE 207. Five second waveforms of typical calling songs of (A) *G. lightfooti*, (B) *G. sotol*, and (C) *G. transpecos*. (A) *G. lightfooti*: (R09-69) Cochise Co., AZ (S09-55), at 24°C; (B) *G. sotol*: (R17-44) from type locality (S17-4), at 24.1°C; (C) *G. transpecos*: (R09-93) Culberson Co., TX (S09-64), at 25°C.

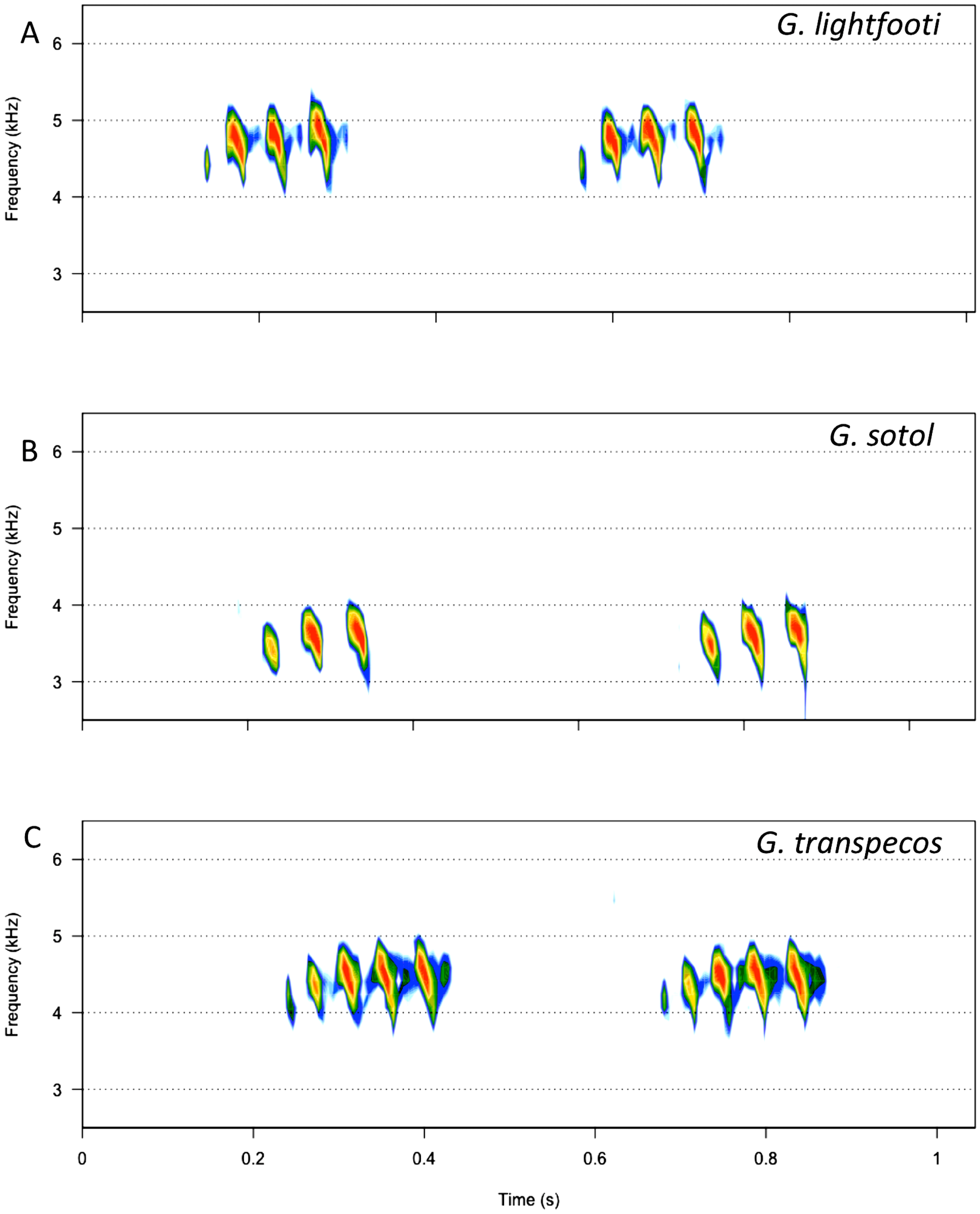

FIGURE 208. One second spectrograms of typical calling songs of (A) *G. lightfooti*, (B) *G. sotol*, and (C) *G. transpecos*, same males as in Fig. 207.

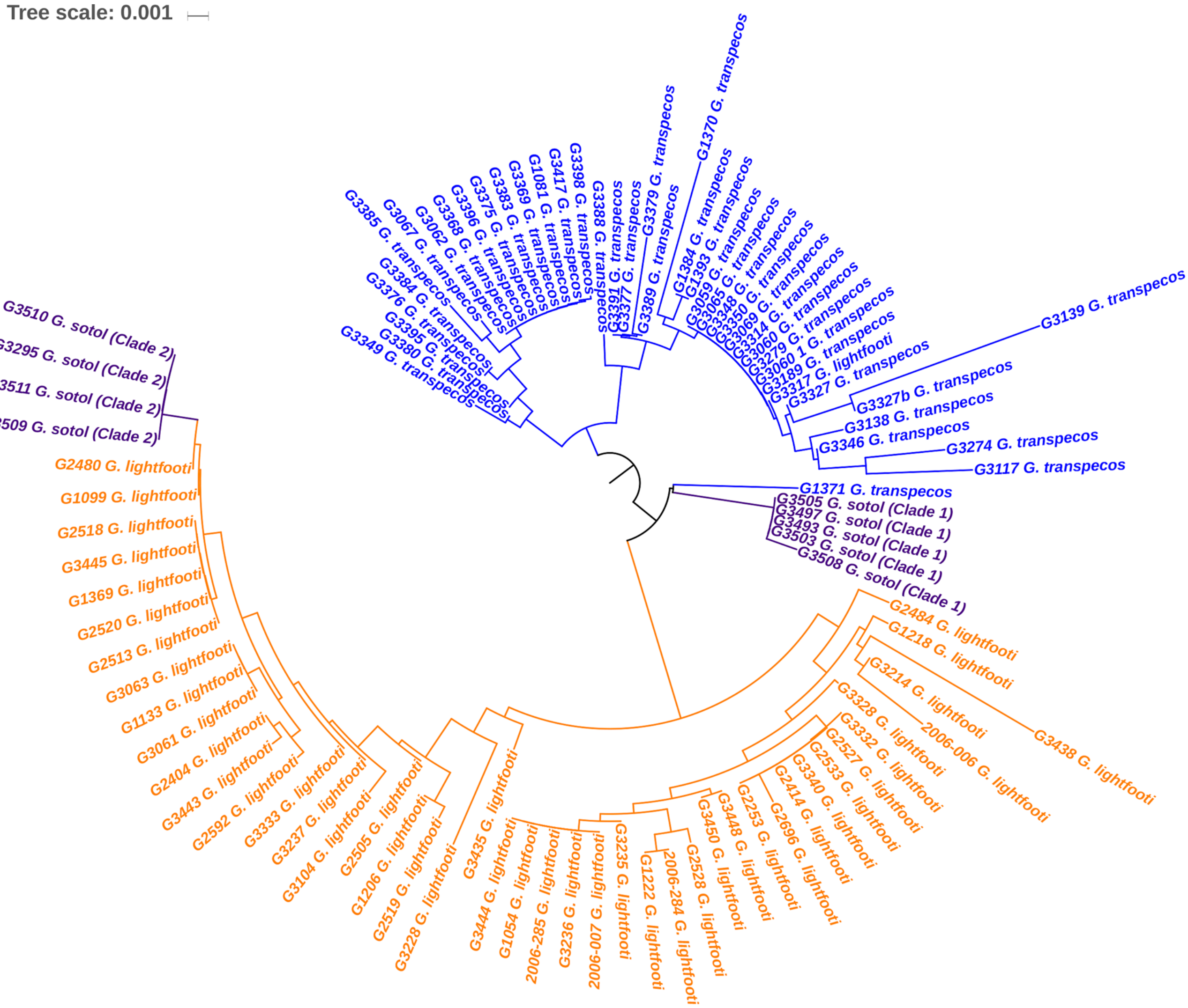

FIGURE 209. ITS2 gene tree. Collection stop numbers for ***G. lightfooti*** samples (orange): S07-61 (G1099, G1206); S07-66 (G1218); S07-67 (G1222); S07-68 (G1133); S09-55 (G1369); S12-19 (G2253); S12-102 (G2404); S12-103 (G2414); S13-13 (G2518, G2528); S13-16 (G2480, G2513, G2519, G2520); S13-18 (G2484, G2696); S13-19 (G2505, G2527, G2533, G2592); S15-49 (G3104); S15-75 (G3061, G3063); S15-100 (G3340); S15-104 (G3328); S15-105 (G3317, G3332); S15-109 (G3333); S15-110 (G3214, G3228, G3235, G3236, G3237); S16-24 (G3435, G3445, G3448, G3450); S16-31 (G3438, G3444); S16-33 (G3443). Collection stop numbers for ***G. sotol*** samples (purple): S15-77 (G3295); S17-4 (G3493, G3497, G3503, G3505, G3508, G3509, G3510, G3511). Collection stop numbers for ***G. transpecos*** samples (blue): S07-36 (G1081); S09-64 (G1370, G1384, G1393); S15-61 (G3189, G3279, G3346); S15-64 (G3314, G3348, G3349); S15-65 (G3117, G3138, G3139, G3274, G3327); S15-68 (G3062); S15-69 (G3067); S15-72 (G3059, G3060, G3065, G3069, G3350); S16-2 (G3376, G3377, G3383, G3384, G3389, G3391); S16-3 (G3379, G3385, G3388, G3395); S16-7 (G3375); S16-8 (G3368, G3417); S16-9 (G3396); S16-10 (G3369); S16-12 (G3398); S16-14 (G3380). Note the two ITS2 clades of *G. sotol*.

suburban neighborhoods. A small (especially when in sandy desert habitats) to large cricket separated, sometimes with difficulty, from similar looking, occasionally sympatric chirping species by a combination of habitat, behavior, female color patterns, DNA, and song. Almost always with short hind wings (Fig. 210); cerci in situ nearly as long as, to just longer than tip of ovipositor; females (and some males) typically with "tegminal bars", a pale longitudinal strip on the anterior dorsal-lateral margins of the forewings (Fig. 210), especially visible when tegmina are dark. Males frequently sing off the ground, in vegetation, especially during the daytime from within *Yucca elata*, and also from within pack rat (*Neotoma* spp.) nests. *Song* (see Fig. 211, R09-69) a medium-fast chirp (frequently over 150 c/m), generally 3-5 p/c, PR 18-29 at 25°C. Distinguished from other US western slow chirping *Gryllus*, some that can be sympatric, as follows: From the *G. montis* complex: the latter occur in sky islands, under a tree canopy, where males have a slower CR and whose cerci are never longer than the ovipositor. Also, despite being at higher, cooler elevations, *G. montis* molts to adult several weeks before *G. lightfooti*. One can conduct elevational transects at several places in Arizona (e.g. Madera Canyon, Kitt Peak, Mt. Lemmon, Hualapai Mt. Park) and hear an almost seamless transition of slow chirpers when descending from tree covered sky island habitats, where *G. montis* lives, to the open grassland-shrub habitats of *G. lightfooti*. Once below tree cover on these elevation-transects, wandering adult females of Arboreal Desert Field Crickets with tegminal bars can occasionally be seen on the roads, although at Hualapai Mountain Road, both species continue to occur sympatrically, in interior chaparral habitat, as Kingman is approached. Separated from sometimes microsympatric *G. longicercus* by no overlap in PR, minimal overlap in tooth number and cerci length, and association with rocky habitats in *G. longicercus*. In elevation-transects on Mt. Lemmon and Kitt Peak, both taxa can occur together in areas of rocky road cuts. Separated from *G. transpecos*, where the two taxa could overlap in western Texas, although no such locality known, by, in *G. transpecos*, cerci in situ almost always longer than ovipositor tip, female tegminal bars usually absent, associated with rocks, small but consistent ITS2 DNA differences, and never climb into vegetation to hide or sing. Separated from *G. saxatilis,* which is microsympatric with *G. lightfooti* in desert washes in the eastern California Mojave Desert at Mt Pass (S91-71) and Halloran (S91-70), by, in *G. lightfooti,* presence of tegminal bar in females, fewer teeth and teeth/mm (but still with overlap), climbing into vegetation, and DNA. Distinguished from *G. veletis* by the latter's shorter cerci and association with more vegetated habitat. Additionally, nymphs and adults of *G. veletis* are never tan-mottled in color, while those of *G. lightfooti* are. Distinguished from *G. sotol*, which is only known from the Organ Mts. of south-central New Mexico, by *G. sotol*'s shorter cerci, non-grassland habitat, and association with sotol. Distinguished from *G. planeta* of the Davis Mts., in western Texas, by the latter's shorter cerci and sky island forested habitat.

FIGURE 210. Holotype male of *G. lightfooti.* Female from Pima Co., AZ (S15-108). Note the presence of tegminal bars (arrow), especially on female.

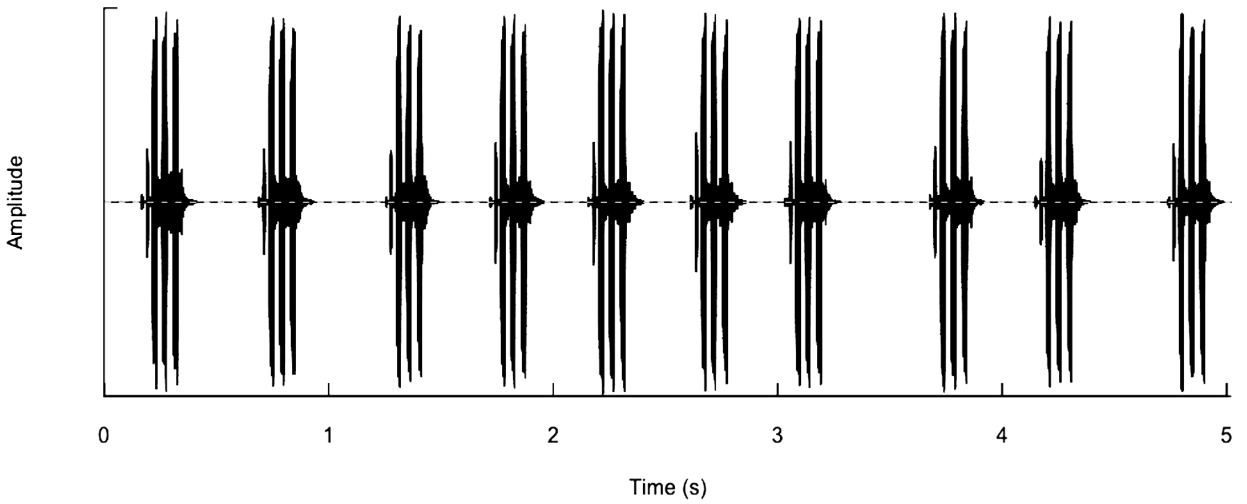

FIGURE 211. Calling song (R09-69) of *G. lightfooti* from Cochise Co., AZ (S09-55), recorded at 24°C.

Holotype. Male (Fig. 210): New Mexico, Dona Ana Co., USDA Jornada Experimental Range, ~5 m E Las Cruces off Highway 70. 3-vii-2015, 4300’, 32° 28’ 33.33” -106° 44’ 10.86”, DBW and DW Weissman. S15-75, R15-139, G3061. 16S GenBank accession # MK446528 BL 17.98, HF 10.0, LC 10.89. Right tegmen removed: 123 teeth, file length 2.8, TL 9.5, TW 4.0. Deposited CAS Entomology #19264.

Paratypes. (Total 259♂ 227♀) **Arizona**: *Cochise Co.*, Apache Pass, 5106’, 32° 09’ 07.8” -109° 28’ 52.6”, 2-vi-2013 (S13-20) 2♂ 2♀. Bisbee, 5500’, 31° 26’ 46.9” -109° 55’ 37.9”, 1-vi-2013 (S13-18) 4♂ 1♀. Fort Bowie parking lot 2 m NE Apache Pass, 4723’, 32° 09’ 23.8” -109° 27’ 09.9”, 2-vi-2013 (S13-19) 13♂ 9♀. Southwestern Research Station, 5423’, 31° 53’ 04.19” -109° 12’ 25.75, 20-viii-2012 (S12-103) 1♂. Willcox Playa, 4155’, 32° 11’ 55.5” -109° 52’ 42.4”, 29-vii-2015 (S15-104) 1♂ 1♀; 4140’ 32° 11’ 57.2” -109° 52’ 32.4”, 28-vi-2009 (S09-55) 4♂ 3♀. *Coconino Co.*, Hwy 89A 1 m S Sedona, 4420’, 30-vi-1994 (S94-36) 1♂ 1♀. *Gila Co.,* Globe, 3660’, 10-vi-2012 (S12-21) 1♂. Miami, 3500’, 16-vi-1990 (S90-50) 1♂. *Graham Co.*, Safford, 2920’, 16-vi-1990 (S90-51) 2♂. Pinaleno Mts, Mt. Graham, Hwy 366 at mile post 116.2, 3700’, 4-vii-1994 (S94-55) 9♂ 6♀; Hwy 366 at mile post 120.6, 5000’, 32° 40’ 10.2” -109° 47’ 20.0”, 10-vi-2012 (S12-19) 4♂; Hwy 366 at mile post 116.9, 3782’, 32° 41’ 40.1” -109° 44’ 59.0”, 28-vii-2015 (S15-100), 7♂ 9♀. Hwy 191 S Safford, around Roper Lake State Park, 4-vii-1994 (S94-56) 1♂. *La Paz Co.,* Alamo Lake, 1400’, 34° 14’ 05.6” -113° 33” 16.1”, 14-ix-2011 (S11-86) 1♂ 1♀. Hwy 60 9.9 m SW Wenden, 1752’, 33° 44’ 15.9” -113° 40’ 35.4, 14-ix-2011 (S11-88) 1♂ 1♀. *Maricopa Co.,* Painted Rock Petroglyph Site, 16-ix-2006, 2♂. *Mohave Co.,* Kingman, 13-vi-2012 (S12-33) 1♀. Hualapai Mt. Road SE Kingman, 5135’ 35° 07.859’ -113° 55.142’, 16-vi-2007 (S07-66) 1♂; 4918’, 35° 08’ 33.6” -113° 55’ 36.2”, 13-vi-2012 (S12-32) 2♂ 2♀. *Pima Co.,* Ajo, 1760’, 20-viii-1998 (S98-74) 2♂ 1♀; 29-vii-2015 (S15-109) 1♂. Hwy 85 8 m S Ajo, 20-viii-1998 (S98-70) 1♂ 1♀. Baboquivari Mts., Brown Canyon, 3960-4080’, 6-vii-1994 (S94-58) 13♂ 6♀; 3786’, 31° 45’ 37.0” -111° 31’ 58.8”, 29-vii-2015 (S15-105) 5♂ 13♀. Hwy 85 13m N Ajo, 1255’, 32° 32’ 44.1” -112° 52’ 48.4, 30-vii-2015 (S15-110) 5♂ 4♀. Hwy 86 W Sells, 2276’, 31° 57’ 25.4 -111° 56’ 46.4”, 29-vii-2015 (S15-108) 2♂ 11♀. Madera Canyon, 4200’, 26-vii-1990 (S90-80) 5♂ 7♀. Mt. Lemmon Recreation Area, Mile 7.5, 4600’, 27-vii-1990 (S90-82) 8♂ 7♀; Mile 9, 5240’, 32° 21’ 21.4” -110° 43’ 34.7”, 27-vi-2009 (S09-51) 1♂. Tucson, 2375’, 18-vi-1990 (S90-53) 4♂ 2♀; 2600’, 27-vii-1990 (S90-84) 2♂; 2780’, 32° 16’ 44” -110° 46’ 18.4”, 27-vi-2009 (S09-52) 1♂. Tucson, 3.9 m N I10, 3040’, 32° 07’ 0.4” -110° 46’ 16.8”, 27-vi-2009 (S09-53) 1♀. *Pinal Co.*, Oracle, 4260’, 18-viii-1998 (S98-64) 1♂. *Yavapai Co.,* Agua Fria National Monument, 3200’, 34° 14’ 50.2” -112° 03’ 28.5”, 31-v-2013 (S13-13) 20♂ 12♀; 3529’, 34° 15’ 57.5” -112° 05’ 28.9”, 21-viii-2012 (S12-106A) 1♂ 3♀. Cottonwood, 3320’, 30-vi-1994 (S94-37) 1♂ 2♀. Sedona, Sky Ranch Lodge Motel by airport, 5120’, 34° 51.146’ -111° 47.415’, 15-vi-2007 (S07-61) 1♂. Hwy 179 eastern outskirts Sedona, 4000’, 31-v-2013 (S13-16) 4♂. Camp Verde, 3146’, 12-vi-2012 (S12-29) 5♂ 2♀. 7 m N Prescott, 5060’, 30-vi-1994 (S94-39) 1♂. *Yuma Co.*, Kofa National Wildlife Refuge, Hwy 95 at mile post 76.8, 10-viii-1988 (S88-88) 1♂; near 33° 14’ 59.93 -114° 12’ 54.40”, 1710’, 10-viii-1988 (S88-87) 5♂ 6♀. Telegraph Pass, mile post 18.6, 676’, 32° 39’ 30.7” -114° 20’ 14.2”, 15-ix-2011 (S11-92) 1♂. **California:** *Imperial Co.,* Algodones Dunes, 240’, 33° 01’ 13.4” -115° 07’ 25.3”, 15-ix-

2011 (S11-91) 2♀. *San Bernardino Co.,* Kelso Dunes, 2500', 13-iii-1985 (S85-28) 2♂, molt to adult late June. Mt. Pass, 4600', 4-viii-1991 (S91-71) 1♂. I15 at Cima Road exit, 3673', 35° 26' 30.54" -115° 40' 24.70", 22-vii-2016 (S16-24) 6♂ 3♀. 13.6 m N I40 on road to Providence Mts. State Rec. Area, 3437', 34° 56' 29.99" -115° 28' 53.30, 23-vii-2016 (S16-31) 4♂ 1F3. First wash n I15 on road to Halloran Springs Microwave Station, 2900' 4-viii-1991 (S91-70) 1♂ 2♀. Essex, washes around town, 2000', 22-vii-1990 (S90-69) 6♂ 1♀. Essex Road, 17.6 m NW Essex, 2900', 5-vi-1989 (S89-29) 4♂ 2♀. **New Mexico:** *Bernalillo Co.,* Albuquerque, Tingley Beach, 4950', 35° 25' 16.35 -106° 44' 33.49", 29-vi-2015 (S15-49) 2♂ 3♀. *Chaves Co.,* Hwy 82 ~33m W Artesia, 4824', 32° 51' 55.02 -104° 58' 51.76", 30-vi-2015 (S15-56) 4♂ 8♀. Hwy 380 7.3 m E Roswell, 3960', 33° 23' 46.4" -104° 22' 32.4", 28-vi-2009 (S09-59) 9♂ 4♀. *Dona Ana Co.,* Las Cruces, 16-vi-1986 (S86-40) 2♂; 27-vi-1988 (S88-58) 1♂. USDA Jornada Experimental Range, ~5 m E Las Cruces off Highway 70, 4300', 32° 28' 33.33" -106° 44' 10.86", 5-vii-1987 (S87-82), DC Lightfoot, 2♂ 6♀; 10-viii-1990 (S90-90) 1♂ 4♀; 3-vii-2015 (S15-75) 6♂ (including holotype) 6♀. *Eddy Co.,* Hope, 4095', 32° 48' 37.73 -104° 44' 15.00, 30-vi-2015 (S15-57) 3♂ 2♀. *Lincoln Co.,* Valle del Sol Municipal Golf Course, 5519', 33° 38' 18.97 -105° 51' 37.79", 30-vi-2015 (S15-55) 1♂ 4♀. *Otero Co.,* Hwy 54 ~16 m N Texas border, 4105', 32° 12' 20.27" -106° 11' 37.48", 3-vii-2015 (S15-74) 10♂ 8♀. *Socorro Co.,* Acamilla rest stop on E side I25 1 m S La Joya, 4850', 15-viii-1993 (S93-68) 2♀. Goat Draw, Los Pinos Mts, 6440', 34° 22' 10" -106° 32' 0", 16-viii-1993 (S93-69) 14♂ 6♀. Sevilleta National Wildlife Refuge, Site 222, 5145', 34° 24' 30" -106° 56' 43", 15-viii-1993 (S93-66) 4♂ 9♀. Sevilleta National Wildlife Refuge, Rio Salado sand dunes, 4500', 34° 18.515' -106° 59.316', 15-viii-1993 (S93-67) 3♂ 1♀. Socorro, 4420', 13-vi-2007 (S07-50) 4♀; 29-vi-2015 (S15-54) 5♂ 6♀. Hwy 60 12 m W intersection Hwy 60 and 47, 4958', 34° 25' 16.35" -106° 44' 33.49", 29-vi-2015 (S15-50) 7♂ 5♀. Hwy 60 at milepost 185.8, 6004', 34° 24' 12.07" -106° 30' 29.16", 29-vi-2015 (S15-53) 4♂ 13♀. Hwy 380 6.8 m W Carrizozo, 5160', 33° 43.276' -105° 57.471', 13-vi-2007 (S07-47) 1♂ 1♀. Hwy 380 37.5 m W Carrizozo, 5200', 33° 53.139' -106° 24.785' (S07-48) 1♂ 2♀. **Texas:** *Culberson Co.,* Guadalupe Mts., 4.4 km NE Pine Springs, 5240' 31° 54.400' -104° 46.920', 13-vii-2001 (S01-63) 5♂ 5♀; 3.2 km SW Pine Springs, 5360', 13-vii-2001 (S01-64) 2♂. Van Horn, 4100', 6-vi-1991 (S91-48) 4♂ 2♀.

Sound records only. **Arizona:** *Maricopa Co*., Aguila, 2100', 23-vii-1990 (S90-71). **Texas:** *Hudspeth Co.,* Cornudas, 4420', 13-vii-2001 (S01-65).

Derivation of name. Named in appreciation of David C. Lightfoot, who first recognized this taxon during field work at the type locality, and who has helped the senior author with companionship, counsel, and comradery for over 40 years. Plus, for all of those times at 4 AM, when asked to help collect just 2 more crickets (and for which he naively continued to believe that I was serious about only collecting just 2 more!).

Geographic range. (Fig. 212). Ranges from the deserts of southeastern CA through central and southern Arizona and New Mexico, into western Texas.

Habitat. From 73m (Algodones Dunes, S11-91) to 1963m (Goat Draw, S93-69), but usually below 1680m and away from dense tree canopy. Vegetation at the Chihuahuan Desert grassland/scrubland type locality includes soaptree yucca (*Yucca elata*), honey mesquite (*Prosopis glandulosa*), tarbush (*Flourensia cernua*), and burrow grass (*Scleropogon brevifolia*). Elsewhere associated with Arizona interior chaparral, dry, rocky streambed bottoms, and at base of vegetation in California sand dune habitats such as Kelso Dunes (S85-28) and Algodones Dunes (S11-91). When driving lower from the sky island, oak covered localities in Madera Canyon (S90-80) and Hualapai Mt Park (near S07-66 and S12-32), where *G. montis* exists, at both sites, in good numbers, one enters more open interior chaparral/grassland habitat. Once around 1676m, faster chirping (when compared with *G. montis) G. lightfooti* are first heard and females, with their distinctive tegminal bar, can be seen wandering on the road. Males frequently daytime sing from pack rat nests, where they occur with females and nymphs, and can be difficult to collect because of cholla jumping cactus sections sequestered by the pack rats.

At Willcox Playa (S15-104), we collected *G. lightfooti* and 2 adult *G. staccato* males singing during afternoon hours from the same dead skirt of a *Yucca elata.* The only other similarly arboreal western *Gryllus* taxon is *G. sotol* at Aguirre Springs, NM (S15-77), where singing *G. sotol* were collected along with one non-singing *G. longicercus* male, in sotol (*Dasylirion wheeleri*), during late afternoon.

Life cycle & seasonal occurrence. One generation/year. No egg diapause: Las Cruces (S86-40 & S88-58); Jornada type locality (S87-82); Mt. Graham (S15-100); and Cima, CA (S16-24). D.C. Lightfoot reports (pers. comm. to DBW, October, 2015) the following for the type locality: "They have one generation a year; that year's eggs hatch late summer (August) with the monsoon rains, slowly grow as nymphs through the winter, probably mostly inactive with cold temps, but active with warm temps, and mature in the late spring (May) and are present as adults through most of the summer. Their life cycle is very similar to *G. veletis*, except they mature about a month later (May/June vs. April/May) and persist as adults through the summer for a month longer (May/June vs. August/Sept.” This information agrees with our oatmeal trail, collecting efforts for *G. lightfooti*: 95% of hundreds of individuals seen 31-v-2013 at Agua Fria National Monument, AZ (S13-13); all 10 individuals collected 2-vi-2013 at Apache Pass, AZ (S13-20); 21 of 22 collected 2-vi-2013 from Ft. Bowie, AZ (S13-19); and 5 of 6 collected 5-vi-1989 from Essex, CA (S89-29), were penultimate or late instars when collected.

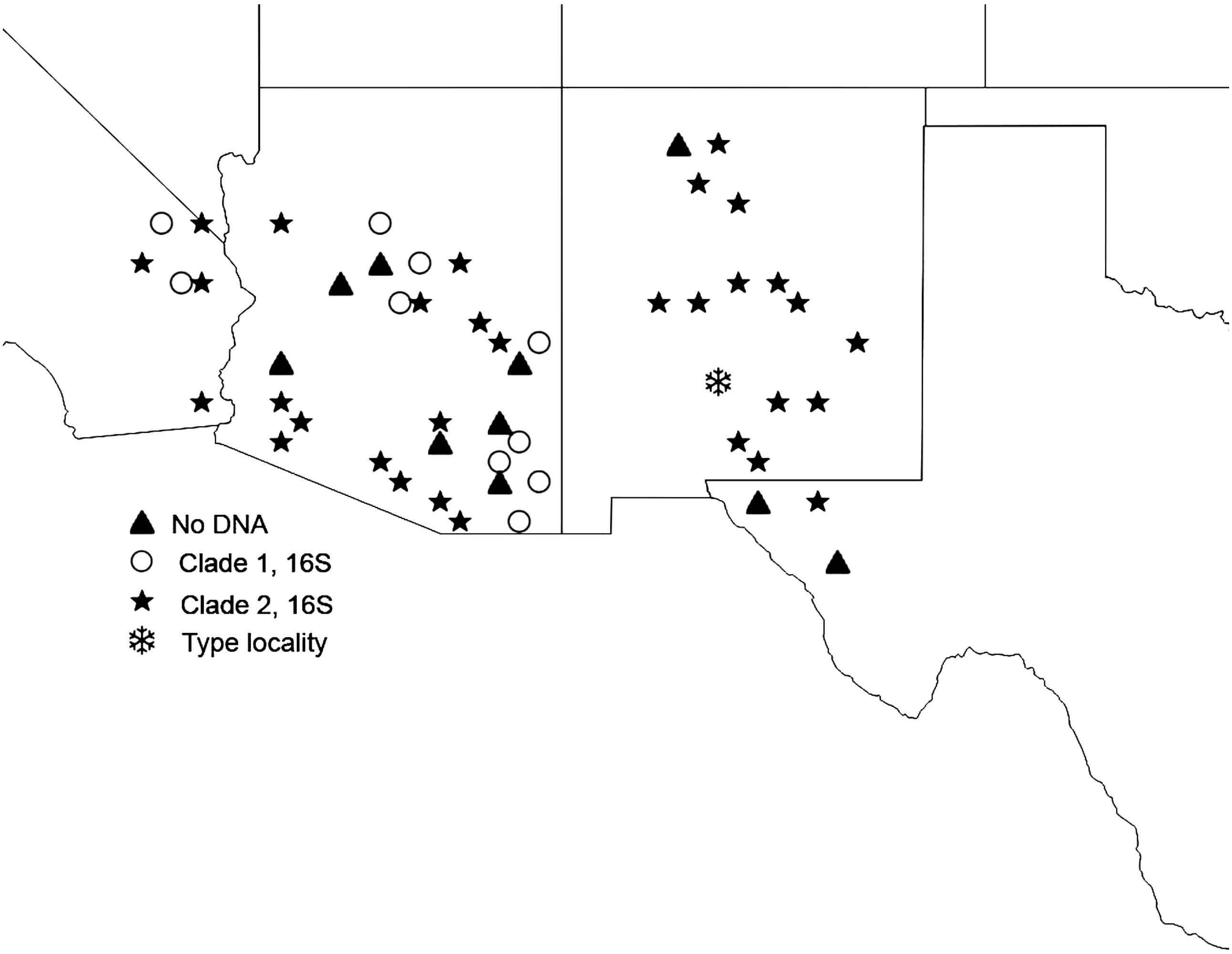

FIGURE 212. Known US distribution of *G. lightfooti* showing distribution of two16S DNA Clades. See discussion of DNA in Barcoding section (p. 16) of this paper.

In the laboratory, all eggs from one female hatch synchronously, when the substrate is kept moist, although nymphs from the same female grow slowly and at different rates from each other, even at temperatures > 25°C. There is no obvious nymphal diapause. On the other hand, when the egg laying substrate is initially not kept moist, and then subsequently moistened, we suspect that eggs may hatch over an extended period of time. In a regime where constant damp sand is provided and nighttime temperatures are kept above 18°C year around, D.C. Lightfoot gets continuous generations and year-round egg laying.

Variation. **Body length:** Adults living within *Y. elata* plants generally smaller than those living elsewhere. **Cerci length vs. ovipositor length:** In females with at least one intact cercus, some 32% have that cercus longer than the tip of the ovipositor in situ. **Color**: Adult specimens generally with dark bodies and lightly tinged, reddish insides of hind femur. Tegminal color varies from black to light brown, with female tegminal bars most noticeable in the former. Occasional males also with tegminal bars. **Hind wing length**: Out of some 485 field-collected individuals, only 6 with long hind wings, as follows: CA: Essex (S90-69, 1♂), Cima (S16-24, 1♂); AZ: Ajo (S98-74, 1♂ 1♀), Kofa (S88-87, 2♀). Laboratory-hatched nymphs raised to adult can yield 50-100% long hind winged individuals of both sexes (D.C. Lightfoot, pers. comm., December, 2015).

DNA. multilocus 2016-038, Jornada type locality. Closest relatives are *G. sotol* and *G. transpecos* (Gray *et al.* 2019).

Discussion. This is one of our most difficult field crickets to identify when away from *Yucca elata. G. lightfooti* is most easily separated from similar sounding and appearing *Gryllus* species by habitat—there is little else common in open, desert Southwest grassland/scrublands. Difficulty arises where it occurs in mixed habitats with grasses, sparse tree cover and rocks. For instance, on Hualapai Mt. Road, Arizona (S90-56), 1524m, 8.4 km NW of Hualapai Park, we collected *G. lightfooti* microsympatric along with *G. montis* and *G. longicercus,* although we could distinguish their songs in the field, mostly by a combination of differing pulse and chirp rates. At Goat Draw, New Mexico, (S93-69), we found *G. lightfooti* microsympatric with *G. longicercus* in a rocky canyon area of pinyon pine—juniper, *Opuntia* cactus and some grasslands.

In such Southwest US mixed-habitats, one has to also consider the widespread slow chirpers *G. veletis* and *G. transpecos.* Using a combination of distribution maps, song analysis, especially PR and CR, file tooth number, arboreal or not, and presence or absence of a female (and sometimes male) tegminal bar should enable identification of most specimens. But probably not all specimens with certainty. DNA analysis may be required in some cases.

This is our most arboreal western field cricket, with the possible exception of the geographically restricted *G. sotol.* Where *G. lightfooti* occurs with *Yucca elata*, the two seem to be intimately associated with male crickets frequently heard chirping, from within plants, during the hottest part of the day when air temperatures exceed 35°C. They prefer the lower dead-portion skirts of living plants as well as those dead plants on the ground. When dead *Yucca* plants not present to search, we have (rarely) broken off a living *Yucca* stalk at ground level, moved the plant into a dirt clearing or onto a nearby road, and by pounding it on the surface, dislodged the crickets, which can then be gathered. We have collected over 15 individuals from one small plant using this technique although they are quick to hop and try to reenter the same *Yucca*. They obviously see well, even at night with just the light from our headlamps. After sunset, they apparently climb down from *Y. elata* and walk around, mostly silently on the ground, as seen on Mt. Graham (S15-100), and observed by D.C. Lightfoot in his laboratory cultures (pers. comm. to DBW, 6/2017).

We wonder if this arboreal behavior provides some or all of the following benefits: relief from hot daytime temperatures when compared with ground dwelling field crickets; protection from nocturnally-active, parasitic tachinid flies; and access to a possible food (and water?) source of the plant itself, including preying on other small arthropods living within the skirt. We suspect that females oviposit into the substrate as in other field crickets. Interestingly, *G. lightfooti* is found in areas of western and northwestern Arizona, southeastern California, and western New Mexico where *Yucca elata* doesn't occur. Conversely, perfectly suitable-looking habitat in western Texas has *Y. elata* but no Arboreal Desert Field Crickets.

Where *G. lightfooti* occurs away from *Y. elata,* males can still be found singing from elevated perches at night: Alamo Lake (S11-86), 1 male 1m up in *Larrea*. When we attempted to capture him, he retreated to base of *Larrea* into a pack rat nest. Town of Van Horn (S91-48), 1 male singing 4m up in a building. Hualapai Mt. Road (S07-67), 1 male 1.5m up in Palo Verde. Open Mohave Desert near Providence Mts. State Rec. area (S16-31), 1 male 0.5m up in shrub. In towns like Las Cruces and Albuquerque, NM, they are common in suburban neighborhoods, and live in bushes and will enter houses and sing from under roof tiles. Also heard in commercial areas of Socorro, NM (S15-54).

D.C. Lightfoot notes the following (pers. comm. to DBW, 6/2017) about his 5th generation, type locality laboratory culture: "They live and sing and mate almost exclusively above the sandy soil bottom of the terrarium, especially during the day. Females wander on the sand floor at night and lay eggs in damp sand. They are highly gregarious, and hang out together, females, males, and nymphs; singing males fight and chase each other a lot but still hang out together. Also, they exhibit a "jerking motion walking behavior" like many camouflaged insects do when they walk (like stick insects and mantises) and they blend in very well with the wood that they live on (tan and brown color). In these aspects, they are totally different from *G. veletis* which I have also kept in the same terrarium. *G. veletis* stay on the ground, are not gregarious, and do not 'jerk walk.'"

Lightfoot reports that juveniles, from the type locality, are distinctly pale tan with mottling. Early instars have black markings on the head, many late instars have dorsum of head black, and all nymphal stages look very similar to *Acheta domesticus* nymphs. They become dark brown/black as adults, but some still retain the black markings on the head adjacent to the eyes. These color patterns are also seen in *G. lightfooti* from Southern CA (S16-31). We have not explicitly compared nymphal color patterns between different *Gryllus* species (but see discussion of striped nymphs under the Longicercus Group, p. 229), although such information might prove phylogenetically relevant.

We have documented parasitoid tachinids *Ormia ochracea* at the following Arizona localities: near Alamo Lake (S11-86), Mt. Graham (S15-100), Willcox Playa (S15-104), Brown Canyon (S15-105), and Painted Rock Petroglyph Site. We believe that the distorted adult sex ratios (e.g. Brown Canyon, S15-105; W of Sells, S15-108) seen later in the season, where adult females greatly outnumber adult males, may be related to the high incidence of tachinid-killed males (Sakaguchi & Gray 2011). Also, not singing at night, when gravid tachinid female flies are most active and acoustically searching for singing male *Gryllus*, should help protect adult males that can still find adult females due to high population densities. DC Lightfoot (pers. comm. to DBW, 6/2017) also reports laboratory males singing more in afternoon and early evening than later at night.

Gryllus sotol **Weissman & Gray, n. sp.**

Organ Mountains Field Cricket
Figs 207–209, 213–215, Table 1

FIGURE 213. Holotype male of *G. sotol.* Female also from type locality (S17-4).

Distribution. Known only from the sky island Organ Mountains of south central New Mexico, above 1520m.

Recognition characters and song. A medium to large, always short hind winged, generally black (except for inside of hind femur) cricket, whose cerci are always shorter than tip of ovipositor in situ (Fig. 213). Intimately associated with sotol, *Dasylirion wheeleri*, from which it frequently sings during the daytime. *Song* (Fig. 214) a slow chirp, usually 3–5 p/c (range 3–6), with a chirp rate of 120–160 (range 82–170) and a PR of 16.5–22.7 at 25°C. Dominant frequency 3463–4746 Hz. Distinguished from other Southwestern slow chirping *Gryllus* as follows: from microsympatric *G. longicercus*, which it greatly outnumbers, by (generally) having non-overlapping and lower file teeth number (Table 1, p. 18), higher PR, and shorter cerci never longer than ovipositor tip in situ (almost always longer in *G. longicercus*). Separated from more eastern, allopatric sister species *G. transpecos* (although some individuals [those in Clade 1—see below] with similar ITS2 DNA [see Fig. 209]), *G. sotol* has more teeth, higher tooth density, shorter cerci never as long as ovipositor tip (almost always longer in *G. transpecos*), slower PR, and habitat: open, lower elevation, drier, rocky Chihuahuan Desert for *G. transpecos* versus higher, cooler, low mountain bajadas and woodlands, with sotol, for *G. sotol*. Additionally, *G. sotol* frequently climbs into sotol while *G. transpecos* is only found on the ground, although sometimes on rocky cliff faces in road cut areas. Separated from lower elevation, also arboreal, later maturing (despite lower elevations and warmer habitat), more open Chihuahuan and Sonoran Desert grassland sister species *G. lightfooti*, although some individuals (those in Clade 2—see below) with similar ITS2 DNA (see Fig. 209), *G. lightfooti*, often associated with *Yucca elata*, have longer cerci usually as long as ovipositor tip in situ, and females usually with light tegminal bar (of 21 *G. sotol* females collected in 2017, only 2 have slight indications of tegminal bars despite their bodies being solid black, which would accentuate any overlying tegmina bar). Additionally, late instar *G. sotol* abdomens frequently with circular, dorsal stripes while those of *G. lightfooti* are usually tan and blotched. Separated from sky island *G. planeta* from the Davis Mts., in western Texas, by the latter's shorter cerci and oak-forested habitat and distinct multilocus DNA (Gray *et al.* 2019). Separated from allopatric, earlier maturing (despite higher, cooler elevation), more western *G. montis* by multilocus DNA (Gray *et al.* 2019), more teeth/mm in *G. sotol*, and habitat, with *G. montis* occurring under mountain-top trees and *G. sotol* occurring in more open Chihuahuan Desert. Separated from more western *G. saxatilis* by the latter's longer cerci, habitat (likes rocks and almost never up in plants) and DNA. Separated from more western *G. vulcanus* by lower, non-overlapping PR in the latter and differences in habitat (sotol obligate vs. lava bed obligate) and multilocus DNA (Gray *et al* 2019). Separated from *G. leei* by habitat (sotol obligate vs. lava bed obligate) and multilocus DNA.

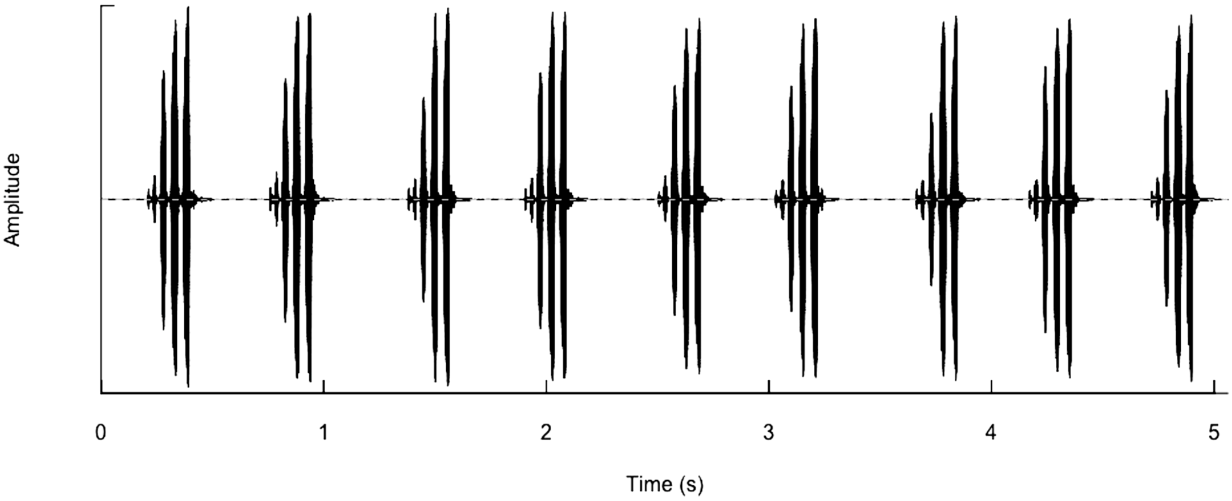

FIGURE 214. Calling song (R17-44) of *G. sotol* from type locality (S17-4), recorded at 24.1°C.

Holotype. Male (Fig. 213): USA, New Mexico, Dona Ana Co., Organ Mountains-Desert Peaks National Monument, Aguirre Springs Campground, 3-vii-2017, 5807', 32° 22' 12.72" -106° 33' 41.18". D.B. Weissman, D.W. Weissman. S17-4, R17-26, DNA (ITS2 and multilocus) sample G3493. GenBank accession # ITS2: MN136862. BL 20.66, HF 11.89, right cercus 12.63. Right tegmen removed: 152 teeth, file length 3.3, TL 10.9, TW 4.3. Type deposited in CAS, Entomology Type #19279.

Paratypes. (total 33♂ 36♀) Type locality, 24-vi-1985 (S85-93), D.C. Lightfoot, 2♂ 3♀; early June, 1994 (S94-29), D.C. Lightfoot, 9♂ 6♀; 3-vii-2015 (S15-77), 4♂ 4♀; 19-v-2017 (S17-4) 17♂ (including holotype) 23♀, most raised from late instars.

Derivation of name. Named for its association with sotol, *Dasylirion wheeleri*, in the Organ Mts. Sotol is a distilled spirit made by a process similar to that for mescal.

Geographical range. Currently known only from the Organ Mts. (Fig. 215), however the Transmountain Road through the Franklin Mountains to the south of the Organ Mountains, should be checked for *G. sotol* in the appropriate habitat. Highest peak there is almost 2194m.

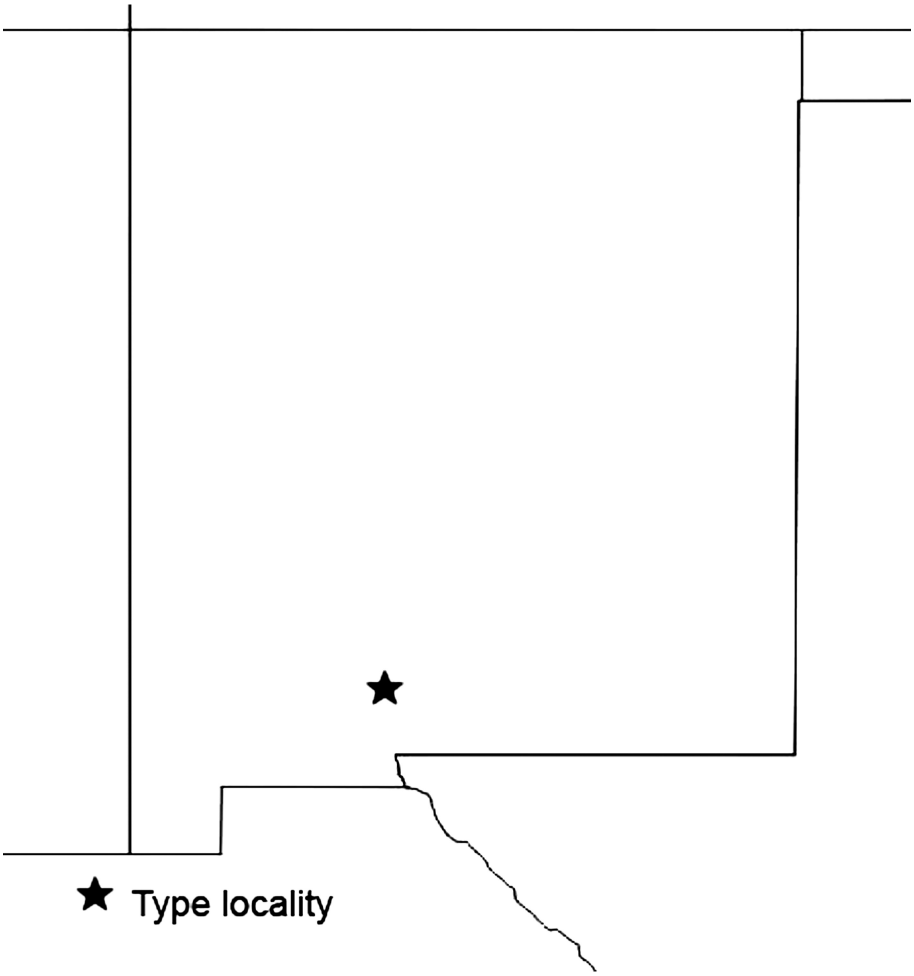

FIGURE 215. Known distribution of *G. sotol*; known only from the type locality in NM despite extensive sampling of nearby regions.

Habitat. Type locality with short oaks and other trees, various shrubs, sotol, and some cactus. The site is at the transition of two Level IV, Chihuahuan Desert ecoregion zones: 24c (Low Mountains and Bajadas) and 24d (Chihuahuan Montane Woodlands). See https://www.epa.gov/eco-research/level-iii-and-iv-ecoregions-state.

Life cycle and seasonal occurrence. No egg diapause (S17-4). Apparently one generation/year in the field, based on our observations of them overwintering as mid-late instars with first adults appearing mid-May. Few adult males heard singing during spring stops in 1994 (early June) and 2017 (May 19th) but oatmeal laid on dirt trails in campground area, during both visits, resulted in many late instars being collected. No singing males were heard during mid to late-summer nighttime visits on 17-viii-1993 (S93-70) and DC Lightfoot visit on 16-ix-2018, consistent with one generation/year. And, most importantly, no nymphs and only 1 adult female came to 7 kg of oatmeal on 16-ix-2018.

Interpretation of this apparently straightforward field situation is complicated by laboratory data: Nymphs collected May 19, 2017, were raised to adult under ambient light conditions, at fluctuating temperatures between 18-30°C, and allowed to mate. Adult females were then isolated in cartons with moist sand, for oviposition, starting on June 13 and June 24. Very good egg hatch commenced on July 8 and July 13, respectively, indicating the absence of an obligate egg diapause. Many, but not all, nymphs in both cultures grew rapidly with the first adults appearing around September 12th in both containers, confirming the possibility of 2 generations/year. Males were heard singing starting on September 16. Still, a fair number of nymphs were only mid-instar in mid-September. So, while this species could have 2 field generations/year, on-site observations are necessary to confirm if those results from 1993 and 2018 are representative of most seasons.

We believe the following could explain this puzzling situation: *Gryllus* eggs need to absorb liquid water, from the substrate, to grow (Hinton 1981). Oviposition into constantly moist sand satisfies this requirement and can result in the rapid hatching of such eggs and the appearance of second generation adults in late summer. But for eggs laid in the field, where Southwestern US monsoon rains typically first arrive in July and August, there may not be adequate time for second generation adults to appear before the arrival of cool fall temperatures, if egg development only first starts with the arrival of moisture. We suspect that if the first rains arrive in July, there will be enough time for some second-generation adults, although their contribution to the following year's population is unknown. What is apparent from the laboratory data is that since many nymphs from first-generation adults grow slowly, there will still be many individuals overwintering as late instars even in years with early July monsoon rainfall. Such a range of maturation dates results in flexibility, depending on rainfall and temperatures, within the population: early hatching would give the nymphs a chance to mature the same summer rather than overwintering as late instars and becoming adults the following spring. We would also like to see research into how long *Gryllus* eggs can remain viable in dry soil, since one predicted result of climate change is increased droughts in certain areas. This information may be particularly relevant in the Southwestern US since Hinton (1981, p. 177) notes that among insects "there are no kinds of eggs that will enter a state of cryptobiosis (i.e. reversible standstill of metabolism) by dehydration at physiological temperatures." Also, do crickets in areas with monsoon rains have more variable instar development than those in California with its predictable summer drought periods and a Mediterranean climate—rainfall regime?

Variation. **Color**: Three 2017, laboratory maturing adult females with a light colored, central, longitudinal belly strip that darkened post-mortem. **Tegmina**: One 1994, laboratory maturing female with tan tegmina.

DNA. Eight males and one female of *G. sotol* were sequenced for ITS2, and yielded 2 clades at the type locality (S15-77 & S17-4) (Fig. 209): 4 males and 1 female (G3493, G3497, G3503, G3505, G3508) were in Clade 1, more similar to *G. transpecos*; and 4 males (G3295, G3509, G3510, G3511) were in Clade 2, more similar to *G. lightfooti*. We suspect that this may be an artifact of poor alignment of ITS2 data (see general DNA discussions, pp 14 & 16). Multilocus sequence data (Gray *et al.* 2019), including individuals from each *G. sotol* ITS2 clade, suggests that *G. sotol* is genetically cohesive and most closely related to frequently arboreal *G. lightfooti* and terrestrial *G. transpecos*.

Discussion. On arrival, between 17:00 and 17:30, at the type locality in 2015 and 2017, males heard singing from sotol plants despite bright, sunny, warm weather. The plants with the most singers were those with live blades near the top but with dead flower stalks and dead skirts on lower three to four feet. Breaking off such plants at ground level and pounding the main stalk on open ground resulted in individuals being thrown onto the ground. Displaced individuals quickly attempted, many times successfully, to jump back into the plant being beaten.

We heard probable *G. sotol* males singing some 90m lower (32° 23' 14.05" -106° 33' 4.83") off Aguirre Springs Road but none could be collected, despite repeated attempts, with oatmeal trails, over several years. Once into more open and dryer Chihuahuan Desert at 1536m, where we found *Yucca elata*, no *Gryllus* crickets, including *G. lightfooti*, were heard. The time was 22:25 and the air temperature was 15.6°C, so the locality should be rechecked later in the season since mid-May, 2017, may be too early for singing *G. lightfooti*.

Oatmeal trail most productive where sotol plants occurred. In fact, this technique was much more successful than collecting later in summer when most of population is adult because, during the latter period, adult males seldom wander and infrequently come to oatmeal trails. Much greater success comes from collecting late instars and raising them to adult, especially at this site where collecting of singing adult males is extremely difficult due to their calling from impenetrable locations under, and within sharp, succulent sotol plants.

This is one of only 2 *Gryllus* commonly associated with an arboreal habitat, and both it and *G. lightfooti* are sister species [Note: several other species do occasionally climb vegetation, and that occurrence is noted under each respective taxon.]

Gryllus transpecos Weissman & Gray, n. sp.

Texas Trans-Pecos Field Cricket
Figs 207–209, 216–221, Table 1

'G. #16' and 'G. #24' of DBW notebooks.

Distribution. Only known from western Texas between the Rio Grande River and the Pecos River.

Recognition characters and song. Medium to large sized, wide head and pronotum, always short hind winged, female tegmina only cover ½ to ¾ of abdomen, cerci in situ typically extend beyond tip of ovipositor. Overall color black (Fig. 216) except for inside of hind femur which is reddish. *Song* (Fig. 217, R09-93) a slow chirp of 4–5 (range 3–7) p/c, CR usually 80–150, PR 20–30 at 25°C. Closely related and similar to both *G. lightfooti* and *G. sotol.* Separated from *G. lightfooti* by, in *G. transpecos*, cerci in situ typically longer than ovipositor tip, female tegminal bars usually absent (Fig. 216), associated with rocks (vs. open grasslands), small but consistent ITS2 DNA differences (Fig. 209), and not known to climb into vegetation to sing. The two taxa could overlap in far western Texas, although no such locality presently known. From Van Horn Pass, where *G. transpecos* is common, to the town of Van Horn (S91-48), where *G. lightfooti* occurs, is some 4 miles distance. The allopatric, Organ Mts., NM, endemic and closely related, *G. sotol* (Table 1, p. 18) has more file teeth, higher tooth density, shorter cerci never as long as ovipositor tip (typically longer in *G. transpecos*), slower PR, and different habitat: open, lower elevation, drier, rocky Chihuahuan Desert for *G. transpecos* versus higher, cooler, low mountain bajadas and woodlands, with sotol (*Dasylirion wheeleri*), for *G. sotol*. Additionally, *G. sotol* frequently climbs into sotol while *G. transpecos* is found on the ground, or sometimes on rocky cliff faces in road cut areas.

FIGURE 216. Holotype male (left) of *G. transpecos.* Female (right) also from Big Bend National Park (S07-37) near type locality.

There are four other slow chirping, frequently rock-associated *Gryllus* species in the Trans-Pecos area that *G. transpecos* must be distinguished from. These four are not closely related to *G. transpecos* and can be separated by DNA (16S, ITS2, and multilocus data). Combinations of morphological, ecological and song characters are also diagnostic, as follows. From sometimes sympatric (at Van Horn Pass and Davis Mts.) *G. longicercus*: *G. transpecos* is distinguished by its larger head, broader pronotum, shorter cerci, lower tooth count and higher pulse rate. From almost sympatric (Davis Mts.) *G. veletis*: *G. transpecos* with longer cerci and different habitat (never in grassland). From sometimes sympatric (Davis Mts., S15-61) *G. planeta*, separated by 5 mostly non-overlapping physical characters (Table 1, p. 18): *G. planeta* has fewer number of teeth and shorter file length, cerci length, tegminal length and tegminal width, and faster chirp rate. From sometimes sympatric (at Big Bend, S85-55) *G. chisosensis*, they are separated by no overlap in number of teeth and PR and minor overlap in teeth/mm and cerci length. The two taxa are also separated by microhabitat in that *G. chisosensis* prefers rocky areas of many rock layers (e.g. talus slopes) while *G. transpecos,* while preferring rocky habitats like rocky road cuts, is not associated with extensive piles of rocks.

From other allopatric, widespread, more western and unrelated, slow chirping US *Gryllus, G. transpecos* is separated from *G. montis* which has shorter cerci, narrower head and pronotum, earlier appearance of adults, different habitats (latter almost always with an overhead tree canopy), and longer ovipositor (Fig. 218).

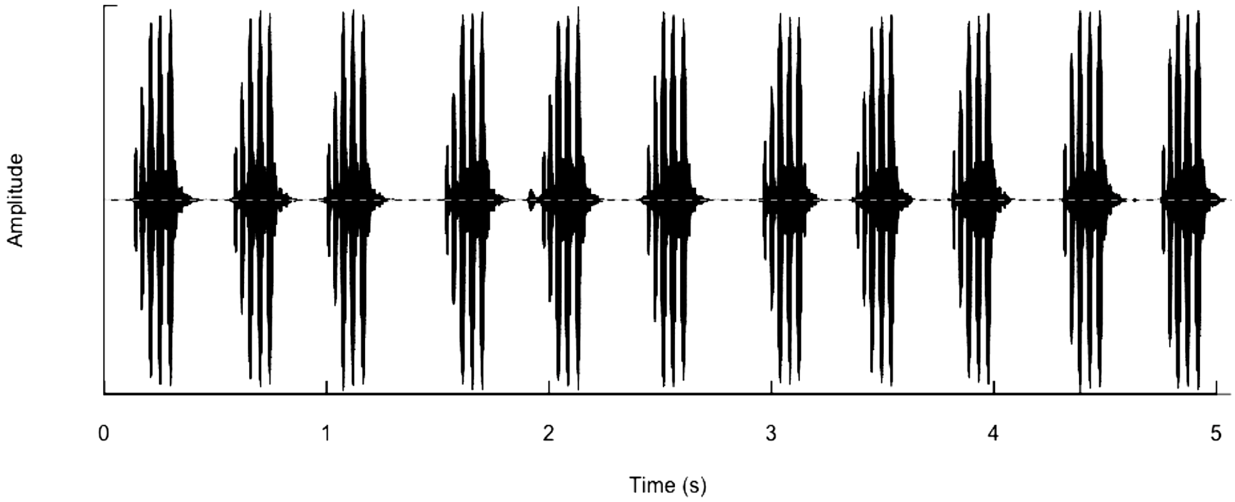

FIGURE 217. Calling song (R09-93) of *G. transpecos* from Culberson Co., TX (S09-64), recorded at 25°C.

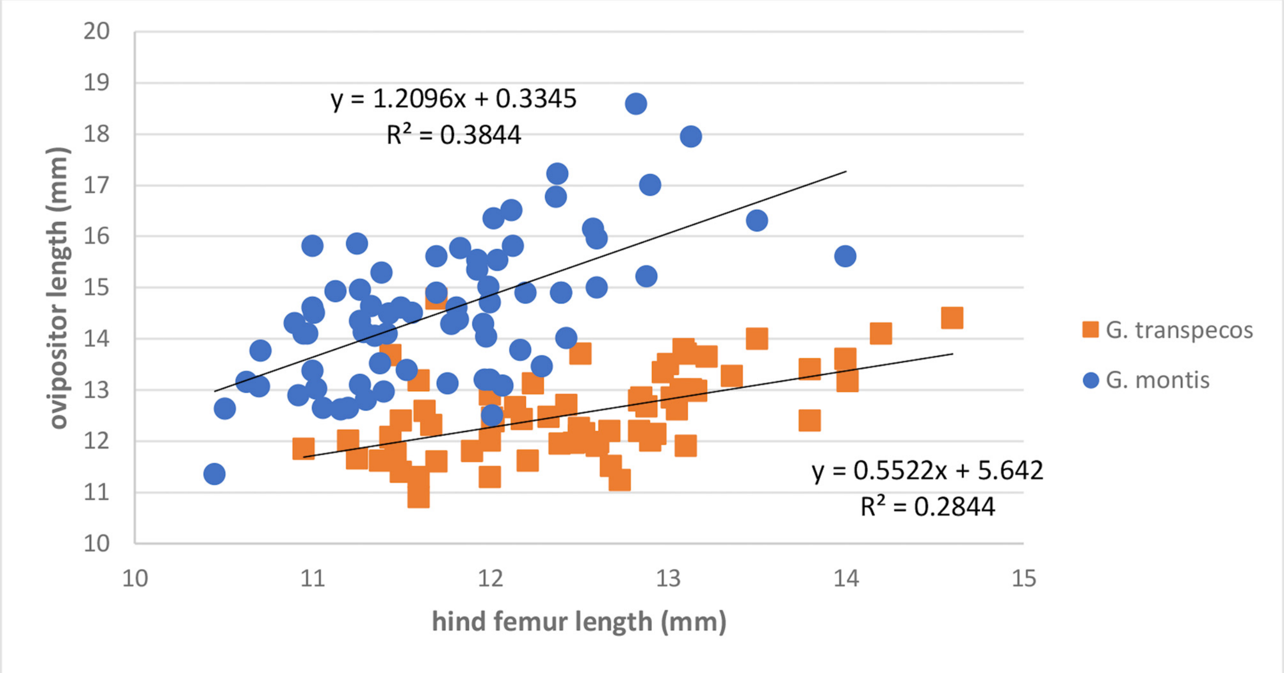

FIGURE 218. Regression hind femur length vs. ovipositor length in *G. transpecos* vs. *G. montis.*

Separated by 800 km from more western *G. saxatilis* which has longer tegmina and longer ovipositor, different multilocus (Gray *et al.* 2019), 16S, and ITS2 (Fig. 209) DNA.

Holotype. Male (Fig. 216). USA, Texas, Brewster Co., Chisos Mts., Big Bend National Park, Grande Village Road to Ranger Station near Lost Mine Trail parking lot, 1.5 m NW ranger station, 12-vi-2007. 5500', 29° 16.471' -103° 17.211'. D.B. Weissman & D.C. Lightfoot. S07-36, R07-95, G1175. 16S ribosomal RNA GenBank accession # MN136663. BL 19.49, HF 12.13, LC 12.36. Right tegmen removed: 142 teeth, file length 3.8, TL 11.9, TW 5.2. Deposited CAS, Entomology type #19273.

Paratypes. (Total: 105♂ 76♀). **Texas,** *Brewster Co.*, Chisos Mts., Big Bend National Park, 5500', type locality, 8-

vi-1985 (S85-55) 13♂ 6♀; 5-vi-1991 (S91-41) 11♂ 7♀; 12-vi-2007 (S07-36) 2♂ 1♀; Panther Junction, 3734', 12-vi-2007 (S07-38), 2-vii-2015 (S15-68) 3♂ 3♀; 18.7 m SE Panther Junction, 9-vi-1985 (S85-57) 1♂; 5-vi-1991 (S91-42) 1♂; Maverick Rd., 3756', 2-vii-2015 (S15-69) 2♂; Rio Grande Village, 2100', 9-vi-1985 (S85-56) 4♂ 1♀; 5-vi-1991 (S91-43) 2♂; Grande Village Road 4.5 m NW ranger station, 4340', 12-vi-2007 (S07-37) 1♂ 3♀; 28-v-2016 (S16-12) 1♂. Hwy 118 24 m S Alpine, 4434', 2-vii-2015 (S15-72) 7♂ 10♀. Hwy 170 8 m W Terlingua, 3000', 27-v-2016 (S16-10) 1♂. Hwy 385 3.3 m S Marathon, 4050', 28-v-2016 (S16-14) 2♂ 1♀. *Culberson Co.,* Van Horn Pass area, 4880', 31° 03' 17.0" -104° 57' 04.4", 12-vi-1985 (S85-65) 6♂ 4♀; 6-vi-1991 (S91-47) 11♂ 11♀; 29-vi-2009 (S09-64) 10♂ 3♀. *Jeff Davis Co.,* Davis Mts., Observatory, 6747', 1-vii-2015 (S15-61) 4♂ 1♀; 2.9 road m below Observatory, 6010', 1-vii-2015 (S15-64) 1♂ 2♀; 3.2 road m below Observatory, 5935', 1-vii-2015 (S15-65) 5♂ 5♀. *Presidio Co.,* Chianti Mts., Hwy 67 Shafter, 3880', 27-v-2016 (S16-3) 4♂; 0.5 m N Shafter, 3856', 27-v-2016 (S16-2) 7♂ 15♀; 2.3 m S Shafter, 26-vi-1986, 3900' (S86-45) 3♂ 2♀. Hwy 170 E. Presidio, 2680', 27-v-2016 (S16-7) 1♂ 1♀. Hwy 170 39 m W Terlingua, 2660' 27-v-2016 (S16-8) 1♂; 30 m W Terlingua, 2600', 27-v-2016 (S16-9) 1♂.

Derivation of name. Trans-Pecos was originally defined, in 1887, by Texas geologist Robert T. Hill, as that portion of Texas west of the Pecos River, which perfectly describes the distribution of this species.

Geographical range. (Fig. 219). Apparently absent from ecologically similar areas of the Guadalupe Mts., Culberson Co., Texas, where we found (S01-63, 64, 65) slow chirpers *G. longicercus* and *G. lightfooti* at lower, dryer elevations, and *G. veletis* at higher (1920m), more mesic Dog Canyon.

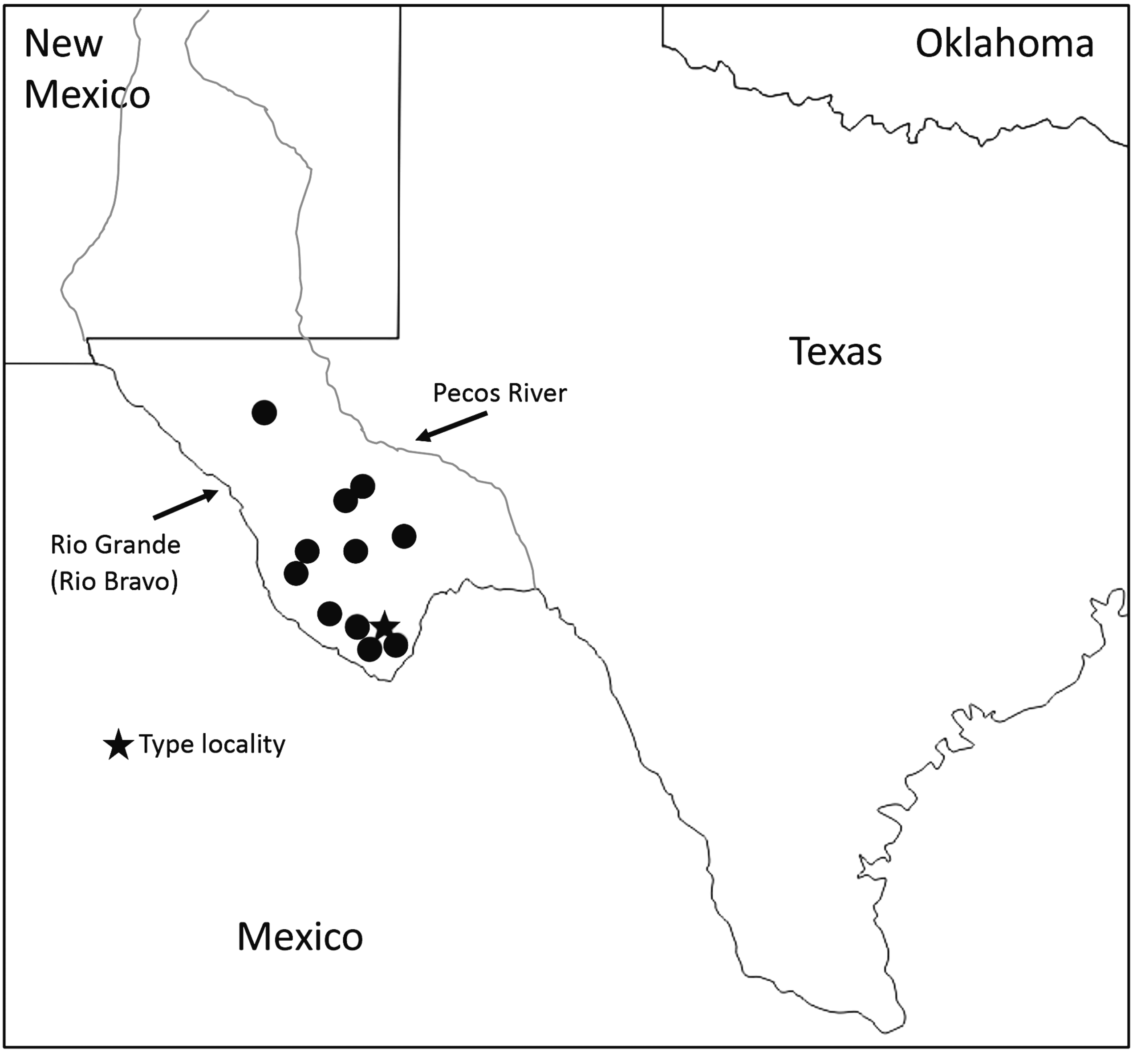

FIGURE 219. Known distribution of *G. transpecos.*

Habitat. Rocky road cuts (S16-2, 16-4); Piñon-juniper-oak woodland (S07-36); Chihuahuan Desert (S07-37) with *Acacia*, sotol, and *Yucca*; and natural, rocky slopes in and around towns (S16-3). Males sing from crevices, holes, under small plants, and under and around rocks. Not known from within any town, where *G. lightfooti* can frequently occur. *G. transpecos* appears to be the ecological equivalent of more western *G. saxatilis.*

Life cycle and seasonal occurrence. No egg diapause: Big Bend (S85-55 and S85-56), Van Horn (S85-65). Probably one generation/year. No nymphs seen at any Brewster Co. locality but most of population south of Shafter (Presidio Co., S86-45) penultimate or last instar when collected on 26-vi-1986.

Variation. Specimens from Big Bend National Park (our 'G. #24') are larger than those from Van Horn Pass (our 'G. #16') (see Table 1, p. 18) and this caused us some initial confusion. Individuals from these two localities differed in temperature corrected pulse rate, with #16 slower than #24 (21 ± 0.4 p/s versus 24 ± 0.4 p/s; $F_{2,22} = 12.02$, $P < 0.001$)); males differed in teeth/mm vs. hind femur length (Fig. 220; $F_{2,30} = 5.5$, $P < 0.01$) and tegmina width vs. hind femur length (Fig. 221; $F_{2,30} = 7.4$, $P < 0.01$). There was no difference in chirp rates, pulses/chirp, or dominant frequency. However, with the addition of individuals from areas other than these two localities, these significant differences disappeared, and we currently attribute this variation mostly to differences in body size, which is consistent with the linear relationships seen in both regressions—i.e. larger crickets have larger body proportions.

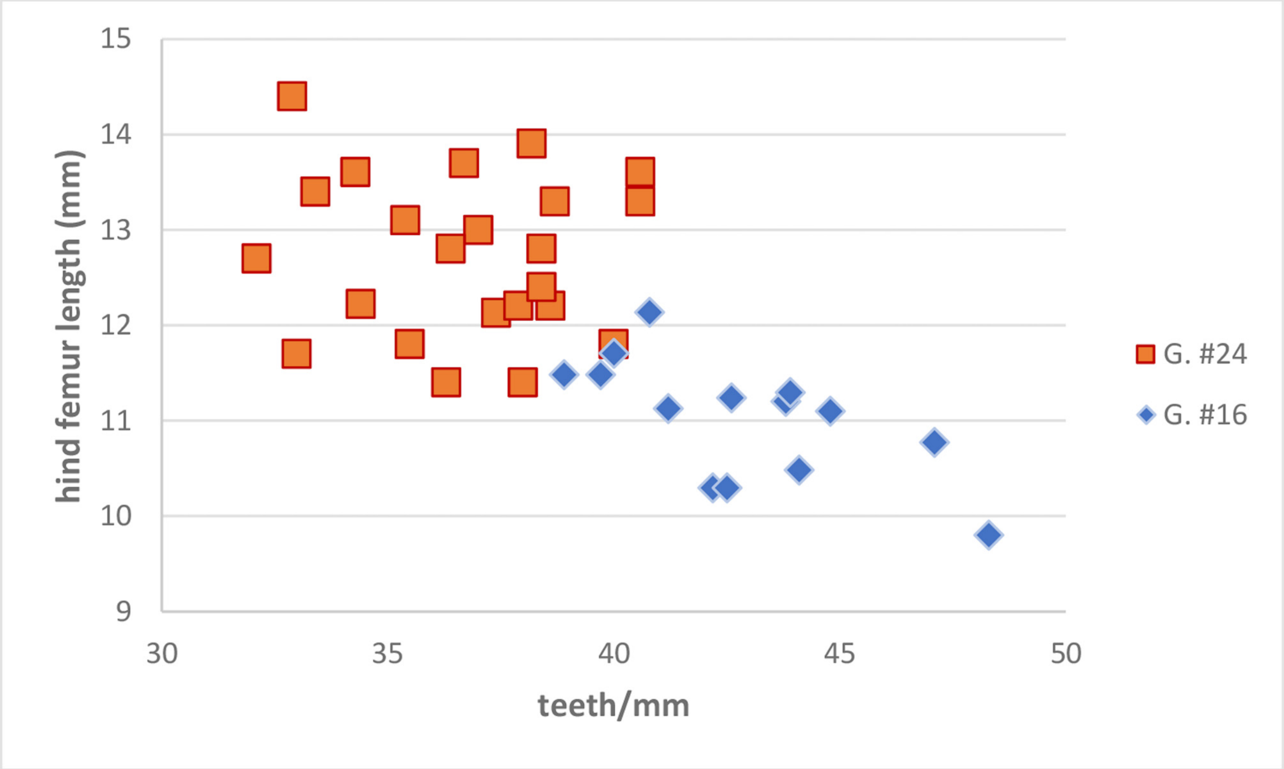

FIGURE 220. Regression of teeth/mm vs. hind femur length in *G. transpecos* populations from Big Bend National Park ('G. #24') vs. Van Horn Pass ('G. #16').

DNA. Multilocus G3062 Big Bend National Park (S15-68) and G3083 Davis Mts. (S15-61) sister species of *G. sotol* and *G. lightfooti* (Gray *et al.* 2019). We note that our confusion re. G. #16 and G. #24 (see above) was compounded by the fact that early 16S sequencing of *G. transpecos* yielded 3 separate clades comprised of individuals from 5.3 km south Marathon (S16-14), individuals from 38.6 km south of Alpine (S15-72), and individuals from Van Horn Pass (S09-64). Subsequent ITS2 sequencing showed these same individuals, from all three sites, to cluster together (Fig. 209, p, 207), hence our combining them together under *G. transpecos*.

Discussion. Can be a relatively common field cricket where found. Singing males easy to approach but stop singing once turning over rocks near them, as opposed to many males of *G. longicercus* that continue to sing while "their" rocks being turned over. Can sing all night and into early morning in Big Bend (S85-55, at 08:30).

Tinkham (1948) discussed the Orthopteran and faunistic zones of the Big Bend Region.

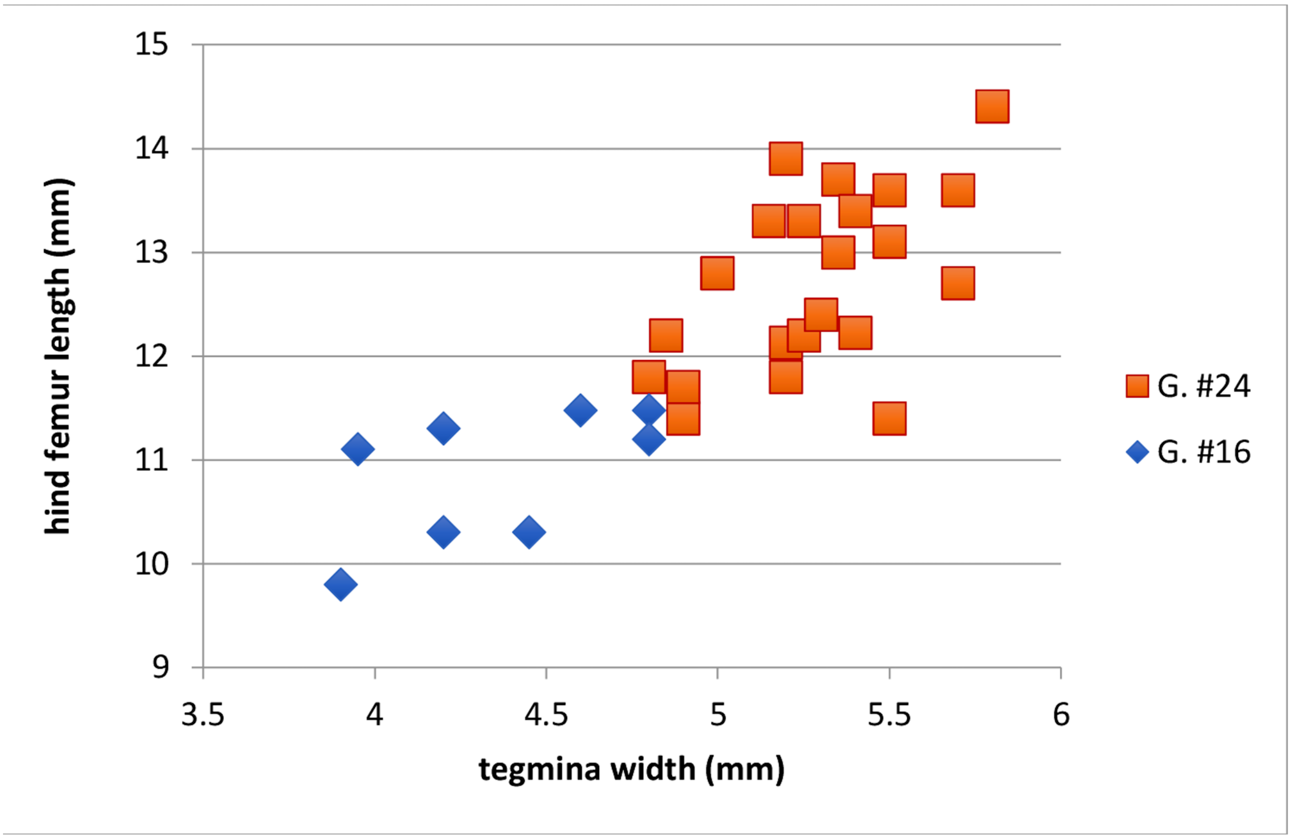

FIGURE 221. Regression tegmina width vs. hind femur length in *G. transpecos* populations from Big Bend National Park ('G. #24') vs. Van Horn Pass ('G. #16').

The Longicercus Group

G. longicercus Weissman & Gray, n. sp. and *G. vulcanus* Weissman & Gray, n. sp.

Sister species of field crickets with exceptionally slow pulse rates within chirped song (Figs 222, 223). *G. longicercus* is widespread in the Southwestern US hotter desert regions; *G. vulcanus* is a morphologically similar, but smaller, cricket restricted to two lava flows in New Mexico. ITS2 does not separate the taxa (Fig. 224); whether or not this is due to incomplete lineage sorting, given a recent derivation of the lava-endemic *G. vulcanus* from *G. longicercus*, or because *G. vulcanus* is simply *G. longicercus* as found on lava, is not entirely clear.

Gryllus longicercus Weissman & Gray, n. sp.
Long Cercus Field Cricket
Figs 206, 222–229, 232, 233, Table 1

'Gryllus #13' of DBW notebooks.
'G. longicercus' of Gray *et al.* (2016a).

Distribution. Southwestern states of Arizona, New Mexico, and Texas, with minor extensions into California, Utah, and Colorado.

Recognition characters and song. A medium to large, usually short hind winged cricket with the longest known cerci in the genus, sometimes exceeding the body length of pinned specimens (male from Kofa [S88-88, R88-172]). Intact cerci always considerably longer than ovipositor in situ (except for individuals from Tijeras Canyon, NM, S19-35). File teeth from ~170–220 (range 155–231). Almost always associated with rocks. *Song* (Fig. 225, R15-159) a slow to medium fast chirp with 4–5 (range 3–6) p/c, PR usually from 9–12 with individual pulses distinguishable by ear and almost countable at 25°C. While *G. longicercus* can occur microsympatrically with several other slow chirping, rock loving, medium to long length cerci, western US *Gryllus,* its low PR makes them immediately identifiable in the field. Morphologically most similar to *G. chisosensis* but the latter, with its unique DNA, restricted to the Chisos Mountains in Big Bend, TX, where *G. longicercus* doesn't occur (nearest population of *G. longicercus* is in the Chinati Mountains, just south Shafter [S16-4] and ~115 km from nearest population of *G. chisosensis).* Microsympatric with the Organ Mountains' endemic *G. sotol* at Aguirre Springs, New Mexico, but separated by non-overlapping pulse rate, DNA, and fewer file teeth in the latter. Morphologically similar to *G. leei* but the latter, only on lava flows in Utah, separated by non-overlapping PR (lower in *G. longicercus),* almost non-overlapping tooth count (higher in *G. longicercus)* and DNA (Gray *et al.* 2019). Also, morphologically similar to *G. vulcanus* but the latter, only on lava flows in New Mexico, is a smaller cricket with fewer teeth, shorter tegmen, shorter cerci, and shorter ovipositor (Table 1, p. 18). Microsympatric with *G. transpecos* but separated by non-overlapping PR (lower in *G. longicercus)* and almost non-overlapping tooth count (higher in *G. longicercus).* Comparing females of *G. transpecos* from Van Horn, TX (S85-65, S09-64) with microsympatric *G. longicercus*, ovipositor in latter shorter than in former despite larger body size (can also separate female *G. transpecos* from female *G. longicercus* because of cerci length in *G. transpecos* are as long as or just longer than the ovipositor in situ). Frequently microsympatric, in road cuts, with *G. lightfooti,* but separated by non-overlapping PR (lower in *G. longicercus)* and almost non-overlapping tooth count (higher in *G. longicercus).* Also, females of *G. lightfooti* difficult to distinguish although the latter usually have a tegminal bar vs. solid black tegmina in *G. longicercus*. Only known to be microsympatric with the more western, slow chirping, rock loving *G. saxatilis* in the Hualapai Mts., Mohave Co., AZ (S90-56), but the two species both occur in Washington Co., UT and could also be sympatric in south-eastern CA around Anza Borrego, San Diego Co. In such localities, the 2 taxa would still separate by pulse rate and DNA.

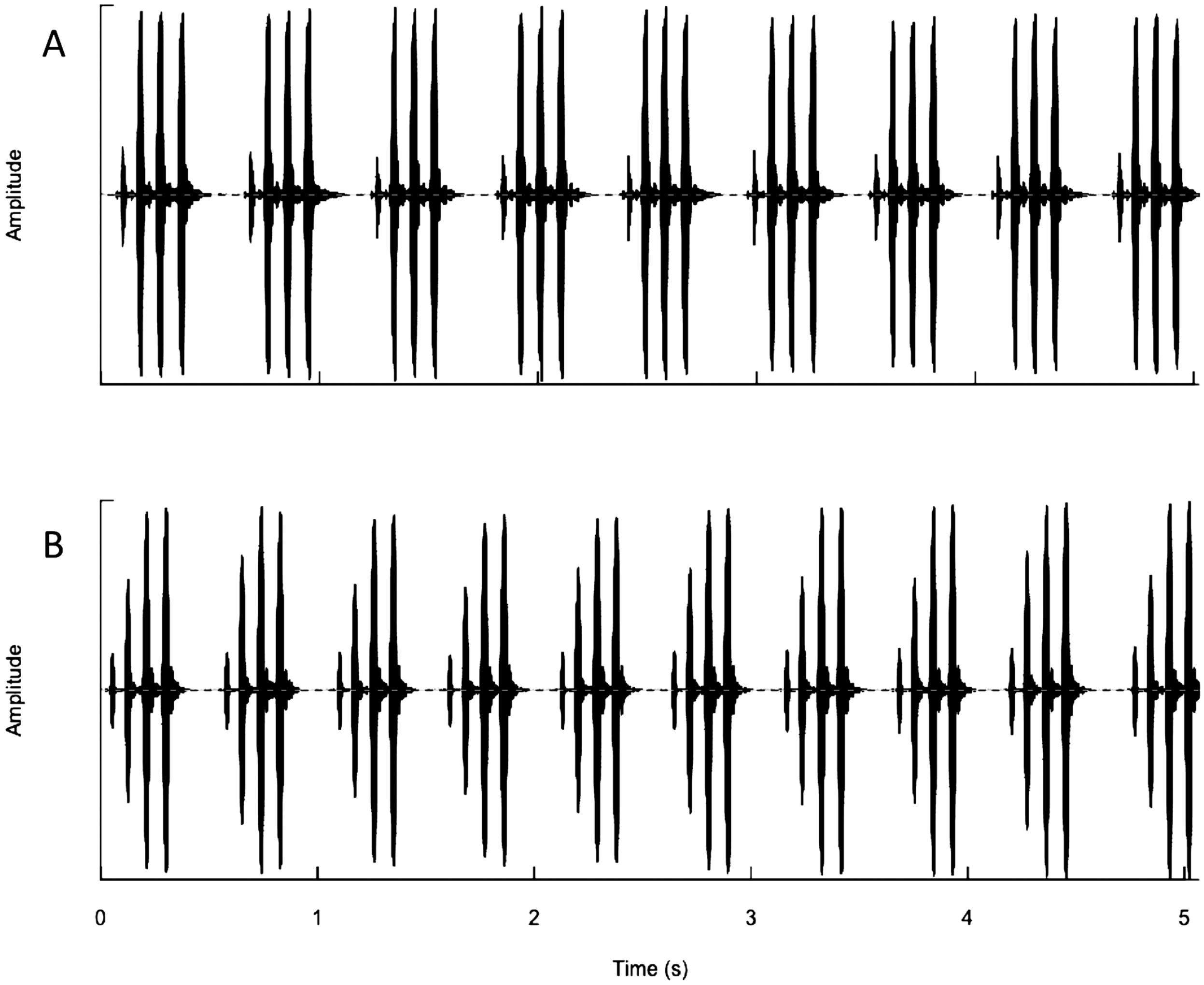

FIGURE 222. Five second waveforms of typical calling songs of (A) *G. longicercus* and (B) *G. vulcanus*. (A) *G. longicercus*: (R15-159) Torrance Co., NM (S15-52), at 25.3°C; (B) *G. vulcanus*: (R07-68) from type locality, at 25°C.

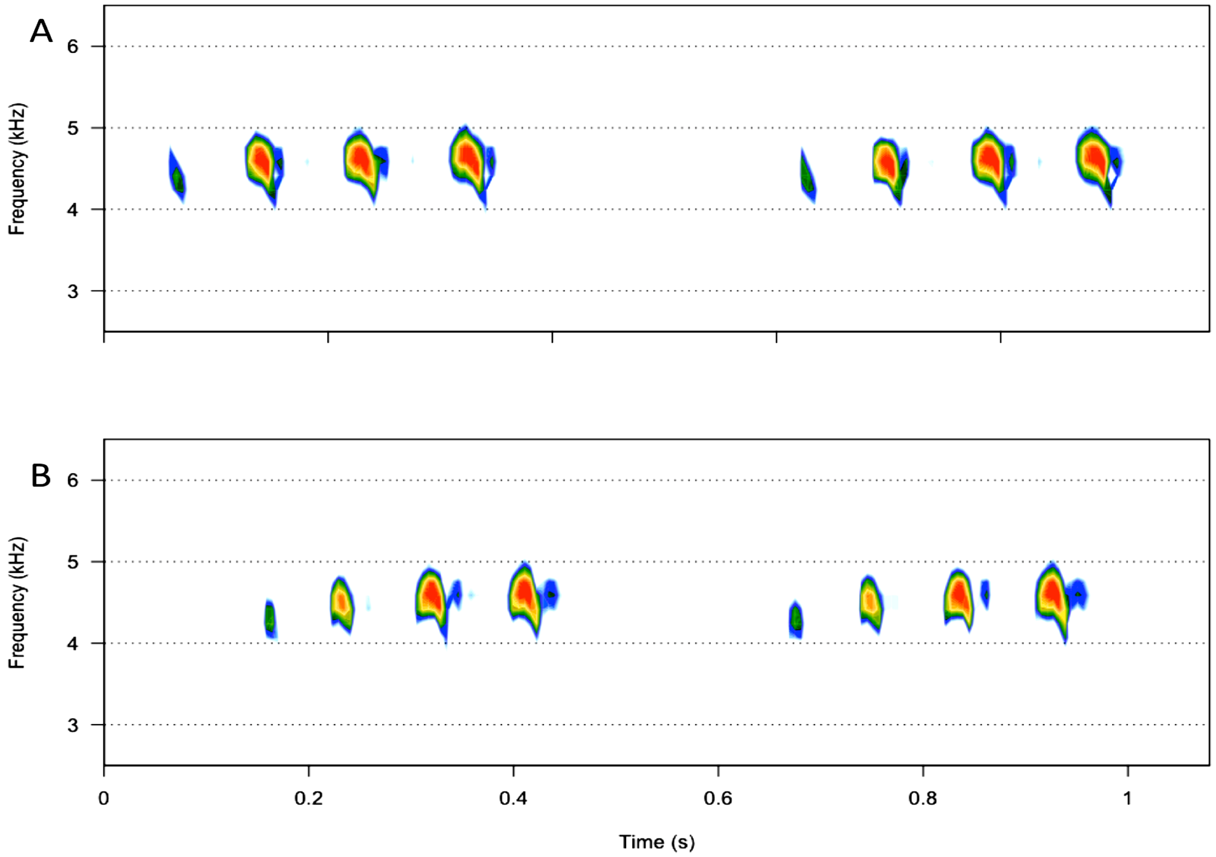

FIGURE 223. One second spectrograms of typical calling songs of (A) *G. longicercus* and (B) *G. vulcanus*, same males as in Fig. 222.

Holotype. Male (Fig. 226): Arizona, Yuma Co., Kofa National Wildlife Refuge, Palm Canyon, 16-ix-2011; molt to adult 25-x-2011. 2100'. 33° 21' 37.8" -114° 06' 22.2". D.B. Weissman, D.W. Weissman. S11-93, R11-185, BL 19.06, HF 11.86, LC 16.48. Right tegmen removed 217 teeth, file length 4.3, TL 13.7, TW 5.4. Type deposited in CAS, Entomology Type #19267.

Paratypes. (Total 217♂ 158♀). **Arizona.** *Cochise Co.,* Bisbee, 5500', 1-vi-2013 (S13-18) 2♂. Portal, 29-vii-1981 4770' (S81-37) 2♂. Chiricahua Mts., Fort Bowie, 4723', 2-vi-2013 (S13-19) 13♂ 6♀. *Coconino Co.,* Sedona, 15-vi-1990, 4400' (S90-49) 3♂ 2♀; 12-vi-1996, (S96-62) 5♂ 1♀. Hwy 89A 1 m S intersection with Hwy 179, 30-vi-1994, 4420' (S94-36) 4♂ 2♀. 2.6 m N Sedona, 25-vi-1980, 4600' (S80-43) 2♂ 2♀. *Gila Co*., Coolidge Dam, 30-vii-1981, 2400' (S81-43) 1♂. *Graham Co.,* 7-10 m NW Bylas, 30-vii-1981, 2800' (S81-42) 1♂; 25-viii-1982 (S82-102) 8♂. Pinaleno Mts., Mt. Graham, 4-vii-1994, 5000' (S94-54) 5♂; 10-vi-2012, 5000' (S12-19) 2♂ 8♀. *La Paz Co.,* 18-35 m N Wenden on road to Alamo Dam, 23-vii-1990, 1200' (S90-70) 3♂ 1♀. *Mohave Co.,* Burro Creek Campground, 1960', 3-iv-2004 (2004-002) 1♂. Quartzsite, 26-vi-1980, 1000' (S80-46) 2♂. Kingman, 3-viii-1991 (S91-68) 1♂; 2-viii-1992, 3700' (S92-113) 1♂ 1♀. Road to Hualapai Mtn. Park SE Kingman, 19-vi-1990, 5000' (S90-56) 3♂ 2♀. *Pima Co.,* Ajo, 20-viii-1998, 1720' (S98-72 & S98-74) 9♂ 6♀; 17-ix-2011 (S11-99) 1♂. Hwy 85 13m N Ajo, 1255', 30-vii-2015 (S15-110) 1♂ 1♀. Baboquivari Mts., Brown Canyon, 31° 45' 37.0" -111° 31' 58.8", 3786', 29-vii-2015 (S15-105) 1♂ 5♀. Kitt Peak, Hwy 386 5.1 m from Hwy 86, 17-ix-2011, 4500' (S11-98) 2♂; Kitt Peak picnic area, 10.5 m from Hwy 86, 8-vi-2013, 6277' (S13-36) 3♂ 1♀. Near Sonora Desert Museum, 28-vii-1981, 2900' (S81-35) 5♂ 2♀. Organ Pipe Cactus National Monument Campground, 8-iv-2004, 1670' (2004-086) 1♂. Santa Catalina Mts., Mt. Lemmon Rec. Area, 27-vii-1990, 2900' (S90-83) 3♂ 2♀; 7-vii-1994, 3500' (S94-61) 1♂; 27-vi-2009, 4820' (S09-51) 1♂. 11-vi-2012, 4675' (S12-23) 10♂ 9♀. Tucson, 27-vii-1990, 2600' (S90-84) 1♂. Why, 20-viii-1998, 1740' (S98-71) 9♂ 5♀. *Santa Cruz Co.*, Madera Canyon, Bog Springs campground, 5010' 19-viii-2004, 6♀. *Yavapai Co.,* Hwy 179 on west side Sedona, 4000', 30-vi-2013 (S13-16) 4♂ 1♀. *Yuma Co.,* Telegraph Pass, 10-viii-1988, 600' (S88-90) 1♂; 17-viii-1998 (S98-62) 4♂ 2♀. Kofa National Wildlife Refuge, Palm Canyon, 10-viii-1988, 2050' (S88-88) 3♂; 4-vi-1989 (S89-26) 1♂ 6♀; 16-ix-2011 (S11-93) 10♂ 35♀. **California.**

San Bernardino Co., Providence Mts. State Recreational Area, 5-vi-1989, 4100’ (S89-28) 2♂ 1♀. Havasu City, 6-vi-1983 (S83-62) 1♂. 14 m N Vidal, 6-vi-1983, 1200’ (S83-63) 1♂. *San Diego Co.,* Road S22 from 2.7 to 10 m SW Borrego Springs, 8-viii-1988, 1800’ (S88-81) 2♂. **Colorado.** *Las Animas Co.,* Trinidad Lake State Park, Carpios Ridge Campground, 6734’, 29-vi-200, 1♂, JA Cole. **New Mexico.** *Bernalillo Co.,* Tijeras Canyon ~2 m W Tijeras, 6000-6600’ (S19-35, S19-37, S19-38), 3-5-vii-2019, 9♂ 8♀, D.C. & K. Lightfoot. *Chaves Co.,* Hwy 380 7.3 m E Roswell at mile post 163.4, 28-vi-2009, 3960’ (S09-59) 3♂ 5♀. Hwy 82 ~33 m W Artesia, 30-vi-2015, 4824’ (S15-56) 7♂ 9♀. *Dona Ana Co*., Organ Mts., Aguirre Springs Rec. Area, 24-vi-1985, 6500’ (S85-93) 2♂; 17-viii-1993 (S93-70) 1♂; 3-vii-2015 (S15-77) 1♂; 19-v-2017 (S17-4) 1♂ 2♀. Tortugas Mts., near UNM, Las Cruces, 23-viii-1982, 4000’ (S82-95 & S82-96) 2♂. *Sandoval Co.,* Jemez Pueblo, 22-viii-1982 (S82-90) 4♂ 2♀; 6-v-1985, 5600’ (S85-50) 3♂. *Socorro Co.,* Los Pinos Mts., Goat Draw 4.5 m N Hwy 60, 16-viii-1993, 6440’, 34° 22’ 10” -106° 32’ 0” (S93-69) 1♂. Hwy 60 34° 24’ 12.07” -106° 30’ 29.16”, 29-vi-2015, 6004’ (S15-53) 4♂ 4♀. Sevilleta National Wildlife Refuge, 15-viii-1993, 5145’ 34° 24’ 30’ -106° 56’ 43’ (S93-66) 4♂ 4♀. *Torrance Co.,* Hwy 60 rocky road cut SW Mountainair, 29-vi-2015, 6037’, (S15-52) 5♂ 2♀. **Utah.** *Washington Co.,* Springdale, 9-viii-1991, 4000’ (S91-94) 1♂. 2 m E of west entrance to Zion National Park, 10-vi-1996, 4220’ (S96-54) 4♂ 3♀. Just west of Zion National Park west entrance, 10-vi-1996, 4060’ (S96-55) 1♂ 1♀. **Texas.** *Culberson Co.,* Guadalupe Mts., 4.4 km NE Pine Springs, 13-vii-2001, 5240’ (S01-63) 9♂ 4♀. I10 8 m W Van Horn, mile post 133, 12-vi-1985, 4300’ (S85-65) 3♂ 1♀; 29-vi-2009 (S09-64) 4♂. *Jeff Davis Co.,* Davis Mts., 30° 40’ 8.73” -104° 02’ 14.72”, 6073’, 1-vii-2015 (S15-63) 2♂ 3♀. *Presidio Co.,* Chianti Mts., Hwy 67 0.5 m N Shafter, 3856’, 27-v-2015 (S15-2) 1♂ 1♀. Hwy 67 just S Shafter, 3920’, 27-v-2016 (S16-4) 5♂ 1♀. *Randall Co.,* Palo Duro Canyon State Park, 12-vi-1988, 3600’ (S88-37) 4♂ 1♀.

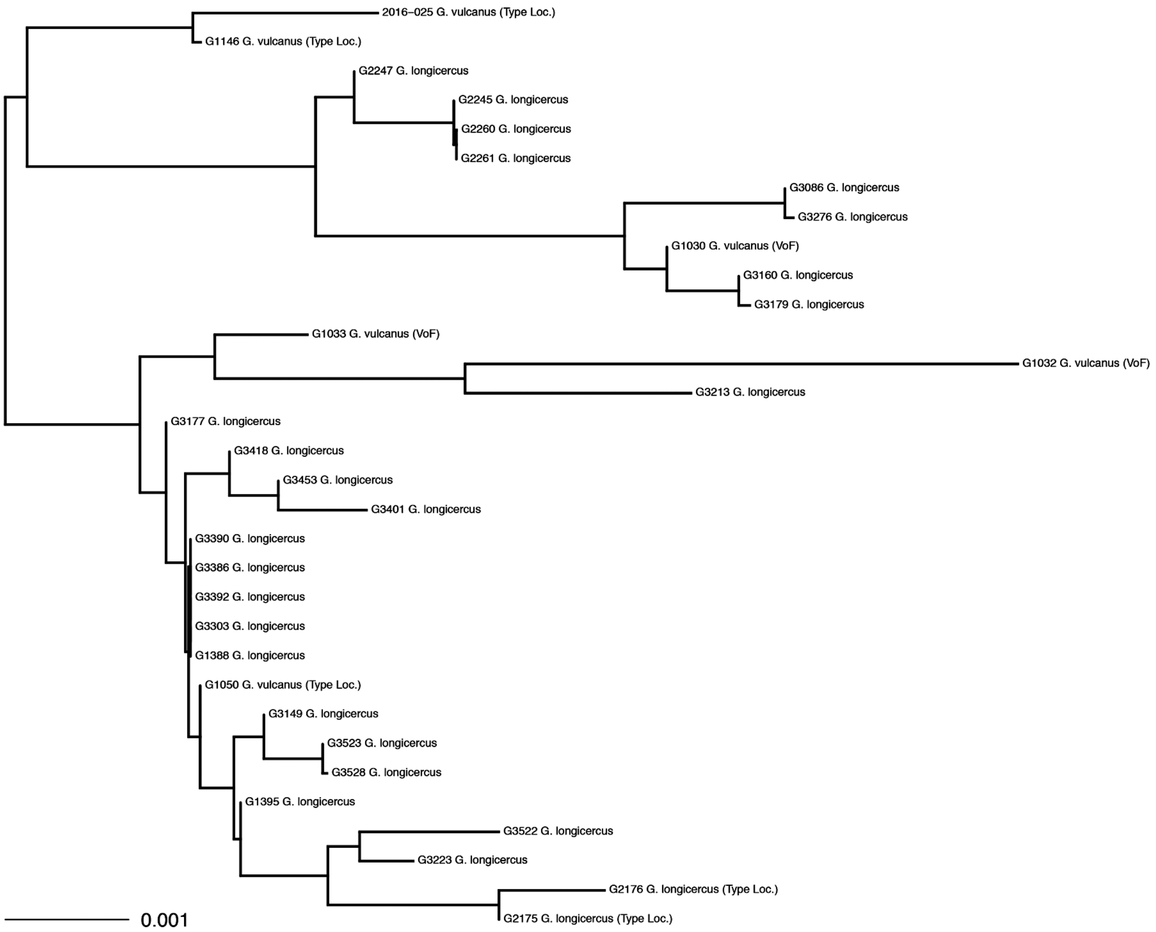

FIGURE 224. ITS2 gene tree. Collection stop numbers for ***G. longicercus*** samples: S09-64 (G1388, G1395); S11-93 (G2175, G2176); S12-23 (G2245, G2247, G2260, G2261); S15-52 (G3086, G3276); S15-56 (G3160, G3179); S15-63 (G3149, G3223, G3303); S15-77 (G3177); S15-110 (G3213); S16-2 (G3418); S16-4 (G3386, G3390, G3392, G3401, G3453); S17-4 (G3522, G3523, G3528). Collection stop numbers for ***G. vulcanus*** samples: S07-46 (G1030, G1032, G1033); S07-52 (G1050, G1146); type locality (2016-025).

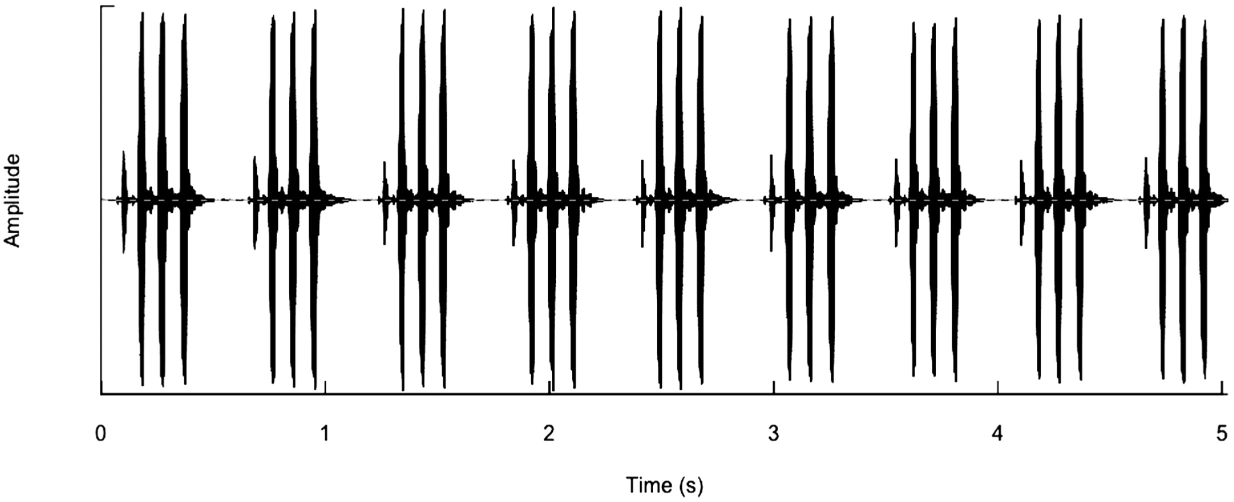

FIGURE 225. Calling song (R15-159) of *G. longicercus* from Torrance Co., NM (S15-52), recorded at 25.3°C.

FIGURE 226. Holotype male (left) of *G. longicercus.* Female (right) also from type locality (S89-26).

Derivation of name. In recognition of their long cerci, which sometimes exceed 19 mm (Ajo [S98-72] and Why [S98-71], Kofa [S11-93], AZ; Shafter, [S16-4], TX) in length and can be longer than body length of a pinned adult male (e.g. Kofa [S88-88]).

Geographic range. (Fig 227). Populations extend into Mexico.

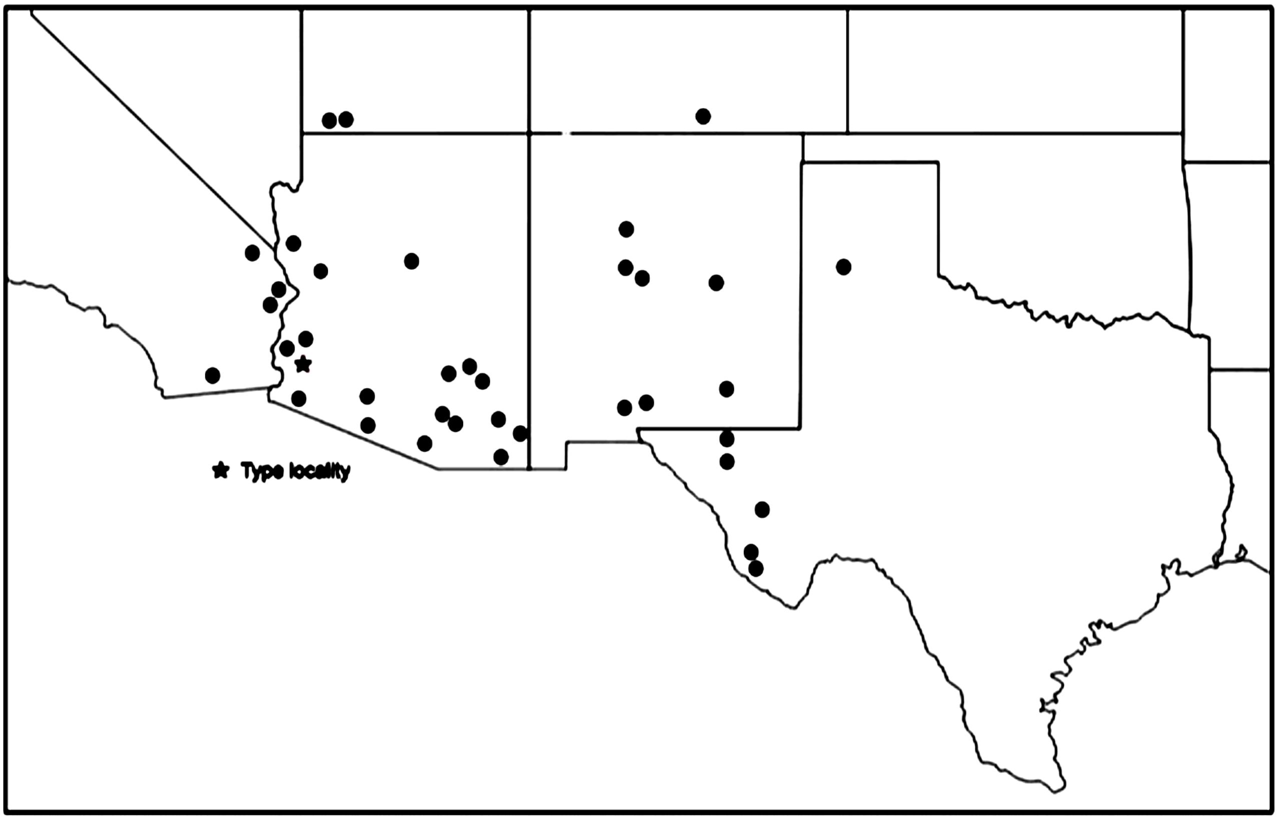

FIGURE 227. Known US distribution of *G. longicercus*.

Habitat. From 183m (Telegraph Pass, AZ, S88-90) to 1980m (Aguirre Springs, NM). Rocky washes, rocky canyons with Joshua tree, *Larrea*, cactus, and *Eriogonum*, oak-juniper grassland with rocks, rocky slopes with pinyon-juniper, rocky road cuts, on ground at base of walls and in cracks on walls and rocky talus slopes. Never found with solid overhead tree cover. Occasionally in towns like Kingman, AZ (S91-68). Also in town in Ajo in cracks at a gas station (S98-72). One male collected from sotol at Aguirre Springs, NM (S15-77), while searching for *G. sotol.*

G. longicercus appears to ecologically replace *G. saxatilis* as one moves east and south into the Sonoran and Chihuahuan Deserts of the Southwest US. Once into western Texas, *G. transpecos,* the ecological equivalent of *G. saxatilis,* can be sympatric with *G. longicercus*

Life cycle and seasonal occurrence. No egg diapause (S88-37). Probably two generations/year, at least at the type locality (Palm Canyon, Kofa National Wildlife Refuge). At the type locality, DAG collected a single adult female 18-iii-2005 (and heard calling males); 12 adult males and 2 adult females 15-iv-2010; a single adult male 5-iv-2013; a single adult male 7-ix-2013 (parasitized by the tachinid *Ormia ochracea*); 6 adult females and 2 late instar females 6-viii-2016 (and heard calling males). Similarly, DBW collected a few singing males there on 4-vi-1989 and saw many more late instars, which started molting to adults in early to mid-July. DBW collected apparent second-generation individuals (7 adult males, many adult females, and many late instars) on 16-ix-2011. Those late instars started molting to adult some 2 weeks later.

We have visited the Ajo/Why, Arizona, area four times after a collecting trip on 20-viii-1998, at which time we collected 15 individuals of *G. longicercus* and 5 other species of *Gryllus.* Our subsequent visits there were on 16-v-1999 (S99-26), 1-viii-2009 (S09-102), 17-ix-2011 (S11-99), and 29-vii-2015 (S15-109) and we only found *G. longicercus* singing during the last 2 visits, and then only one male each time. Apparently, rainfall has a significant effect on when certain species of Sonoran Desert field crickets appear.

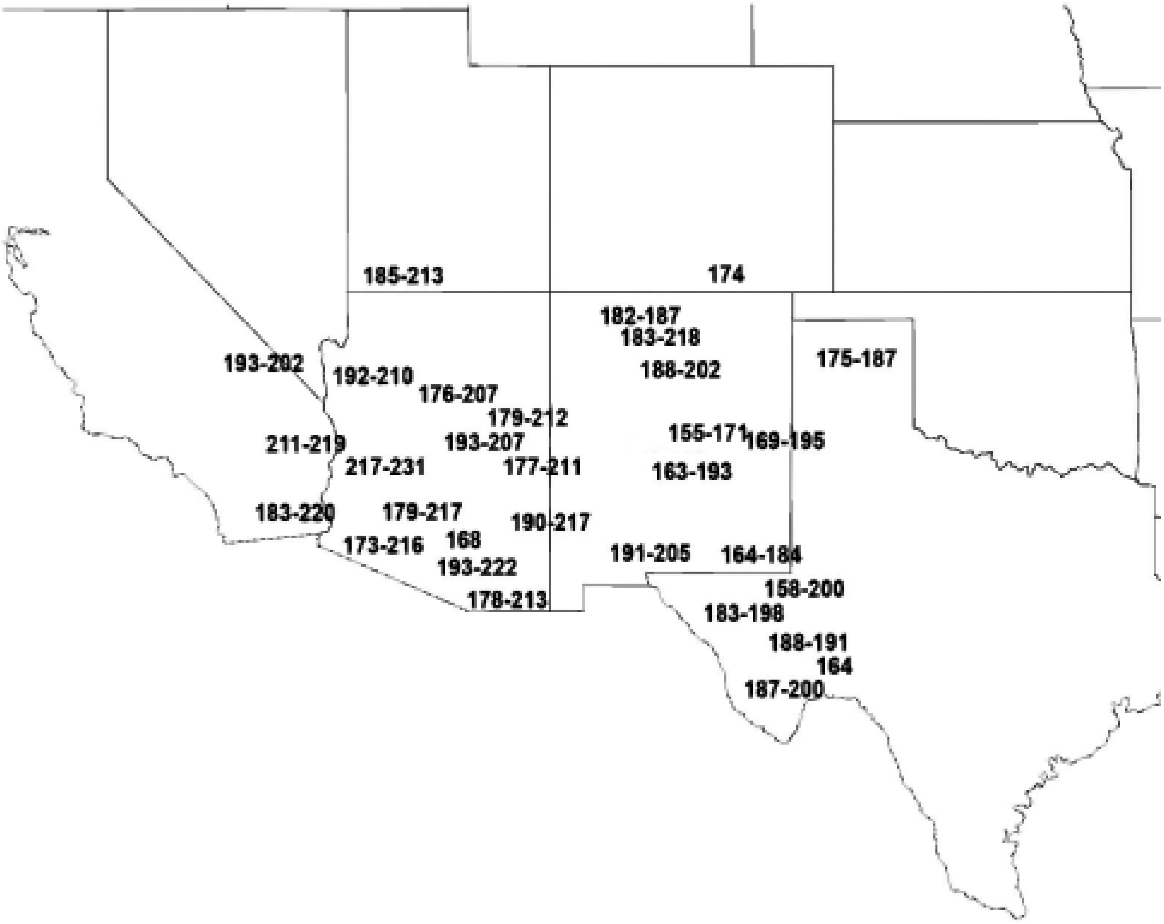

FIGURE 228. Map of *G. longicercus* file tooth counts showing geographic variation. Counts vary from 155 (Mountainair, NM, S15-52) to 231 (Quartzite, AZ, S80-46).

During June, Arizona field trips, we collected many more late instar nymphs than adults at the following localities: Mt. Graham (S12-19), Mt. Lemmon (S12-23), and Fort Bowie (S13-19).

Variation. **Female tegmina length:** The large series of 35 females from the type locality, where *G. longicercus* is usually the only field cricket present [highly flight-capable *G. staccato* also found there once, 15-iv-2010 (DAG 2010-017 female, 2010-018 male)], demonstrates a range from long (most specimens) tegmina almost reaching the tip of the abdomen to very short ones covering about ½ of the abdomen. Both conditions are seen in other populations where several females have been collected. **Hind leg color:** In most specimens, entire hind leg is dark except for reddish area on inside of hind femur. All individuals from Washington Co., Utah, and near Roswell, New Mexico (S09-59), have the entire hind leg reddish colored. **Hind wing length:** Most field collected adults with short hind wings although many adults in towns of Ajo/Why, Arizona, with long hind wings. Additionally, over 70% of type locality late instar nymphs collected on 16-ix-2011 (S11-93) had long hind wings after molting to adult in the subsequent 2-4 weeks while all, simultaneously, field-collected adults from there were short winged. **Length of cerci in situ:** In *G. longicercus,* cerci usually considerably longer than ovipositor except for the high elevation (1830m) population from Tijeras Canyon, NM (S19-35), where the intact cerci in 4 females did not exceed the tip of the ovipositor. In fact, the two longest ovipositors in any females, from any population of this species, were from this site, perhaps indicating that the winters there are extremely cold. Two other females from 300m higher (S19-37) in the same area both had cerci longer than the ovipositor. **Number of file teeth:** Varies from 155-231 over its US range (Fig. 228), which is considerably more than the tooth range of 30-40 seen in most other *Gryllus* species. Significantly, a male from Mountainair, New Mexico (S15-52) with the fewest number of teeth (155) known for this species, sang (R15-341) with a pulse rate of 10.8 at 26°C. Both his 16S and ITS2 DNA mapped with other *G. longicercus.* Three other males from Mountainair had 162, 164, and 171 file teeth. **Song:** Male (Fig. 229A, R93-153) from Sevilleta Refuge, NM (S93-66) with 7-9 p/c and PR 8.6. R09-112 (Fig. 229B) from Van Horn, TX (S09-64) with 9-30 p/c (most similar to a trill) and PR 11.8. **Overall population characteristics:** The population from 11.7 km E Roswell (S09-59) was unusual in several ways: (1) adults with brown-reddish heads compared with usual black heads. (2) Singing males were very wary and readily stopped singing when approached. They resumed singing only after much delay, even though air temperatures ~22°C. (3) Males made no chirping noises as we turned over rocks trying to collect. In most cases, in most other populations, males continue to sing after they have climbed down into their rock pile while we are moving rocks aside to locate them. (4) These males jumped well and readily while we were trying to collect them. Multilocus analysis maps a male from there (S09-59) with individuals from the type locality of Palm Canyon, AZ (2016-039), and Shafter, TX (S16-4). **Tegminal markings:** rare males and females have a light tegminal bar.

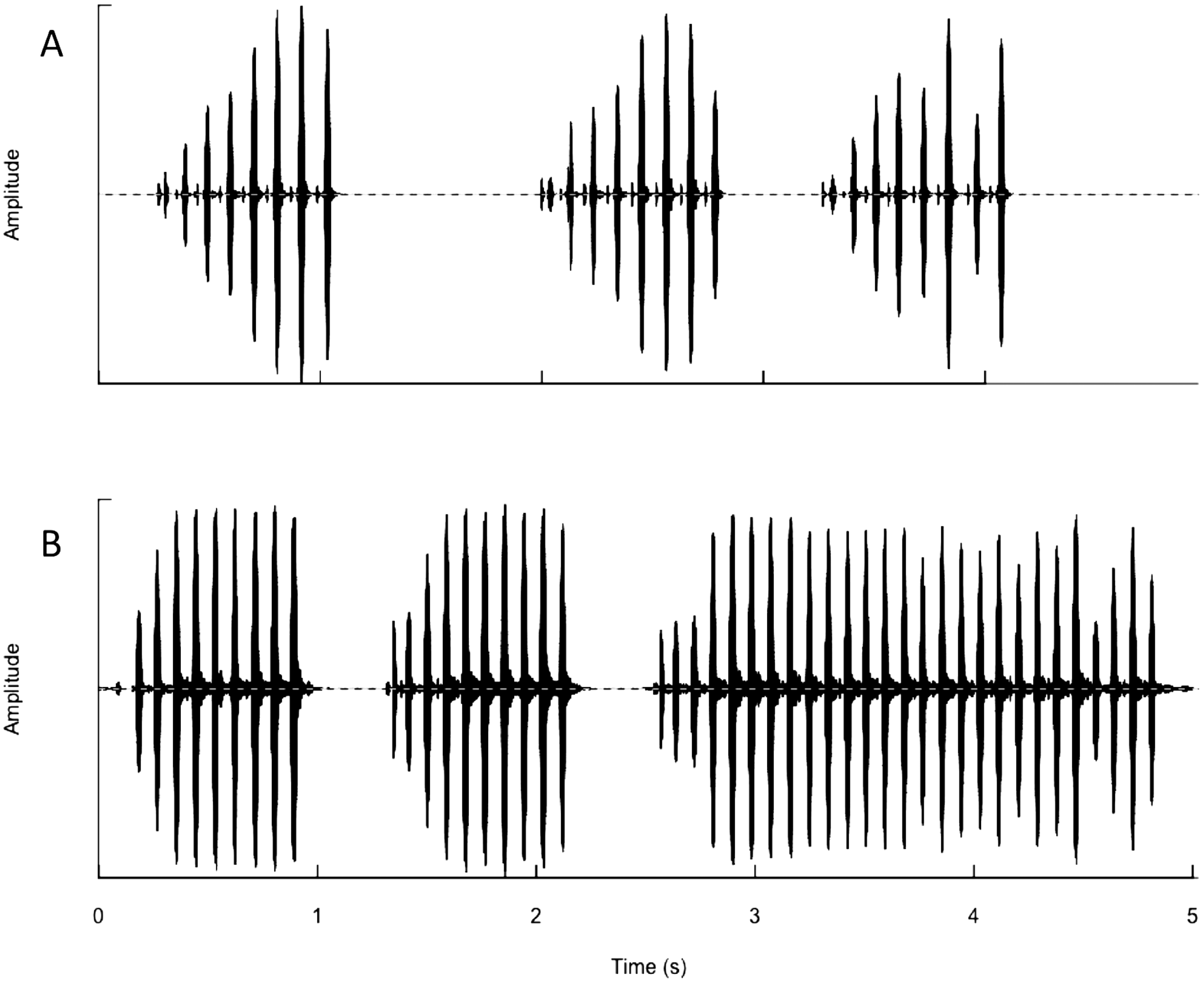

FIGURE 229. Atypical "trill" calling song of *G. longicercus*: (A) (R93-153) from Socorro Co., NM (S93-66), recorded at 22°C; (B) (R09-112) from Culberson Co., TX (S09-64), recorded at 28°C.

DNA. Multilocus 2016-039 (Kofa, type locality of Palm Canyon); G1433, 7.3 m E Roswell, NM (S09-59); and G3386, Shafter, TX (S16-4) are sister species (Gray *et al.* 2019) to New Mexico lava restricted *G. vulcanus* 2016-025 from El Malpais; and G1030, from Valley of Fires State Park (S07-46).

Discussion. Behaviorally, most male *G. longicercus* continue chirping while turning over rocks attempting to capture them, a characteristic fairly unique to this taxon but also sporadically seen in other rock chirping species. Oatmeal trails do well to attract adult females and even some adult males. Adult males sometimes climb and sing: 1 male singing 1.5m up in shrub at Palo Duro Canyon State Park, TX (S88-37).

Of the 7 adult males (probably only two or three were actually singing) collected at the type locality of Palm

Canyon (S11-93) on 16-ix-2011, all were parasitized by the tachinid *Ormia ochracea*. Five males had 1 fly larva, one male had 2 larvae, and one male had 4 larvae. Of the many adult females and late instars of both sexes collected concurrently, none were parasitized. One of two males from Kitt Peak (S11-98) parasitized with one *Ormia ochracea* larva.

Late instars of *G. longicercus* have contrasting, banded abdomens, a common juvenile character of many species in the two rock-chirping groups: Longicercus Group and Saxatilis Group, and also seen in *G. lightfooti*.

Gryllus vulcanus **Weissman & Gray, n. sp.**

New Mexico Lava Field Cricket
Figs 222–224, 230–235, Table 1

'Gryllus #41' in DBW notebooks.

Distribution. Known only from two lava flows in central New Mexico.

Recognition characters and song. A small to medium, always short hind wing, almost totally black (except for inside of hind femurs which can be reddish colored) *Gryllus* with medium length cerci longer than ovipositor tip in situ (Fig. 234), and a file tooth count greater than 160. *Song* (Fig. 230, R07-68) usually with 4–5 p/c (range 3–7), PR < 14 and pulses almost countable at 25°C. Distinguished from only other US obligate lava field cricket, *G. leei,* from Utah, in minimal overlap in number of teeth (Fig. 231, Table 1, p. 18), no overlap in pulse rate, and different DNA (Gray *et al.* 2019).

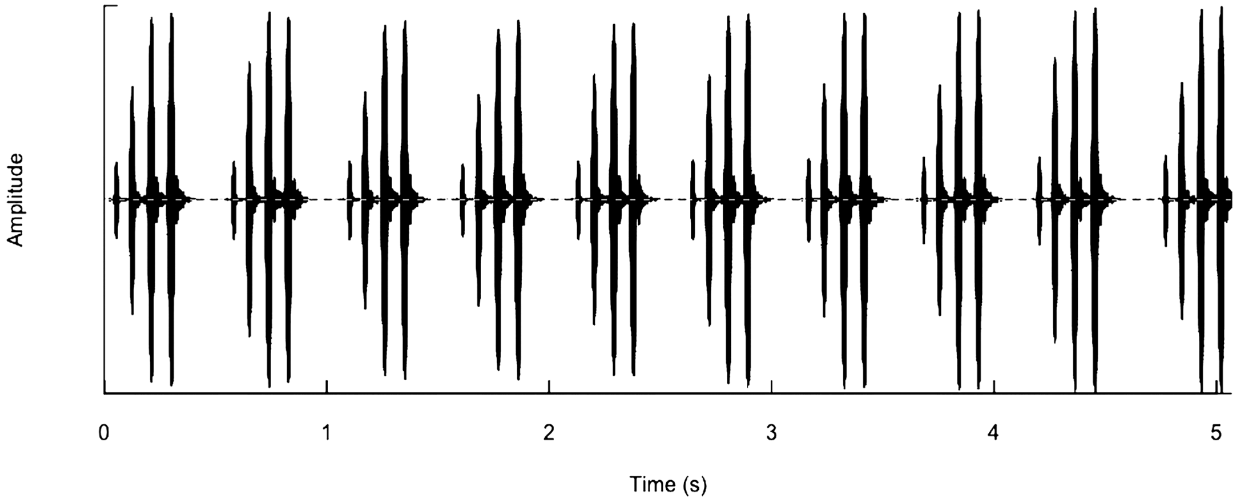

FIGURE 230. Calling song (R07-68) of *G. vulcanus* from type locality, recorded at 25°C.

Morphologically and genetically most similar to sister species *G. longicercus* but *G. vulcanus* matures earlier (despite being at higher elevation), is smaller with fewer file teeth (Fig. 232), shorter cerci, habitat (only on lava as opposed to rocky areas), and shorter ovipositor (Fig. 233).

From microsympatric, off-lava *G. veletis* at the type locality, the two taxa are easily separated (Table 1, p. 18) by cerci length and pulse rate.

Holotype. Male (Fig. 234). USA, New Mexico, Cibola Co., El Malpais National Monument adjacent to Hwy 117 at mile post sign 31 [or 31 m S I40], 14-vi-2007, 2161m. 34° 47' 17.16" -107° 56' 13.92" DB Weissman, DC Lightfoot, S07-52, R07-81 & 84, G1146. 16S ribosomal RNA GenBank accession # MK446541; ITS2 GenBank accession # MK441986. BL 17.72, HF 10.56, RC 11.53. Right tegmen removed: 171 teeth, file length 3.4, TL 10.3, TW 4.4. Type deposited in CAS, Entomology Type #19275.

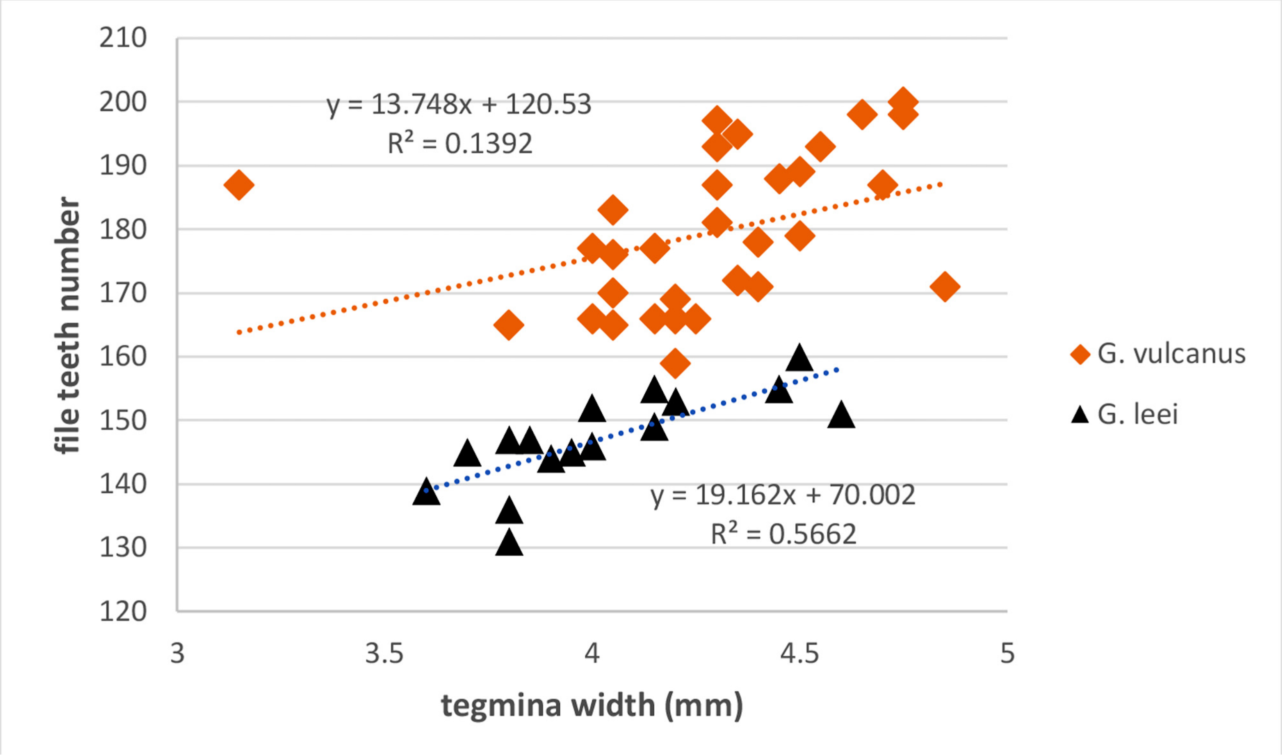

FIGURE 231. Regression tegmina width vs. file teeth number in *G. vulcanus* vs. *G. leei*.

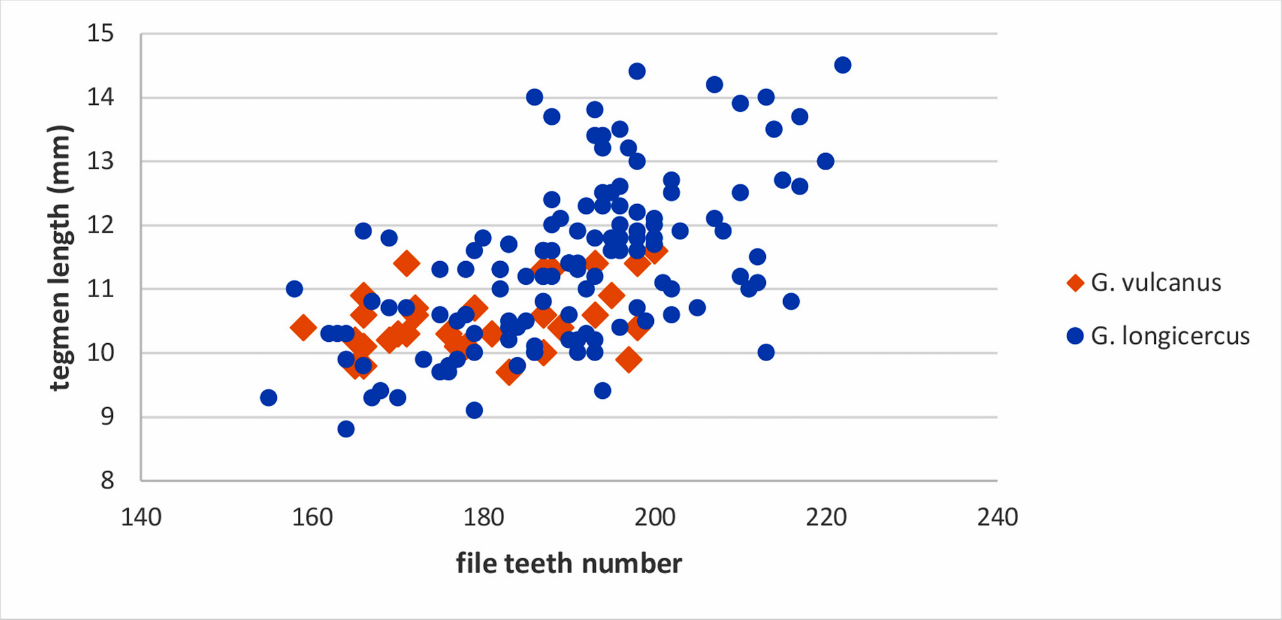

FIGURE 232. Regression file teeth number vs. tegmina length in *G. vulcanus* vs. *G. longicercus.*

Paratypes. (Total: 36♂ 22♀). **New Mexico**, *Cibola Co*., El Malpais National Monument, type locality, 6870’, 18-viii-1993 (S93-71) 6♂ 4♀; 1-vii-1994 (S94-41) 2♂; 1-vii-1994 (S94-42) 2♂; 14-vi-1996 (S96-68) 12♂ 2♀; 14-vi-2007 (S07-52) 2♂ 1♀. *Lincoln Co.,* Valley of Fires State Park along Hwy 380, 5 m W Carrizozo at mile post 60, 5090’, 33° 42.115’, -105° 56.249’, 2-vii-1994 (S94-48) 9♂ 8♀; 13-vi-2007 (S07-46) 3♂ 7♀.

Derivation of name. Named with reference to ancient Roman myth: Vulcan (Latin: Vulcanus) is the god of lava and smoke, including the fires of volcanoes, because lava flows have created this cricket’s habitat.

Geographic range. (Fig. 235). The two known localities are separated by about 210 km distance and are not connected by any lava flows visible on Google Earth.

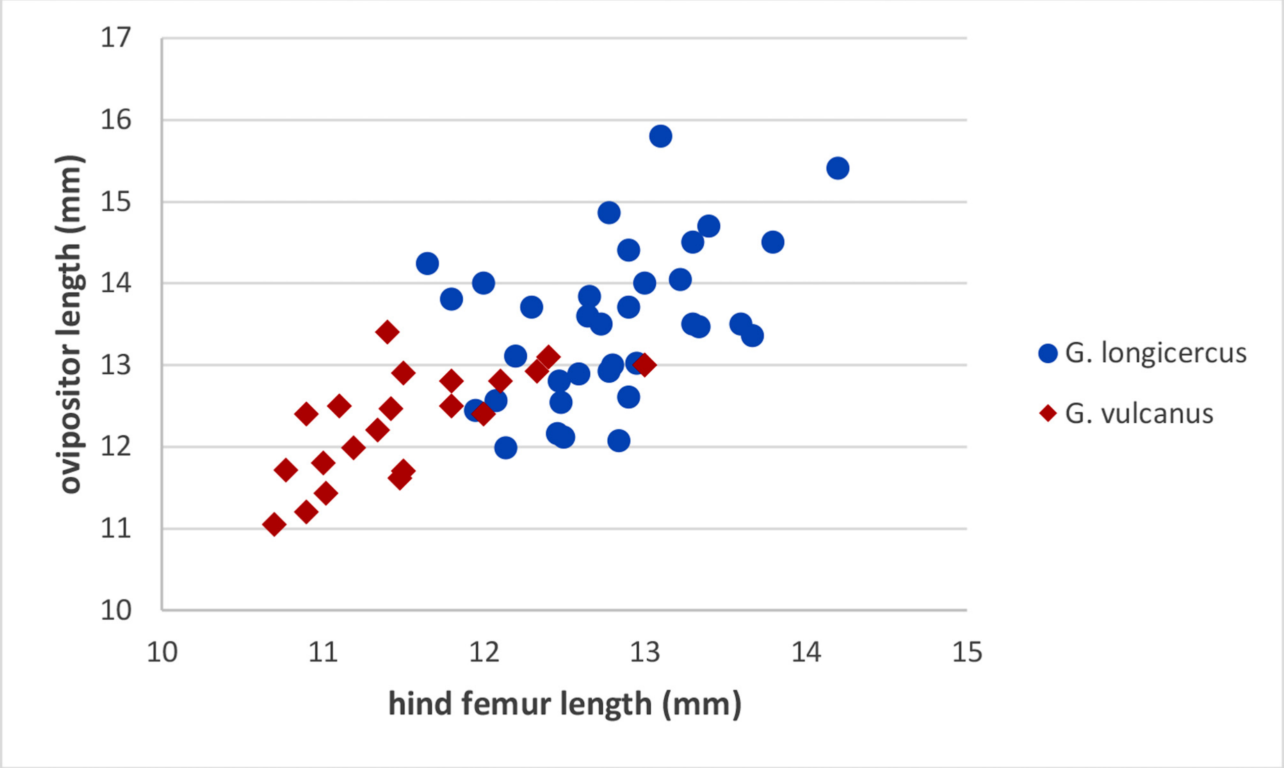

FIGURE 233. Regression hind femur length vs. ovipositor length in *G. vulcanus* vs. *G. longicercus.*

FIGURE 234. Holotype male (left) of *G. vulcanus.* Female (right) also from type locality (S07-52).

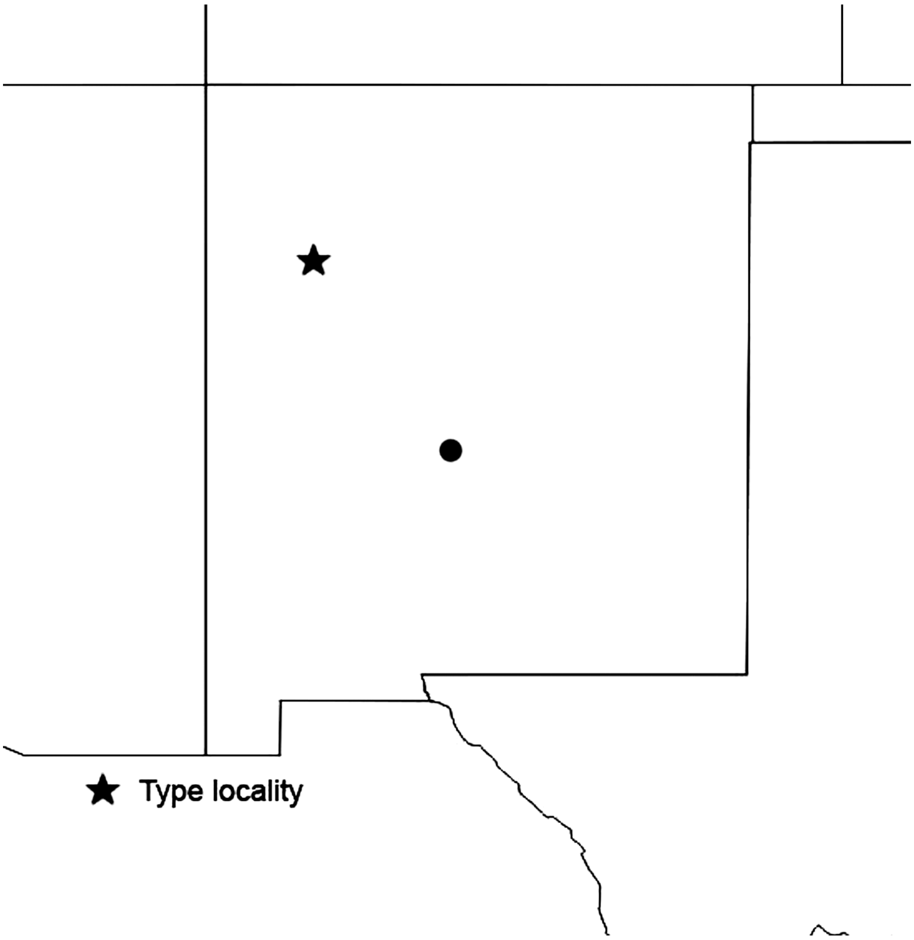

FIGURE 235. Known distribution of *G. vulcanus.*

Habitat. From 1550-2094m elevation. Both lava flow sites are well vegetated with various annuals, shrubs and small trees. The type locality site has bordering grazed grasslands on sandy substrate with pinyon-juniper woodlands nearby.

Life cycle and seasonal occurrence. One generation/year. Adults known from mid-June to mid-August with most August individuals having damaged cerci. It appears that the higher elevation type locality individuals mature before those from Valley of Fires given the presence of many nymphs seen at S07-46 (13-vi-2007) and none ever seen at the type locality on similar dates.

Variation. **Body size:** lower elevation (1550m elevation) Valley of Fires adults somewhat larger than type locality (2094m elevation) adults.

DNA. Multilocus 2016-025 (type locality) and G1030 (Valley of Fires State Park, S07-46) sister species (Gray *et al.* 2019) to *G. longicercus* from Kofa Mts., Arizona (2016-039, type locality), G1433 (New Mexico, S09-59) and G3386 (Texas, S16-4). ITS2 does not separate *G. longicercus* and *G. vulcanus* (Fig. 224). 16S shows minimal variation either within or between these taxa (509 bp of 16S; N = 10 *G. vulcanus*; N = 69 *G. longicercus*; mean ± SD Tamura-Nei distance: within *G. vulcanus* = 0.0019 ± 0.0018, within *G. longicercus* = 0.0016 ± 0.0018, between *G. vulcanus* and *G. longicercus* = 0.0018 ± 0.0018) and does not separate them.

Discussion. We contemplated the possibility that *G. vulcanus* is simply *G. longicercus* on lava, given the fact that multilocus DNA analysis shows them as sister species. They do separate with the regression of hind femur length vs. ovipositor length (Fig. 233), but this could be explained by the simple fact that *G. longicercus* is a larger cricket. A similar result, and possible explanation, is seen (Fig. 232) when regressing number of file teeth vs. tegmen length. Despite these results, we have decided to treat them as separate species because of two factors: (1) *G. vulcanus*, despite living at higher, cooler elevations, appears to reach adulthood before most populations of *G. longicercus.* Specifically, the entire type locality population of *G. vulcanus* was adult by mid-June and by mid-August, many individuals had damaged cerci, apparently indicating old adult age. In contrast, during several early to mid-June, Arizona field trips, we collected more late instar *G. longicercus* nymphs, than adults, at the following localities: Mt. Graham (S12-19), Mt. Lemmon (S12-23), and Fort Bowie (S13-19), despite these localities being lower and warmer than the New Mexico *G. vulcanus* sites. (2) Lava flows are not a typical *Gryllus* habitat, as confirmed by our extensive checking of such areas. *G. leei,* from west-central Utah, appears to be another lava exception and is isolated to the Black Rock Desert of western Utah.

Although we treat *G. vulcanus* here as separate from *G. longicercus*, further work is clearly warranted. Especially given the similarity in song, pre-zygotic reproductive isolation, to the extent that it exists, may be driven solely by ecology and/or phenology. Given that the two known lava flow localities in New Mexico are not connected and are of very different ages, we suspect that the two flightless *G. vulcanus* populations represent separate derivations from *G. longicercus*; this also could be tested in future work. DNA markers more sensitive than ITS2 and 16S would be required (e.g. SNPs).

The type locality is part of the 3,000-year-old McCarty lava flow: http://geoinfo.nmt.edu/tour/federal/monuments/el_malpais/zuni-bandera/pahoehoe.html (Laughlin *et al*. 1993). However, volcanism in adjacent areas dates as far back as 115,000 years (Laughlin *et al.* 1994). There are many deep lava cracks and fissures from which *G. vulcanus* sing, making their song soft and the crickets difficult to collect, despite their boldness. With patience, singing males can frequently be coaxed from deep cracks with a slim twig, as they do not dive down. Nevertheless, collecting time is better spent walking the edges of the lava flow at night after laying of an oatmeal trail there during the late afternoon. One male singing from a crack in the ground several meters from lava's edge at El Malpais (S96-68).

Many fewer singing males at Valley of Fires in 2007 (S07-46) than in 1994. At Valley of Fires State Park, there are fewer and more shallow cracks in the surface lava and more dirt and grassy areas within the lava flow area when compared to the type locality. This lava flow has been dated to ca. 5,200 ±700 years of age (Dunbar 1999). At Valley of Fires all crickets were in the open with many males singing totally exposed away from cracks but still on lava. They were also easy to approach while singing and active jumpers. Many singing males had females near them. In 2007 (13-vi-2007, S07-46), several medium instar nymphs, and adult females, were seen walking around.

The Saxatilis Group

G. saxatilis Weissman & Gray, n. sp.; *G. leei* Weissman & Gray, n. sp.; *G. makhosica* Weissman & Gray, n. sp.; *G. navajo* Weissman & Gray, n. sp.

Sister species of western chirping crickets with similar songs (Figs 236, 237). Most easily separated from each other by habitat and geography: *G. saxatilis* widespread in dry rocky areas west of the Rockies; *G. leei* restricted to lava in Utah; *G. makhosica* restricted to badlands clay habitats in South Dakota; *G. navajo* restricted to the red sandstone region of the Colorado Plateau in Utah and Arizona. At least three additional cryptic species may exist within the Saxatilis Group. Poorly separated by ITS2 DNA (Fig. 238); both COI and 16S likewise proved unhelpful.

Gryllus saxatilis **Weissman & Gray, n. sp.**

Western Rock-Loving Field Cricket
Figs 205, 236–246, 248, Table 1

Gryllus pennsylvanicus of Weissman *et al*., 1980.
'Gryllus #2' of Rentz & Weissman, 1981.
'G. #2, #11, #22, #38', 'G. mojave', 'G. tulare', 'G. mormoni' of DBW notebooks.

Distribution. Widespread in the western US, west of the Rocky Mountains.

Recognition characters and song. A small to large, short or long hind winged, medium-long cerci rarely longer than ovipositor in situ, slow chirping cricket usually associated with rocky habitats. *Song* (Fig. 239, R15-372) with 3–5 p/c (range 2–7), 50–280 c/m, PR 14-25. Separated from the following western slow chirping *Gryllus* as follows: From *G. longicercus*, which has a distinctive, non-overlapping lower PR, and has more file teeth, longer cerci, and different DNA. From *G. lightfooti* which has a tegminal bar in females, shorter male tegmina, not usually associated with rocks, faster chirp rate, fewer file teeth, and different DNA. From *G. montis* which occurs at higher elevations

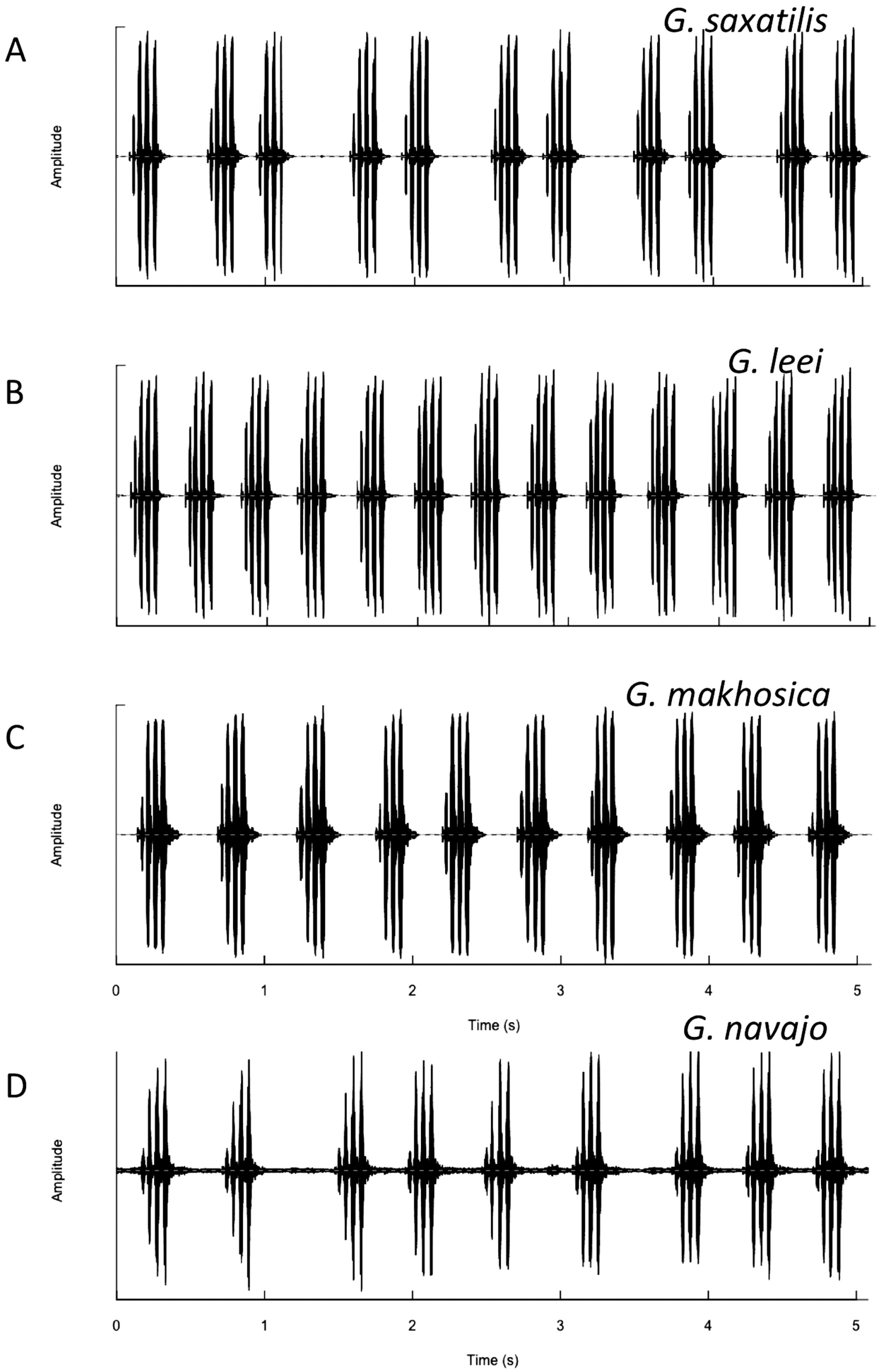

FIGURE 236. Five second waveforms of calling songs of (A) *G. saxatilis*, (B) *G. leei*, (C) *G. makhosica*, and (D) *G. navajo*. *G. saxatilis*: (R15-372) from type locality (S15-114), at 25.5°C. *G. leei*: (R17-7) from type locality (S17-6), at 24.5°C. *G. makhosica*: (R09-95) from type locality (S09-89), at 24.5°C. *G. navajo*: (R07-61) from Coconino Co., AZ (S07-56), at 25°C.

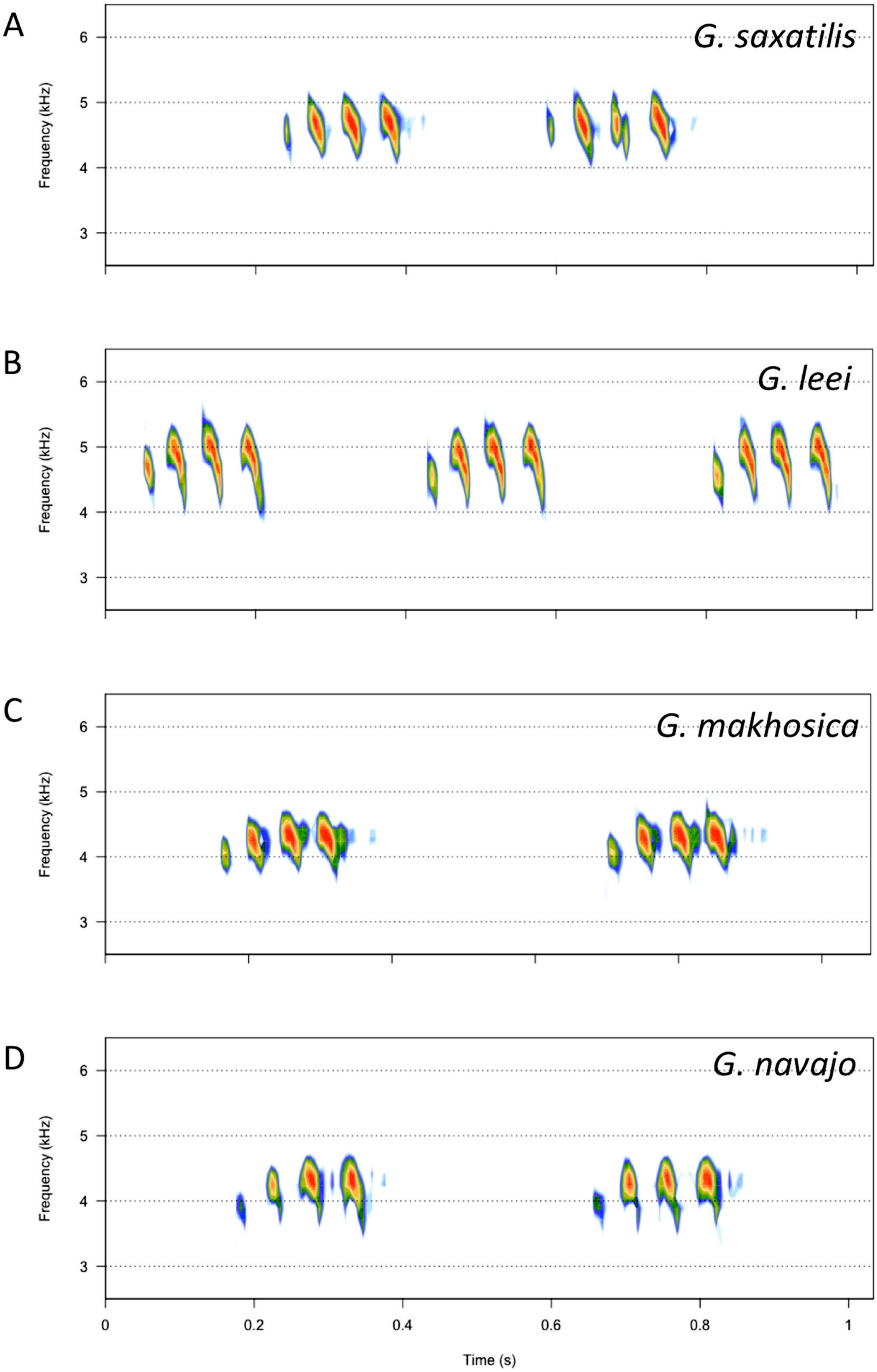

FIGURE 237. One second spectrograms of (A) *G. saxatilis*, (B) *G. leei*, (C) *G. makhosica*, and (D) *G. navajo*, same males as in Fig. 236.

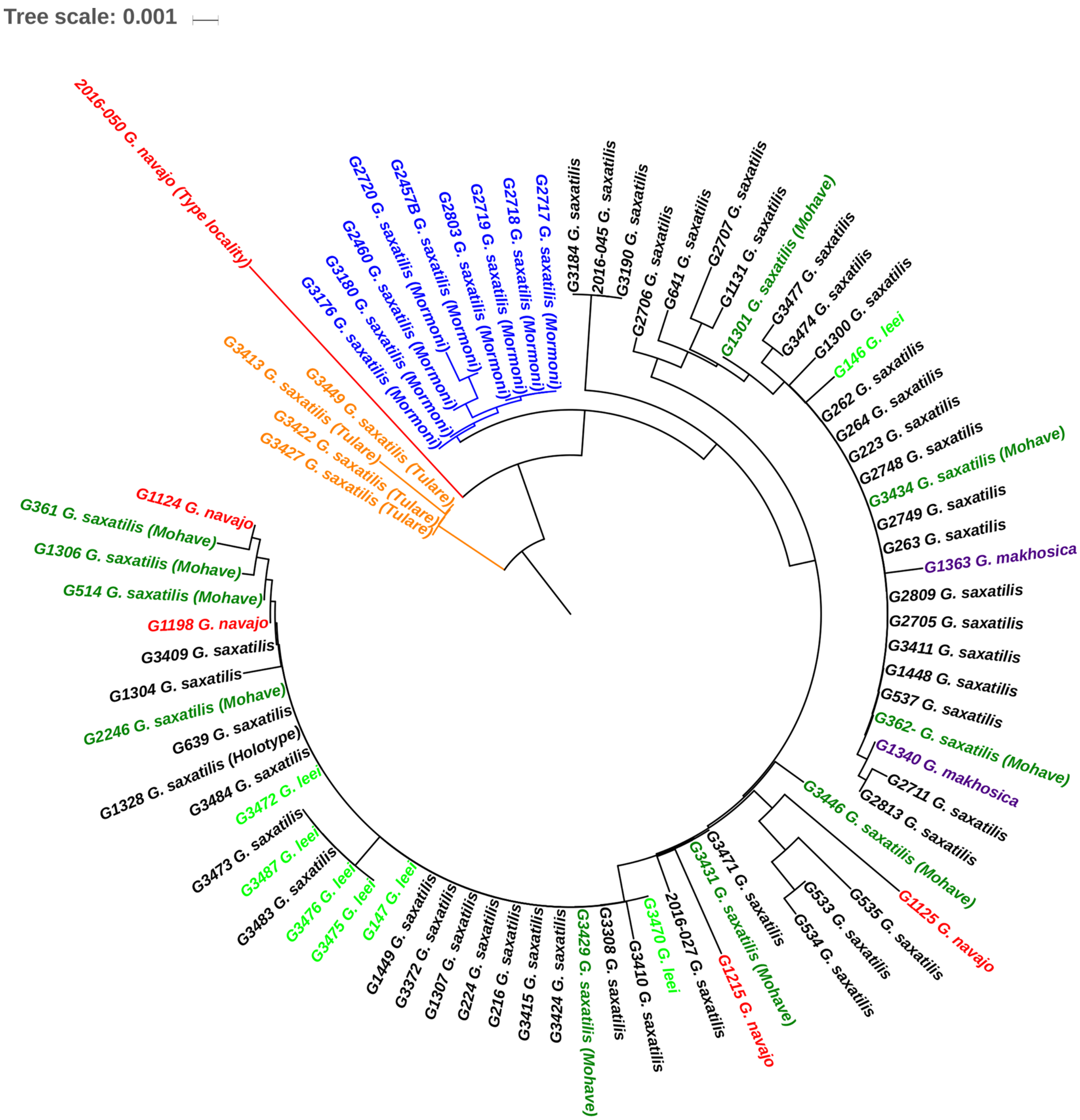

FIGURE 238. ITS2 gene tree, color coded to highlight species and potential cryptic species warranting further study. Collection stop numbers for ***G. saxatilis*** legs: S04-51 (G216); S04-62 (G223, G224); S04-74 (G262, G263, G264); S04-121 (G361, G362); S05-109 (G514); S06-5 (G535); S06-21 (G533, G534, G537); S06-105 (G639, G641); S07-64 (G1131); S09-22 (G1306); S09-28 (G1300); S09-29 (G1304, G1307); S09-32 (G1301); S09-43 (G1328); S09-131 (G1449); S09-141 (G1448); S12-34 (G2246); S13-10 (G2457B, G2460, G2717, G2718); S13-10A (G2719, G2720); S13-79 (G2705, G2706, G2707, G2711); S14-30 (G2748, G2749); S14-61 (G2809, G2813); S14-77 (G2803); S15-87 (G3176, G3180); S15-89 (G3184, G3190); S15-90 (2016-045); S15-93 (G3308); S15-96 (G3372); S16-17 (G3409, G3410, G3411, G3415); S16-18 (G3429, G3431); S16-21 (G3413, G3422, G3427, G3449); S16-23 (G3434, G3446); S16-33 (G3424); S17-7 (G3471, G3473, G3474, G3477, G3483, G3484); La Verkin overlook, Washington Co., UT (2016-027). Collection stop numbers for ***G. leei*** legs: S01-28 (G146, G147); S17-6 (G3470, G3472, G3475, G3476, G3487). Collection stop numbers for ***G. makhosica*** legs: S09-89 (G1340, G1363). Collection stop numbers for ***G. navajo*** legs: S07-56 (G1124, G1125, G1198, G1215); Goblin Valley, Emery Co., UT (2016-050).

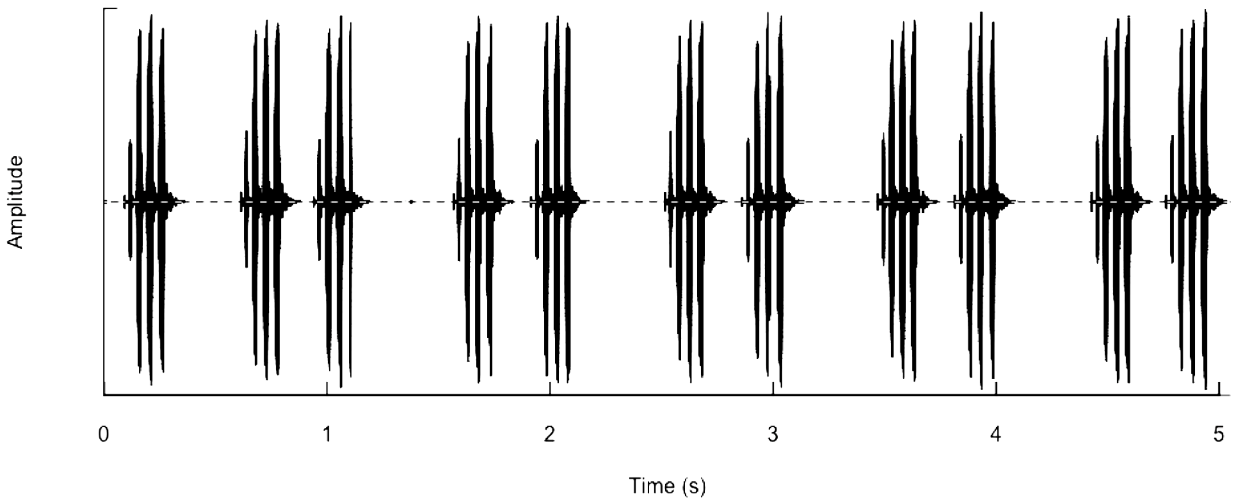

FIGURE 239. Calling song (R15-372) of *G. saxatilis* from type locality (S15-114), recorded at 25.5°C.

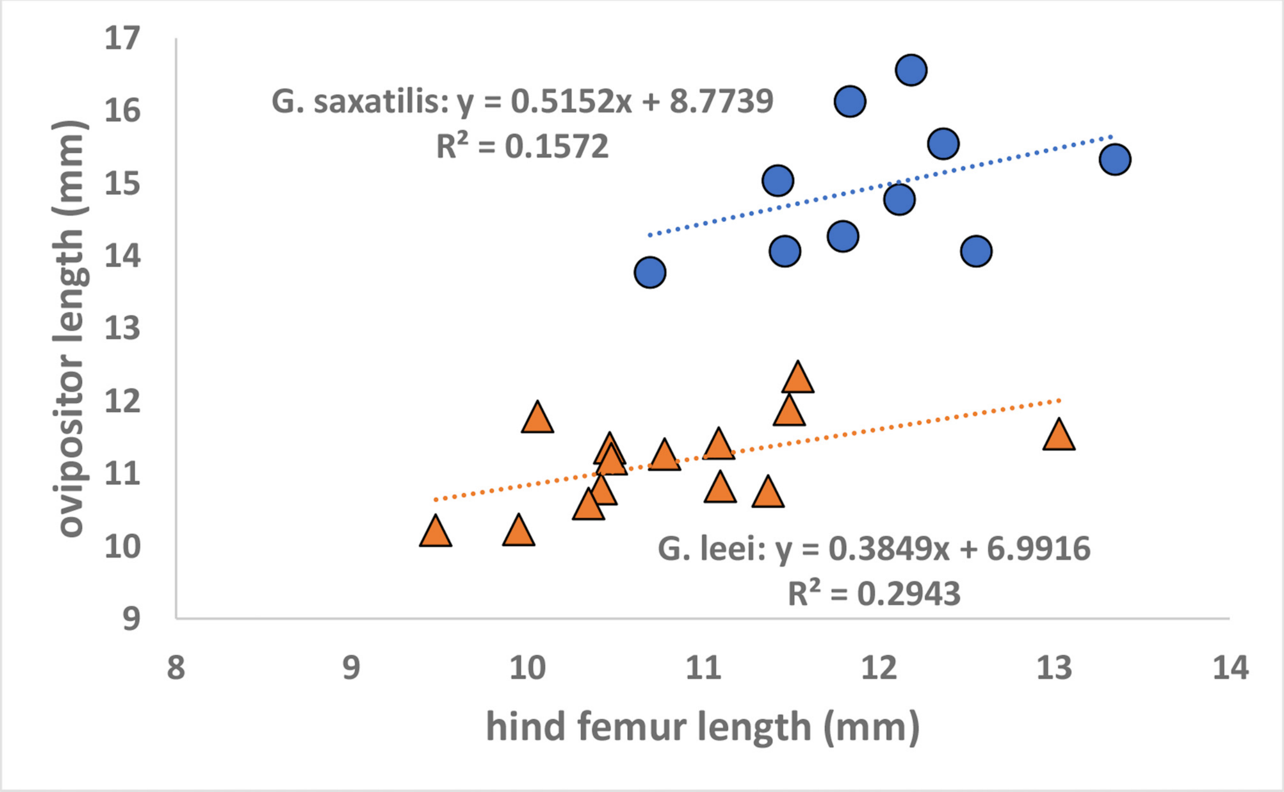

FIGURE 240. Regression of hind femur length vs. ovipositor length in *G. saxatilis* vs. *G. leei.*

under forest canopy and has different DNA. From *G. navajo* of red rock sandstone badlands in Utah and Arizona, the latter usually reddish in color with very long antennae in some populations reaching past tip of abdomen (e.g. Coconino Co., AZ, S07-56), cerci always longer than hind femur and, in certain populations, usually longer than ovipositor tip in situ. From Utah lava restricted *G. leei,* which are smaller crickets with shorter tegmina and longer cerci that always extend beyond the tip of the ovipositor, a rare situation in *G. saxatilis.* Ovipositor ~4–5 mm longer in *G. saxatilis* than in *G. leei* even when controlling for body size by regressing against hind femur length (Fig. 240; $F_{1,21}$ = 84.8. P<0.001; N = 14 *G. leei*; N = 10 *G. saxatilis*).

From South Dakota Badlands National Park *G. makhosica* which has long antennae extending well past tip of ovipositor and cerci longer than ovipositor in situ. The nearest population of *G. saxatilis* is ~580 km to the west near

Cody, WY, where the latter lives in rocky areas and seldom climbs more than a meter vs. the deep cracks in clay badlands, up to 10 m above the canyon floor, that *G. makhosica* frequently inhabits.

Holotype. Male (Fig. 241). California, Santa Clara Co., Mt. Hamilton, observatory area, 4040’, 7-vi-2009, 37° 20.384’ -121° 38.632’, D.B. Weissman. S09-43, R09-46, G1328. 16S GenBank accession # MK446492; ITS2 GenBank accession # MK441923. BL 23.74, HF 13.45, LC 14.57. Right tegmen removed: 174 teeth, FL 4.5, TL 15.1, TW 5.7. Type deposited in CAS, Entomology type #19272.

FIGURE 241. Holotype male (left) *G. saxatilis.* Female (right) also from type locality (S97-62)

Paratypes. (Total 776♂ 300♀) **CANADA. British Columbia,** Haynes Ecological Reserve Hwy 97 3 m N Osoyoos, 1200’, 26-viii-2000 (S00-27) 5♂ 7♀; 19-vi-2004 (S04-62) 4♂ 8♀. **USA. Arizona.** *Coconino Co.,* Lees Ferry, 19-v-1987 (S87-35) 4♂. *Mohave Co.,* Kingman, 3700’, 2-viii-1992 (S92-113) 9♂ 25♀. Hualapai Mt. Road 1.8 m NW Hualapai Mt. Rec. Area, 5850’, 16-vi-2007 (S07-64) 1♂. Quartzsite, 1000’, 26-vi-1980 (S80-46) 2♂ 1♀. **California.** *Calaveras Co.,* Hwy 26 3.3 m SW West Point, 14-v-2005, 740m (S05-51) 1♂. *Colusa Co.,* Hwy 20 at mile post 10.9, 547’ 5-viii-2014 (S14-61) 2♂. *Contra Costa Co.,* Mt Diablo State Park, 3800’, 13-vii-1982 (S82-37) 4♂; 13-viii-1994 (S94-96) 2♂; 17-viii-1996 (S96-78) 2♂. *Fresno Co.,* Jacalitos Canyon, 840-1020’, 29-viii-1981 (S81-76) 1♂; 9-iii-1982 (S82-2) 1♂; 6-iii-1992 (S92-33) 1♂; 3-vi-1997 (S97-54) 6♂ 1♀; 29-viii-1998 (S98-83, 84, 85) 8♂ 1♀; 18-viii-2001 (S01-97, 98, 99, 100) 19♂ 2♀; 4-v-2003 (S03-31 & 32) 2♂. *Inyo Co.,* Alabama Hills W Lone Pine, 4240’, 8-x-1995 (S95-110) 1♂. Big Pine, 4000’, 8-x-1995 (S95-112) 3♂ 1♀; 27-vi-2017 (S16-18) 4♂ 4♀. Bishop, 4150’, 16-iii-1996 (S96-13) 1♂; 28-viii-2005 (S05-99) 1♂ 7♀. Death Valley National Monument, Furnace Creek, -186’, 5-vi-1983 (S83-60) 2♂; 25-vi-1992 (S92-61) 2♂. Stovepipe Wells, 5’, 5-vi-1983 (S83-59) 1♂; 25-vi-1992 (S92-62) 2♀; 1.9 m W Wildrose Ranger Station, 3700’, 23-vi-1980 (S80-27) 2♂; Hwy 178 3.5-7 m E west boundary of Monument, 4050-5000’ (S80-29) 2♂. Lone Pine, 3400’, 7-x-1995 (S95-107) 5♂ 2♀; 22-viii-1998 (S98-78) 1♂; 29-viii-2005 (S05-105) 6♀. Panamint Springs, 1920’, 8-x-1995 (S95-108) 1♂. Shoshone, 25-vi-1992 (S92-60) 4♂ 3♀. White Mts., Westgard Pass, Hwy 168, 1.4 to 6.7 m W Summit, 5540-7271’, 17-ix-1998

(S98-98 & 98-99) 4♂ 1♀; 27-vi-2017 (S16-17) 4♂. Whitney Portal Rd 8 m W Lone Pine, 6300’, 29-viii-2005 (S05-104) 2♂; just below main campgrounds, 8200’, 5-viii-1978 (S78-119) 1♂. Hwy 395 8-9 m N Bishop, 4400-4700’, 4-vi-1983 (S83-55) 10♂; 26-vi-1992 (S92-64) 7♂ 1♀. Hwy 395 11.2-11.5 m N Bishop, 4600’, 20-viii-2009 (S09-142) 9♂ 2♀. *Kern Co.,* Jawbone Canyon off Hwy 14, 3000’, 16-iii-1980 (S80-1) 1♂. Hwy 14 30 m N Mojave, 3100’, 18-viii-1982 (S82-68) 1♂. Mojave, 2756’, 28-viii-1983 (S83-117) 3♂; 17-iii-1996 (S96-18) 1♂; 28-v-2009 (S09-32) 1♂. Tehachapi, 4147’, 21-vii-2015 (S15-93) 2♂. Oakcreek Rd. 2.2 m E Tehachapi Willow Springs Rd., 28-v-2009 (S09-29) 7♂ 4♀. Hwy 58 26 m E Mojave, 2400’, 27-viii-1982 (S82-108) 1♂. Short Canyon ~10 m NW Inyokern, 3800’, 9-vi-1983 (S83-69) 5♂. Hwy 178 3.2 m NW Hwy 14, 3928’, 21-vii-2015 (S15-94) 2♂. Hwy 178 19.4 m W Hwy 14, 3064’, 21-vii-2015 (S15-95) 1♂. Hwy 178 8 m E Lake Isabella, 2720’, 21-vii-2015 (S15-96) 3♂ 6♀. *Kings Co.,* Tar Canyon, 1040’, 18-iv-2003 (S03-19) 3♂ 2♀. *Lake Co.,* Hwy 20 near mile post 40.72, 1402’, 5-viii-2014 (S14-62) 4♂. *Lassen Co.,* Hwy 36 1 m W Susanville, 4429’, 29-viii-2003 (S03-92) 3♂; 7-viii-2014 (S14-74) 3♂. *Los Angeles Co.,* San Gabriel Mts. Hwy N6 1.35 m NW Devil’s Punchbowl, 4400’, 8-vi-1983 (S83-67) 4♂; Henninger Flats, 2580’, 25-ii-2001 (S01-9) 1♂ 1♀. Santa Catalina Island, Avalon, Hermit Gulch Campground, 500-900’, 10-vii-2018 (S18-25) 3♂ 5♀; Middle Ranch, 7-viii-1972, 7♂; Mills Landing, 15-vi-1971, 4♂. Santa Monica Mts., Hwy 27 8 m N Hwy 1, 1000’, 24-vi-1992 (S92-59) 2♂. Santa Clara River, dry river bed near Acton, 2710’, 29-VI-2003 (S03-74) 2♂ 2♀. 21-viii-2006 (S06-84) 1♂ 3♀; 28-v-2009 (S09-26) 1♀. *Madera Co.,* Coarsegold, 2213’, 20-vii-2015 (S15-89) 9♂. Hwy 41 3.2 m N Oakhurst, 3500’, 27-viii-1982 (S82-111) 1♂. Hwy 41, mile post 16, 1169’, 20-vii-2015 (S15-90) 1♂ 1♀. *Mendocino Co.,* Hwy 162 4 m E Longvale, 1000’, 2-viii-1980 (S80-59) 3♂. *Modoc Co.,* Hwy 299 2 m W Cedarville, 5210’, 30-viii-2003 (S03-97) 1♂. Hwy 299 3.9 m E Hwy 395, 5000’, 30-viii-2003 (S03-95) 1♂. Hwy 299 12.8 m E Hwy 395, 5810’, 30-viii-2003 (S03-96) 1♂. *Monterey Co.,* Hwy 198 27 m NW Hwy 33, 2180’, 3-vi-1997 (S97-55) 1♂. *Riverside Co.,* Blythe, 400’, 26-vi-1980 (S80-47) 3♂. Joshua Tree NM, Cottonwood Springs, 2975’, 14-vi-1980 (S80-6) 3♂. Whitewater Canyon, 24-iv-1982 (S82-14) 1♂; 6-iv-1991 (S91-13) 6♂ 1♀. Hwy 74 3 m SW Palm Desert, 1740’, 26-v-2009 (S09-20) 1♂. *San Benito Co.,* Pinnacles National Monument, Chalone Campground, 12-viii-1982 (S82-45) 1♂. *San Bernardino Co.,* Afton Canyon, 1-v-2005, 1400’ (S05-50) 1♂. Baker, 1000’, 4-viii-1991 (S91-72) 2♂ 2♀; 5-v-2003 (S03-38) 2♂; 30-viii-2005 (S05-110) 3♂. Barstow, 2420’, 21-viii-1998 (S98-77) 1♂ 1♀. Havasu Lake, 6-vi-1983 (S83-62) 7♂. Halloran Springs Microwave Station, 4200’, 4-viii-1991 (S91-69) 11♂ 10♀. First wash off I15 on road to Halloran Springs Microwave Station, 2900’, 4-viii-1991 (S91-70) 2♀. Kokoweef area, 35° 24.917’ -115° 30.166’, 5010’, 30-viii-2005 (S05-109) 1♂. Lake Arrowhead, 5100’, 14-vii-1991 (S91-57) 2♂; 20-vii-1994 (S94-64) 3♂. Ludlow Exit off I40, 2060’, 16-viii-1998 (S98-60) 5♂ 5♀. Mt. Pass, 4600”, 4-viii-1991 (S91-71) 1♂; 22-vii-2016 (S16-23) 2♂ 1♀. Newberry Springs, 2160’, 16-viii-1998 (S98-59) 1♂ 1♀. Yucca Valley, 3160’ 26-v-2009 (S09-22) 3♂ 1♀. Truck stop, I40 exit at Goffs, 23-vii-2016 (S16-32) 4♂ 1♀. Hwy 18 near Cushenbury Mitsubishi Cement Plant, 4500’ 27-v-2009 (S09-25) 6♂ 6♀. Hwy 95 14 m NW Vidal, wash area, 1200’, 6-vi-1983 (S83-63) 4♂. *San Diego Co.,* Hwy 79 1.5 m S Hwy 8, 3220’ 5-vi-1997 (S97-58) 2♂. *Santa Barbara Co.,* Anacapa Island, West Island, 23-vi-1971, 1♂. Santa Cruz Island, Field Station, 320’, 11-vi-1970, 6♂ 1♀; 14-vi-1972, 6♂; 5-ix-1973, 2♀; 11-vii-2004 (S04-64) 2♂; Prisoner’s Harbor, sea level, 11-vii-2004 (S04-65) 1♂. Santa Ynez Mts., Lake Cachuma, 2100’, 4-vi-1997 (S97-56) 6♂. Santa Ynez Mts., Hwy 154, 1050-1300’, 24-vii-1981 (S81-26) 2♂; 23-vi-1992 (S92-57) 4♂ 1♀. *Santa Clara Co.,* Mt. Hamilton, 4040’, 10-iv-1982 (S82-7) 1♂; 9-vi-1982 (S82-22) 4♂; 7-vi-1997 (S97-62) 10♂ 6♀; 7-vi-2009 (S09-43) 3♂ (including holotype) 1♀; 27-viii-2015 (S15-114) 3♂. Mt. Umunhum, 3306’ 5-vii-2018 (S18-20) 9♂ 6♀. *Shasta Co.,* Lake Shasta, Bridge Bay Rd yacht area, 4-viii-1980 (S80-67) 3♂. Shasta Dam Visitor’s area, 4-viii-1980 (S80-66) 3♂. *Trinity Co.,* Hwy 299 3.5 m (S14-67) and 10.9 m (S14-68) E Humboldt Co. line, 626’-1390’, 6-viii-2014, 6♂. Hwy 299 28.8 m E Humboldt Co. line, 1255’, 6-viii-2014 (S14-70) 2♂. **Colorado.** *Moffat Co.,* Dinosaur National Monument, Lodore Canyon, Limestone River Campground, 5105’, 5-viii-2012, 1♂. **Idaho.** *Elmore Co.,* Hwy 51 12 m S Mt. Home, 2400’, 12-vi-2004 (S04-41) 3♂. Hwy 51 10.3 m S Hwy 67, 26-vi-2014 (S14-30) 4♂ 2♀. *Owyhee Co.,* Bruneau Dunes State Park, 2660’, 7-vi-1996 (S96-39) 1♂. Hwy 51 1 m N Bruneau, 2900’, 7-vi-1996 (S96-38) 3♂. Hwy 51 at mile post 49.6, 4540’, 7-vi-1996 (S96-36) 9♂ 8♀. Hwy 51 13 m SE Mt. Home, 2780’, 7-vi-1996 (S96-40) 4♂. *Washington Co.,* Weisel Dunes OHV Play Area, 27-vi-2014 (S14-34) 3♂. **Nevada.** *Churchill Co*., Fallon, 4000’, 16-ix-1998 (S98-95) 2♂ 2♀. Fallon Range Training, 4133’, 17-vii-2018, 38.918846° -118.196263° (S18-32) 1♂ 2♀, A. Abela. Fallon Range Training, 4974’, 17-7-2018, 39.15550° -118.341317° (S18-33) 7♂ 2♀, A. Abela. Fallon Range Training, 5997’, 20-vii-2018, 39.444553° -118.046063° (S18-36) 2♂, A. Abela. *Clark Co*., Cottonwood Cove, 750’, 24-vi-1980 (S80-36) 6♂ 1♀. Henderson, 2000’, 24-vi-1980 (S80-35) 2♂. Indian Springs, 4300’, 3-viii-1992 (S92-114) 1♂. Las Vegas, 15-viii-1998 (S98-57) 5♂ 1♀.

Spring Mts., Lee Canyon Rd, at intersection with Hwy 95, 3600’, 15-viii-1998 (S98-56) 2♂. Lee Canyon Rd. at mile post 8.8, 6000’, 2-viii-1991 (S91-60) 10♂ 8♀; 15-viii-1998 (S98-55) 1♀; 5-ix-2006 (S06-105) 3♂. Searchlight, 3540’, 24-vi-1980 (S80-37) 1♂; 23-vii-2016 (S16-33) 3♂. *Humboldt Co.,* Hwy 95 4 m N Winnemucca, 4480’, 9-vi-1996 (S96-45) 2♂; 17-iv-1998 (nymphs reared to adult) (S98-22) 3♂ 2♀; 2-iii-2005 (nymphs reared to adult) (S05-27) 2♂. Hwy 290 11-11.8 m N Paradise Valley, 6220-6460’, 8-vi-1996 (S96-43) 12♂ 3♀. Hwy 140 ~12 m W Denio Junction, 4200’, 28-vi-1992 (S92-70) 10♂ 4♀. *Lincoln Co.,* Panaca, 4900’, 20-viii-1982 (S82-80) 1♂. 7 m E Panaca, 6000’, 20-viii-1982 (S82-81) 3♂. Pioche, 6000’ 20-viii-1982 (S82-79) 1♂. Hwy 319 4.1 m W Utah state line, 6140’, 18-viii-2009 (S09-131) 1♂. Hwy 319 10.6 m W Utah state line, 6280’, 18-viii-2009 (S09-132) 2♂ 1♀. *Mineral Co.,* Mina, 4360’, 4-ix-1999 (S99-98) 2♂. Hwy 95 just S Mina, 4680’, 18-iv-1998 (nymphs reared to adult) (S98-25) 2♂ 2♀. Hwy 395 5 m S Hawthorne, 5200’, 26-vi-1992 (S92-65) 5♂ 2♀. *Nye Co.,* Beatty, 3300’, 22-viii-1998 (S98-80) 5♂ 7♀. Currant Summit, 6999’, 19-viii-2009 (S09-140) 5♂ 1♀. Tonopah, 6140’, 10-x-1995 (S95-115) 5♂ 1♀; 4-ix-1999 (S99-99) 1♂; 19-viii-2009 (S09-141) 1♂. *Pershing Co.,* Rye Patch State Rec. Area, 4050’, 27-vi-1992 (S92-67) 3♂. Rye Patch Dam road exit, 4000’, 27-vi-1992 (S92-68) 9♂ 6♀. *Washoe Co.,* Reno, near intersection I80 and Stoker St., 5000’, 23-viii-2002 (S02-63) 7♂ 2♀; 31-viii-2003 (S03-99) 6♂ 3♀; early May, 2004 (S04-31) 9♂ 2♀. Hwy 447 22.5 m S Gerlach, 4300’, 3-vi-1983 (S83-50) 2♂. *White Pine Co.,* outskirts Baker, 5380’, 9-vi-1996 (S96-49) 5♂ 3♀. Hwy 488 3.1 m W Baker. 6020’, 9-vi-1996 (S96-48) 9♂ 5♀. Hwy 488 5 m W Baker, 6440’, 9-vi-1996 (S96-47) 2♂. **Oregon.** *Harney Co.,* 10.7 m S Burns at mile post 10.7, 4100’, 14-vi-2004 (S04-51) 5♂ 1♀. Hwy 205 16.6 m NW Fields, 4720’, 2-vi-1997 (S97-52) 17♂ 6♀. *Josephine Co*., Store Gulch Campground, 900’, 27-vi-1992 (S92-80) 1♂ 1♀. 2.6 m E Store Gulch Campground, 1300’, 30-v-1983 (S83-36) 11♂ 7♀. 8 m W Selma, 800’, 27-vii-1992 (S92-79) 1♂ 6♀. *Lake Co.,* Alkali Lake, 2-vi-1983 (S83-46) 3♂. Hwy 31 at mile post 62.7, 5200’, 17-VI-2004 (S04-57) 2♂. *Sherman Co.,* John Day Dam, 24-vi-1983 (S83-100) 2♂. Hwy 97 0.7 m SE Biggs, 220’, 31-v-1997 (S97-47) 5♂ 2♀. Hwy 97 14.8 m S Biggs, 1460’, 31-v-1997 (S97-48) 3♂. *Wasco Co.,* Hwy 97 23 m N Madras, 2160’, 31-v-1997 (S97-49) 2♂. **Utah.** *Box Elder Co.,* Hwy 30 1 m N Hwy 69, 4700’, 20-vi-1987 (S87-50) 12♂ 8♀. *Grand Co.,* Moab, 25-iv-2006 (S06-21) 4♂. *Juab Co.,* Eureka, 23-v-2015 (S15-13) 1♂ 1♀. *Kane Co.,* 6.4 m up road to Zion Narrows, 6740’, 9-viii-1991 (S91-93) 1♂ 1♀; 10-vi-1996 (S96-51) 7♂ 3♀. *Millard Co*., Copley’s Trail ~8 m E Fillmore, 6300’, 31-vii-1992 (S92-104) 2♂ 1♀. Fillmore, E Canyon Rd. 0.9 m E Business I15, 4920’, 31-vii-1992 (S92-103) 4♂ 1♀; 18-v-2001 (S01-30) 3♂ 2♀; 20-v-2017 (S17-7) 14♂ 7♀. S. Canyon Rd. 1.8 m E Business I15, 5040’, 18-v-2001 (S01-31) 1♂ 1♀. S. Canyon Rd. 8.1 m E Business I15, 5820’, 18-v-2001 (S01-32) 2♂. Hwy. 6 at mile post 41, 39° 2’ 9.8” -113° 20’ 15.7”, 5239’ 23-v-2015 (S15-15) 6♂ 7♀. *San Juan Co.,* Hwy 191 4 m S Moab, 21-vi-1987 (S87-58) 2♂. Hwy 191 9 m N Monticello, 6200’, 21-vi-1987 (S87-60) 2♂. *Tooele Co.,* Dugway Proving Grounds, Granite and Sapphire Mts., 1400m, 24-27-viii-2013 (S13-79) R. Delph, 7♂ 4♀. Johnson Pass, Hwy 199 between mile posts 11.6-15.2, ~6000’, 20-vi-1987 (S87-52) 4♂; 30-vii-1992 (S92-92) 7♂; 9-ix-2004 (S04-105) 2♂. Stockton, 5390’, 9-ix-2004 (S04-106) 2♂; 23-v-2015 (S15-11) 1♀. Tooele, 23-v-2015 (S15-10) 1♀. *Uintah Co.,* Hwy 149 0.5-1.4 m S Dinosaur National Monument, 5000’, 10-ix-1999 (S99-128) 3♂. *Washington Co.,* Hurricane, 3420’, 20-iv-1999 (S99-12) 5♂ 1♀. St. George, 3040’, 19-v-1995 (S95-39) 11♂ 1♀. Zion National Park, 4440-5640’, 10-vi-1996 (S96-52 & 53) 3♂. La Verkin, 3420’, 11-ix-2004 (S04-121) 9♂ 5♀. Hwy 9 1-2 m NE La Verkin, 3700’, 9-viii-1991 (S91-95) 1♂; 10-vi-1996 (S96-57) 5♂. **Washington.** *Grant Co.,* Ephrata, 1240’, 30-v-1997 (S97-46) 9♂ 5♀. Wanapum Dam Reservoir, 750’ 1-vi-1983 (S83-44) 6♂ 2♀; 1300’ (S83-43) 2♂. Hwy 155 ~6 m S Grand Coulee, 1600’, 30-v-1997 (S97-44) 2♂ 3♀. Hwy 17 2 m N Soap Lake, 1120’, 27-viii-2000 (S00-32) 10♂. Hwy 17 14.1 m N Soap Lake, 1220’, 27-viii-2000 (S00-31) 1♂. Hwy 155 6.5 m N Coulee City, 1660’, 30-v-1997 (S97-45) 3♂. *Lincoln Co.,* Hwy 2 ~10 m W Davenport, 2260’, 30-v-1997 (S97-40) 4♂. Hwy 174 4.5 m SE Grand Coulee, 1760’, 30-v-1997 (S97-41) 3♂. **Wyoming.** *Fremont Co.,* Hwy 20 ~13 m N Shoshone, 4810’, 18-vii-2011 (S11-70) 7♂ 4♀. *Park Co.,* 3.1 m W Cody, 5200’, 2-viii-1997 (S97-104) 6♂ 2♀; 16-vii-2004 (S04-74) 4♂ 1♀.

Derivation of name. “saxatilis” is Latin for “found among rocks,” in reference to this species’ most typical habitat.

Geographic range. Fig. 242. Also into northern Baja California, Mexico. Only known populations east of the Continental Divide are those in Wyoming.

Habitat. Tolerant of widely varying ecological conditions from elevations between -57m (Furnace Creek, Death Valley National Monument, CA S83-60) to over 2200m (Inyo Co., Westgard Pass, S98-98 & S16-17) up to around 2500m at Whitney Portal campgrounds (S78-119), but almost always associated with rocks. Occasionally in cracks of buildings (Halloran Springs Microwave, S91-69) or debris piles in dry river bed bottoms (Jacalitos Canyon, S01-

100). Rarely climbs >1-2m in vegetation, but one male singing from palm tree 10m above ground at Furnace Creek (S83-60). Does climb within rocks along cliff faces (e.g. Long Canyon, Burr Trail, Boulder Co., Utah; Checkerboard Mesa, Zion National Park, Kane Co., Utah); also in rocks supporting railroad tracks in Mojave, CA (S83-117).

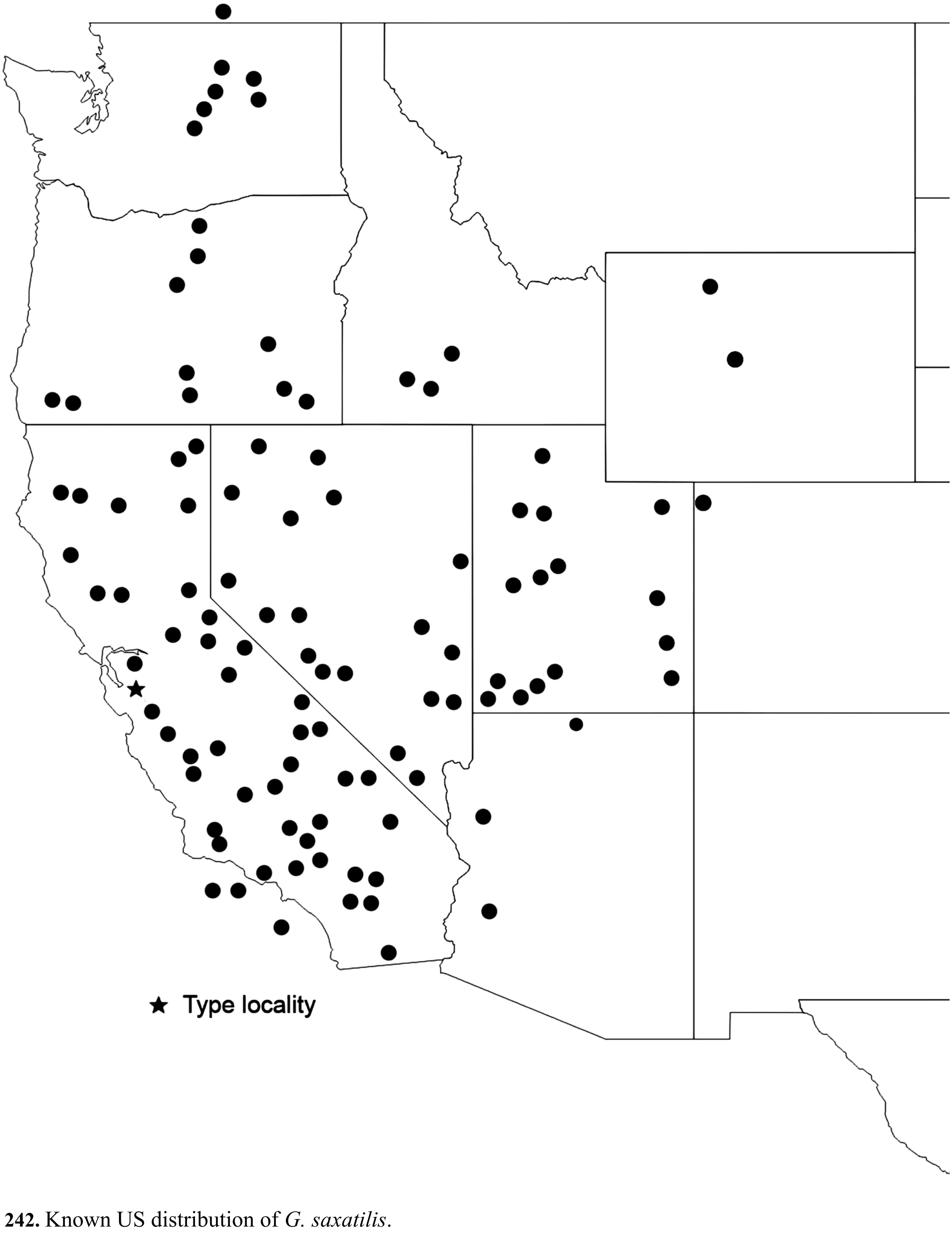

FIGURE 242. Known US distribution of *G. saxatilis*.

Life cycle and seasonal occurrence. No egg diapause: UT, Box Elder Co. (S87-50); CA, Halloran Springs Microwave (S91-69); Reno, NV (S02-63, S03-99); British Columbia (S04-62); NV, Current Summit (S09-140); UT, Dugway Proving Grounds (S13-79); UT, Millard Co., Fillmore (S17-7). Probably one generation/year in Southern and Central California as adults present in May but almost none heard singing by August, which is when a second generation, if present, would be maturing. On the other hand, there appears to be 2 generations/year in Reno, Washoe Co., NV. In early May, 2004 (S04-31), singing males were heard throughout town. We collected 9♂ 1♀ and 1 last instar ♀ that soon molted to adult. On 23-viii-2002 (S02-63) we collected 7♂ 2♀ along with 2 mid-late instars, but singing males were geographically restricted. Eggs from those 2 adult females had no diapause. On 31-viii-2003 (S03-99) we collected 6♂ 2♀ and 3 mid-late nymphs. Eggs from those females also had no diapause. One collected female nymph was a last instar 3-xi-2003 and an adult 1-v-2004 (in a laboratory minimally heated during the winter). Further work over several years with more sampling, and variable rainfall, is needed to interpret this pattern.

Variation. **Body color:** Generally dark (Fig. 243) but reddish individuals known (Fig. 243, CA, Jacalitos Canyon, S01-97). **Hind wing length:** see "Discussion" below. **Number file teeth:** Varies from 122-190 (Fig. 244), a greater range than typically seen in a *Gryllus* species with a more limited distribution. **Tegminal bars** present in certain populations**:** 2 of 7 field collected adult females from UT, Millard Co., Fillmore (S17-7); in both sexes from CA, Kern Co., Tehachapi (S09-29).

FIGURE 243. Color variation in *G. saxatilis*, moving left to right: left long hind winged 'G. mohave' (Baker, CA, S03-38); middle long hind winged 'G. mohave' (Kingman, AZ, S92-113); right *G. saxatilis* (Fresno Co., CA, S01-97).

DNA. G. saxatilis falls within a clade of closely related western chirping species that we recognize here as *G. saxatilis, G. leei, G. makhosica,* and *G. navajo.* Multilocus G3310 Mt. Hamilton, CA (S15-114—type locality for *G. saxatilis*); G3484 Fillmore, UT (S17-7—locality of *G. saxatilis* nearest [14 km east] to type locality of *G. leei*); G3431 Big Pine, CA (S16-18—'G. mojave', where all 12 collected individuals had long hind wings); and G1131 Kingman, AZ (S07-64—'G. mojave') all map (Gray *et al.* 2019) in a group of rock chirpers along with Utah *G. leei,* South Dakota *G. makhosica*, Arizona and Utah *G. navajo,* and California 'G. tulare' and 'G. mormoni'. Individuals of *G. saxatilis* from Mt. Pass, CA, (S16-23), near Goffs, CA (S16-32), and Searchlight, NV (S16-33) all have the same 16S sequence that we found in 'G. tulare'. ITS2 (Fig. 238, p. 236) does a poor job resolving within the *S*axatilis Group, specifically *G. makhosica*, *G. leei*, and *G. navajo* ITS2 sequences are intermingled with *G. saxatilis*. Ironically, the 'tulare' and 'mormoni' forms, which we do not recognize here as distinct species, are better resolved by ITS2 than the taxa we do recognize. Further work is clearly warranted; analysis of SNP data from rad-seq on a large series of *G. saxatilis* and *G. navajo* is already underway (Collosi *et al.*, in prep.), see discussion under *G. navajo*, p. 258.

Discussion. This species was initially split into several groups, mostly for convenience, based on geography and some physical differences. All populations in California, Oregon, and Washington west of the Sierras and Cascades were called 'G. #2'. Those populations in California, Oregon, and Washington east of the Sierras and Cascades, and those collected in southern Idaho and Nevada were designated 'G. #11'. Populations from Utah, northern Arizona, and Wyoming were labeled 'G. #22'. And lastly, those individuals not always associated with rocky habitats but with human habitation, and with long hind wings and small heads, from the Great Basin and Mojave Desert areas of California, southern Nevada and adjacent Arizona, were called 'G. #38' or 'G. mojave'. While we suspect that cryptic species may exist within this geographically diverse assemblage, we are not able to separate them either morphologically or with DNA profiles. All have similar songs and have been included as paratypes under *G. saxatilis*.

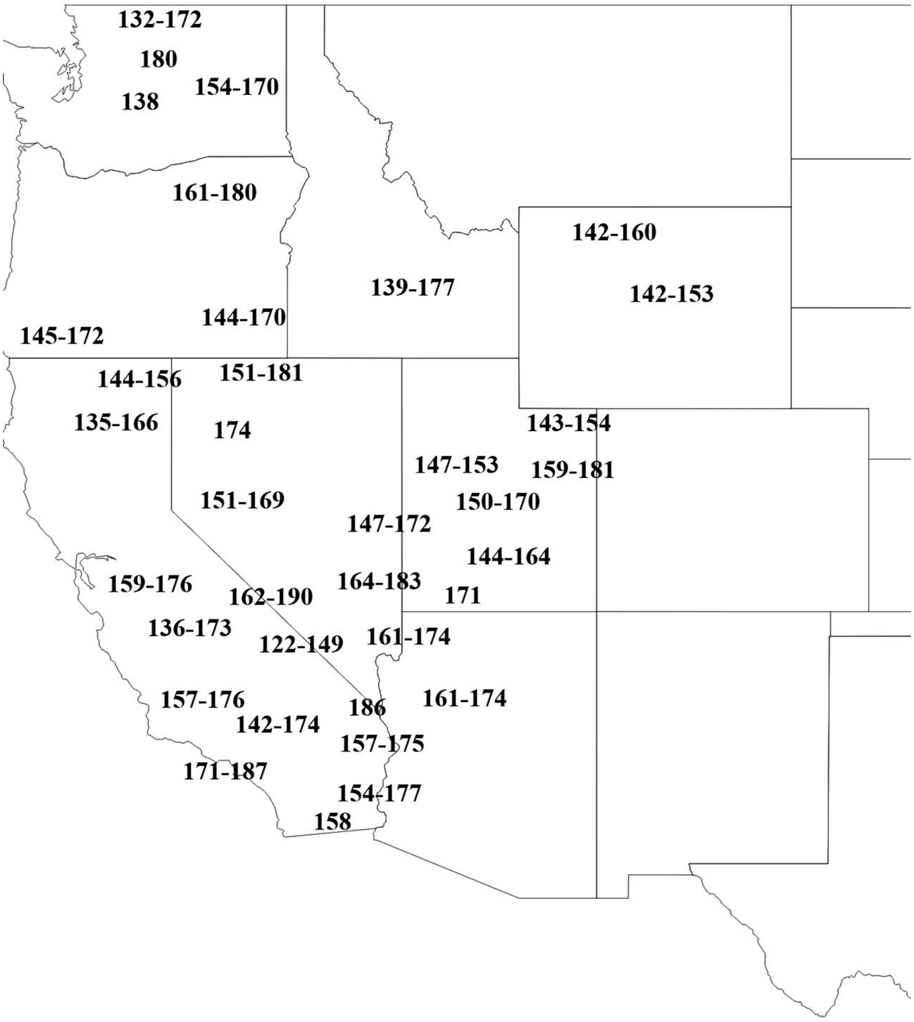

FIGURE 244. Distribution map of file tooth number in *G. saxatilis.* Counts vary from 122 (Tulare Co., CA, S03-28) to 190 (Big Pine, CA, S16-18).

Still, the most likely cryptic taxon are those individuals considered to be 'G. mojave' based on the common, but not universal, reduced head width and almost universal presence (Fig. 243) of long hind wings (e.g. all 9 males and 25 females from Kingman, AZ (S92-113); all 11 males and 10 females from Halloran Springs (S91-69) and, in total, 97 of 120 males [81%] and 84 of 85 females [99%] from the Great Basin and Mojave Desert, where we considered all collected *G. saxatilis* to be 'G. mojave'. Most of these just discussed, long hind-winged individuals were from areas of human influence, either adjacent to or within town boundaries or outside towns but associated with human structures. In contrast, a nice series of 14 individuals of *G. saxatilis*, collected by A. Abela in undisturbed Great Basin Desert habitat, Churchill Co., NV (S18-32, 33, 36), all had short hind wings. Also, only one of 8 males and the only female from another undisturbed, (high elevation—2216m) locality, Westgard Pass, CA, on the western edge of the Great Basin, had long hind wings. And away from the Great Basin and Mohave Deserts, only 6 of 530 adults (~1%) had long hind wings. It thus appears that a combination of living with human influence within and near the Great Basin and Mojave Deserts, favors adults with long hind wings.

On the 21-km-long road between Hualapai Mt. Rec. Area and Kingman, Arizona, going from 2042m to 1128m, there are 4 species of medium sized, medium-long length cerci, slow chirping *Gryllus* species. *G. montis* is highest in the pine-oak forest, but extends into the higher elevation interior chaparral as low as 1585m. Once out of the forest driving almost due west through interior chaparral, faster chirping *G. lightfooti* is heard starting at 1738m and heard into Kingman. *G. longicercus* starts at 1646m, drops out at 1433m, and is then heard again in Kingman. *G. saxatilis* was first heard in 1992 (S92-113), on the outskirts of Kingman, at 1128m, in large numbers (9 males and 25 females, all with long hind wings. In 2007 (S07-64), only one male *G. saxatilis*, with long hind wings, heard and collected at 1783m. Three species (*G. montis, G. longicercus,* and *G. saxatilis*) heard microsympatric, in both 1990 (S90-56) and 1991 (S91-65), at 14 km SE Kingman at 1646m.

Five tachinid *Ormia ochracea* emerged from 1 male near Palm Desert, CA (S09-20); one *O. ochracea* emerged from a male from Corn Springs, Riverside Co., CA (33.625, -115.333) collected 10-iv-2015—seasonally among the earliest *O. ochracea* we have encountered. One, two, and three tachinid *Exoristoides johnsoni* emerged from three males from Fallon, NV (S98-95). One tachinid *E. johnsoni* emerged from each male, both collected as nymphs, from 6.4 km N Winnemucca, NV (S98-22). For such a widespread species, this is a surprisingly low parasitism rate. Perhaps this rate is reduced by having only 1 early-season generation/year, before the tachinid fly numbers become significant.

One female *G. saxatilis*, Oregon, Josephine Co., 13 km W Selma (S92-79) with horsehair worm. One male, California, Tulare Co. (S03-27) with mermithid worms (see Poinar & Weissman 2004).

Occasional males continue to sing while turning over rocks attempting a capture—a behavior also seen in *G. longicercus*.

Two geographically restricted areas of *G. saxatilis* give us pause, based primarily upon DNA results. We gave individuals from these two areas tentative names, and we now discuss them: 'G. mormoni' is from the area around Folsom Lake, CA, and 'G. tulare*'* is from Tulare Co., CA. They both have 16S, ITS2, and multilocus DNA sequences distinctive from other *G. saxatilis* and from each other. Since neither can be morphologically or ecologically separated from typical *G. saxatilis*, and in the absence of any vicariant physical barrier, we tentatively place them together with the nominate species and discuss them below, but do not consider them paratypes. Comparing 'G. mormoni' vs. 'G. tulare', they can be separated by DNA (Fig. 238), almost non-overlapping teeth/mm (Table 1, p. 18), non-overlapping file teeth vs. tegmina width (Fig. 245), and little overlap between hind femur length vs. ovipositor length (Fig. 246), although the latter could be the simple result of larger body size in 'G. tulare'.

'G. mormoni' Known only from around Folsom and Placerville, in California's Sacramento Valley, that portion of the California Central Valley that lies to the north of the Sacramento-San Joaquin River Delta. Medium sized, generally black, narrow pronotum, medium length cerci and always short hind wings. Song a slow chirp (1.5-2.5 C/S), 4-5 P/C, PR 17-21 at 25°C. Separated from nominate *G. saxatilis* by DNA (Fig. 238) and the narrower tegmina in 'G. mormoni' (Table 1, p. 18). Additionally, paratype *G. saxatilis* not known from the Central Valley floor proper but only in foothills of adjacent mountain ranges to the west (e.g. Jacalitos Canyon near Coalinga, Fresno Co.; Tar Canyon near Kettleman City, King Co.); to the north (e.g. Lake Shasta, Shasta Co.); and east (West Point, Calaveras Co.).

Specimens studied. (23♂ 18♀). **California.** *El Dorado Co.,* 4.7 air miles NE Placerville, Mosquito Rd near mile post 5.64, 8-viii-2014, 519m, 38° 46' 34.76" -120° 45' 08.57' (S14-77) 4♂ 1♀. *Sacramento Co*., Folsom, intersection of Folsom Blvd. and Hwy 50, 174', 19-vii-2015 (S15-87) 6♂ 2♀; Folsom, intersection of Folsom Blvd. and Blue Ravine Rd., 19-vii-2015 (S15-88) 5♂ 7♀. Folsom Lake SRA, Beal's Point area near Folsom Dam, 463', 6-v-2013, 38° 43' 06.61" -121° 10' 10.18", 29-iii-2005 (S05-38) 2♂, collected as mid instars; 6-v-2013 (S13-10A) 6♂ 8♀.

Derivation of name. Named for Mormon Island, a California mining community that developed, starting in 1848, after gold was discovered on the south fork of the American River. The community was subsequently razed and covered with water from Folsom Lake, which formed in 1955, after the construction of Folsom Dam. Due to California's record drought from 2012-2017, parts of Folsom Lake were exposed, where we collected a nice series in 2015. Mormon Island is designated as California Historical Landmark #569.

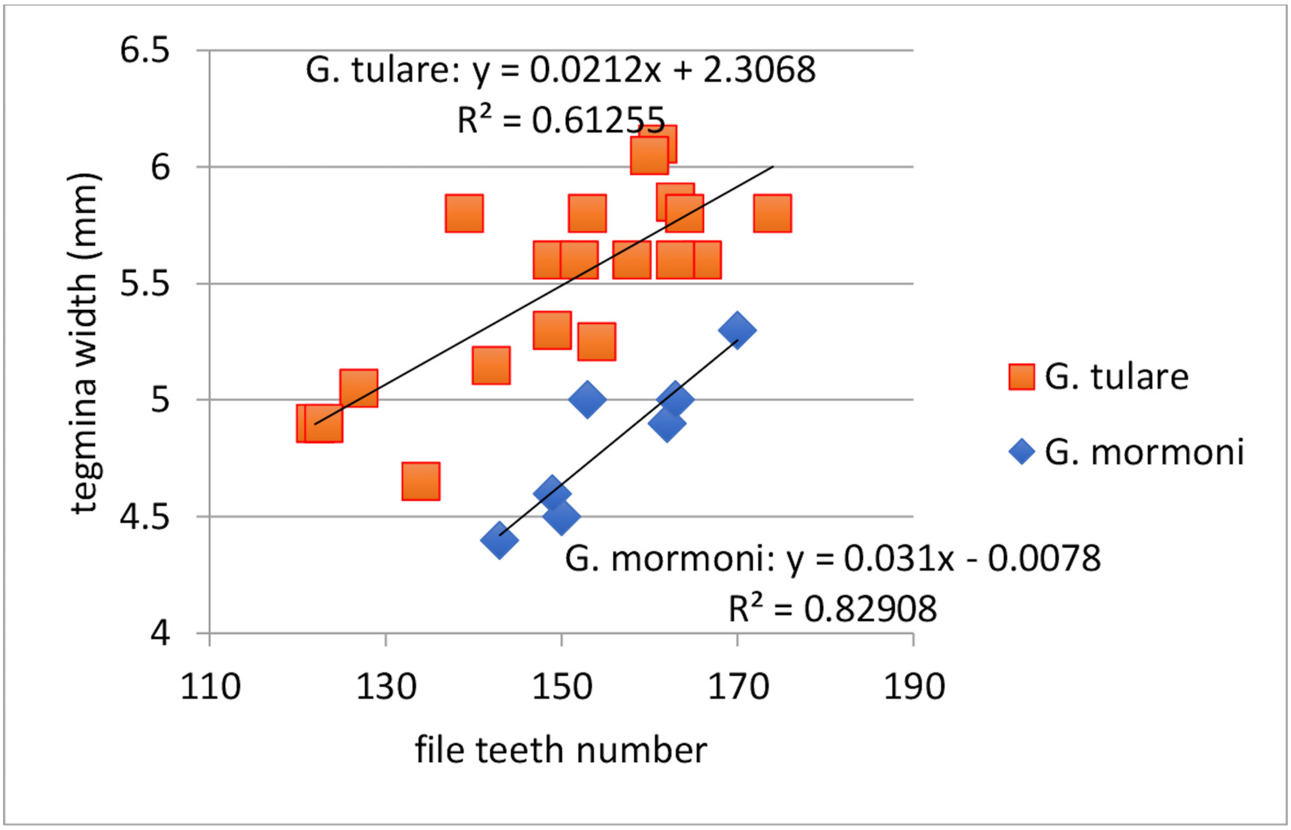

FIGURE 245. Regression of file teeth number vs. tegmina width in 'G. tulare' vs. 'G. mormoni' showing absence of overlap.

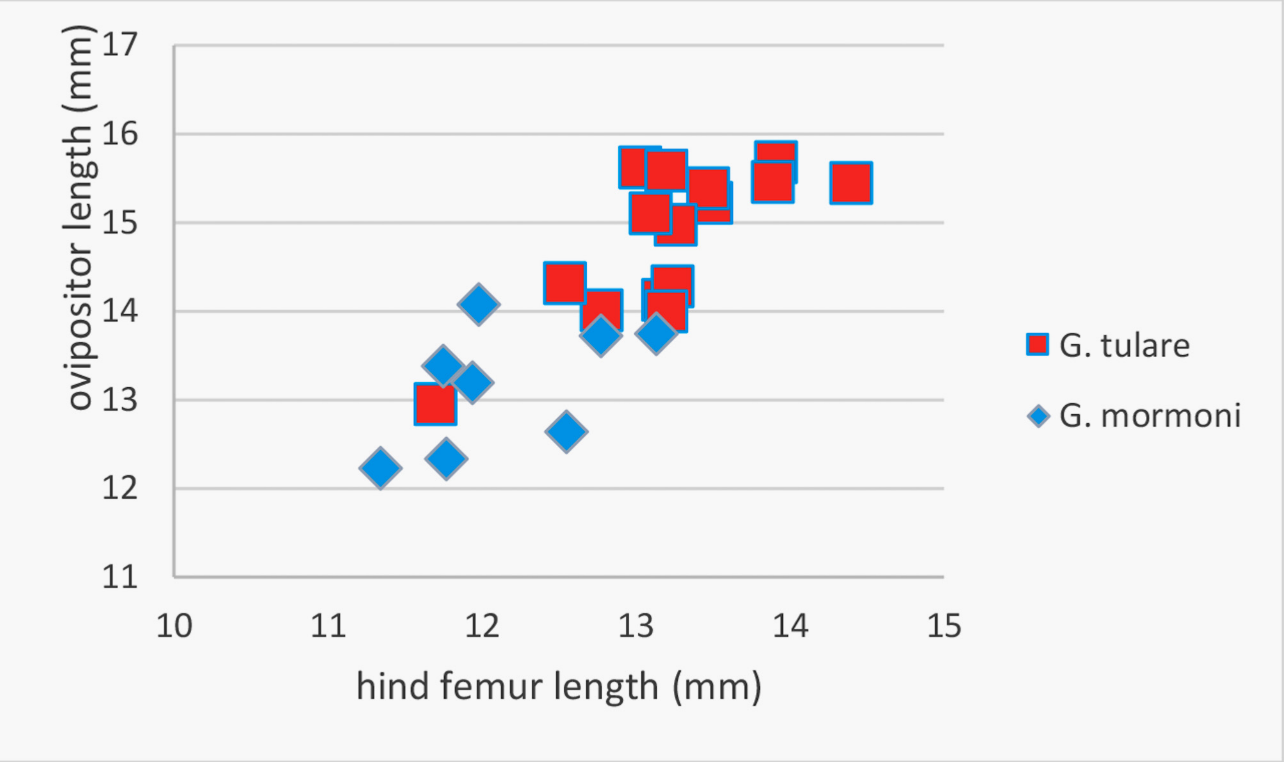

FIGURE 246. Regression of hind femur length vs. ovipositor length in 'G. tulare' vs. 'G. mormoni' showing minimum overlap.

Habitat. The Folsom Lake locality is open, short grassland, with rocks, lying in the completely dry, exposed part of "Folsom Lake", which may have been submerged in 2019 after an above-average rainfall year. A few males also singing from under adjacent rocks at the base of Folsom Dam. Similar sounding males also singing within oak-woodland of Folsom Lake SRA but none collected and species identity not confirmed as similar sounding *G. veletisoides* also occurs in the area. The two localities within Folsom city limits (S15-87, S15-88) were open areas with dirt and few rocks, the latter adjacent to the railroad tracks. Mosquito Road is 37 air km from the first locality and more typical habitat of *G. saxatilis* comprised of oak woodland with dirt road banks but few rocks. Crickets were heard for some 3 km along Mosquito Rd. between 511m and 684m elevation.

Life cycle and seasonal occurrence. No egg diapause (S14-77). One generation/year with nymphs overwintering as mid-late instars since late-instars present in late March and adults present and singing in early May. F_1 nymphs, from laboratory laid eggs, started molting to adults, in May, one year after they were laid.

'G. tulare' Only known from Tulare Co., California, always with short hind wings. Song a slow chirp (3) 4 (5) p/c, 90-225c/m, PR 15.2-23.8 at 25°C. Separated from nominate *G. saxatilis* by DNA (Fig. 238).

Specimens studied. (31♂ 17♀). **California.** *Tulare Co.,* Hwy 190 3.2 m E Springville, 1620', 20-viii-2006 (S06-81) 1♂. Hwy 190 6.5-10 m E Springville, 2320-3460', 29-v-2009 (S09-34, 35) 17♂ 13♀. Hwy 190 0.5 m W Pierpoint Springs, 4700', 4-v-2003 (S03-27) 2♂ 2♀. Hwy 190 5.4 m W Pierpoint Springs, 3700', 4-v-2003 S03-28) 5♂. Hwy 198 4.4 m E Lemon Cove, 725', 28-vi-2016 (S16-21) 6♂ 2♀.

Habitat. From 221-1433m elevation. Habitat typical for *G. saxatilis*: oak-woodland borders, chaparral, road cuts always associated with rocks.

Life cycle and seasonal occurrence. One generation/year, egg diapause not checked but undoubtedly absent as adults present in late spring. Mid-late instars seen early May (S03-27 & 28) and a last instar female seen late May (S09-35) when most of population adult.

Variation. **Cerci length:** Longer than ovipositor in situ in only one female (S09-34). **Color:** Hind femur normally varies from small reddish area medially where attaches to body to entire femur reddish with rest of hind leg black. Two males (S03-27 and S06-81) with entire hind legs reddish. **File teeth:** Vary from 122–174. All of these males have medium length cerci and DNA consistent with 'G. tulare.' The three *G. saxatilis* males with the fewest teeth (122–149, see Fig. 244, p. __) are in this 'G. tulare' group (S03-28, W Pierpoint Springs), collected on 4-v-2003, and raised through the last few instars in the laboratory.

Gryllus leei Weissman & Gray, n. sp.

Utah Lava Field Cricket
Figs 231, 236–238, 240, 247–250, Table 1

Distribution. Known only from lava flows in the Black Rock Desert of west-central Utah.

Recognition characters and song. A small-medium, always short hind winged, generally black, shiny pronotum, small headed, short ovipositor, cerci always longer than ovipositor in situ *Gryllus* (Fig. 249). *Song* a chirp (Fig. 247, R17-7) of usually 4 (range 3–5) p/c, PR 17.5–22, CR 105–200 (range 98–225). Most importantly, because multilocus *G. leei* maps close to multilocus *G. saxatilis,* we can separate the two even though they are found only ~14 air km from each other, as follows: *G. leei* is smaller (S01-28, S17-6), with the longest body-length individual being shorter than the smallest individual of *G. saxatilis* (S01-30, S17-7), with good sample sizes from both populations. If the same species, it then logically follows that *G. leei* might have (see Table 1, p. 18) fewer file teeth, shorter files and shorter tegmina, and (non-overlapping) shorter ovipositors than nearby *G. saxatilis.* What doesn't necessarily follow is that *G. leei* has proportionally longer cerci, almost non-overlapping teeth/mm, and a different dominant frequency calling song. For the latter, 24 males from the type locality (S17-6) had a dominant frequency from 4017–5211 Hz while 15 males *G. saxatilis* from nearby (S17-7) had a dominant frequency of 3593–4097 Hz. Most male *G. leei* (20 of 22–91%) with 3–4 (rarely 5) harp veins while 12 of 13 (92%) nearby *G. saxatilis* have 4–5 (rarely 3) harp veins. Additionally, the cerci are longer, in situ, than the tip of the ovipositor in all 14 type locality females of *G. leei* while shorter than the tip in all 10 females of nearby (S17-7) *G. saxatilis.* This trend is confirmed when we regress ovipositor length on hind femur length (as an indicator of body size) (Fig. 248; hind femur: $F_{1,20}$ = 87.72, $p < 0.0001$, species: $F_{1,20}$ = 81.16, $p < 0.0001$, species*hind femur $F_{1,20}$ = 0.10, $p = 0.748$).

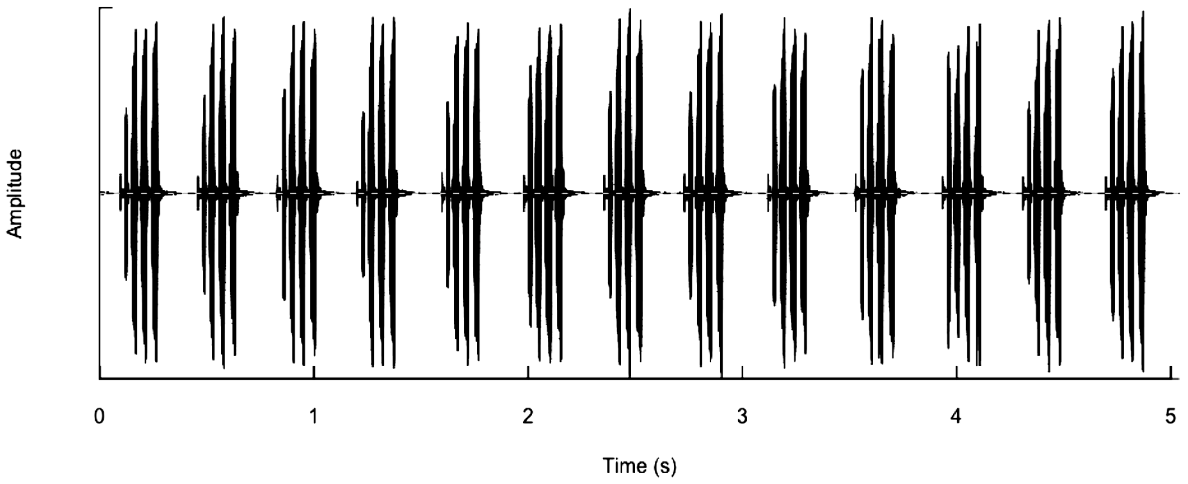

FIGURE 247. Calling song (R17-7) of *G. leei* from type locality (S17-6), recorded at 24.5°C.

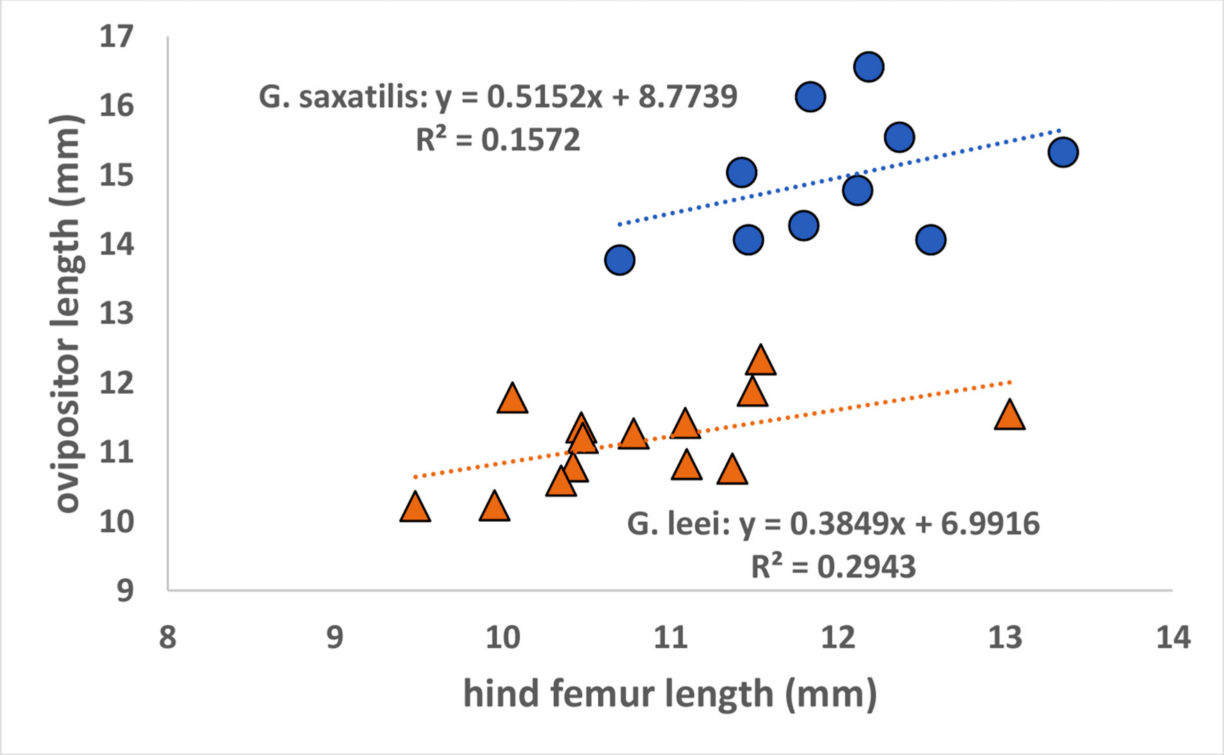

FIGURE 248. Regression of hind femur length vs. ovipositor length in *G. saxatilis* vs. *G. leei* from populations separated by only 14 kilometers.

If individuals from both populations were the same species, even if with different body lengths, we would expect them to fall on the same regression line with a similar Y axis intercept. Apparently living in lava flows favors a shorter ovipositor than living off of lava, even if both species probably oviposit into the soil. There is also evidence that these smaller and lower elevation *G. leei* (S17-6) may molt to adult before *G. saxatilis* in central Utah (S17-7): 29 of 37 (78%) *G. leei* individuals collected on 20-v-2017, at 1418m, were adult while 12 of 24 (50%) *G. saxatilis* individuals collected on the same date, at 1598m, were adult. On the other hand, perhaps the larger *G. saxatilis* simply take longer to become adult because they are larger, as indicated by their longer hind femur lengths.

Distinguished from a number of allopatric lava and rock-associated *Gryllus* as follows: From New Mexico lava *G. vulcanus*, no overlap (Table 1, p. 18) in number of teeth and PR and different DNA. From rock *G. longicercus*, almost no overlap in number of teeth, PR, cerci length, and DNA. From allopatric eastern Utah *G. navajo* by habitat (sandstone badlands vs. lava), general body and tegmina color (reddish vs. black), antennae length longer than body in *G. navajo*, and the Pahvant Mt. Range and Sevier Plateau between the two species. From allopatric South Dakota badlands *G. makhosica*, no overlap in file length, teeth/mm, tegmina length and width, hind femur length, ovipositor length and PR. From allopatric Texas rock *G. transpecos*, distinguished by *G. leei*'s smaller size, slower PR, shorter ovipositor, habitat, and DNA with the nearest populations separated by some 1110 km. *G. veletis* sympatric with *G. leei* but can be easily separated by the former's shorter cerci which never approach the ovipositor tip in situ, being located away from lava, and more robust, larger body size.

Holotype. Male (Fig. 249): Utah, Millard Co., 2.05 m NW Flowell and 8.5 m NW Fillmore, 20-v-2017, 4653', 38° 59' 52.30" -112° 27' 32.94". D.B. Weissman, D. W. Weissman. S17-6, R17-6. DNA sample G3480. BL 17.44, HF 9.46, RC 11.07. Right tegmen removed: 3 harp veins, 144 teeth, file length 2.8, TL 9.5, TW 3.9. Type deposited in CAS, Entomology Type #19277.

FIGURE 249. Holotype male (left) of *G. leei*. Female (right) also from type locality (S17-6).

Paratypes. (Total: 30♂ 14♀). Same locality data as holotype: 18-v-2001 (S01-28) 7♂ 4♀; 20-v-2017 (S17-6) 23♂ 10♀.

Etymology. Named for Vincent F. Lee of the CAS, for helping to collect the initial series and for never complaining, during many field trips, when asked to help collect "one more cricket" at 04:30.

Geographical range. See Fig. 250. Known only from the type locality.

Habitat. Many males sing from deep crevices and cracks, within vegetated lava flows, where they are almost impossible to catch, even using water for flushing. Fortunately, a good number of juvenile and adult males and females were under lava rocks that were resting on soil, around edges of main lava flow. Walking into the lava field at night, we heard males singing more than 50 meters from lava's edge on 20-v-2017, although not as common as on the lava's perimeter. Utah's Black Rock Desert volcanic field is a heterogeneous mix of flows from 6.1 MYA with continuous activity from 2.7 MYA to the present, including the most recent eruptions 720 years ago (USGS: https://volcanoes.usgs.gov/volcanoes/black_rock_desert/).

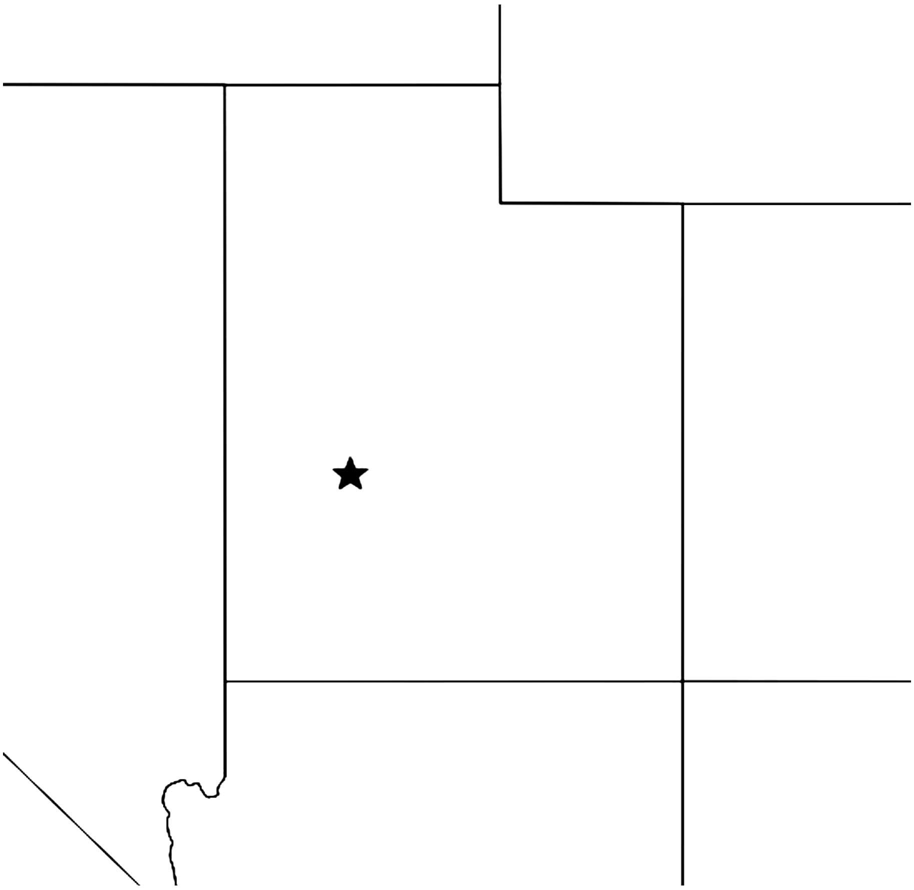

FIGURE 250. Known distribution of *G. leei.*

Life cycle and seasonal occurrence. No egg diapause (S17-6). Probably one generation/year, overwinter as late instars with first adults probably appearing in early-May. No nymphs seen when series collected 18-v-2001, despite a cool, wet spring in Utah. On 20-v-2017, we collected 22 adult males, 7 adult females, and 8 late instars. Also listened here 19-iv-1999 and 11-ix-1998 (apparently too late) without hearing any singing males.

One generation/year also supported by these observations: Adults collected May 20th were maintained together under ambient light conditions, at fluctuating temperatures between 18-30°C, and allowed to mate. Females were then isolated in cartons with moist sand, for oviposition, starting on May 30. Very good egg hatch commenced on June 26, indicating the absence of an obligate egg diapause. Many, but not all, nymphs in both cultures grew rapidly with the first adults appearing around September 12th in both containers, confirming the possibility of 2 generations/year. Still, a fair number of nymphs were only mid-instar in mid-September. So, while this species could have 2 generations/year, on site observations support a univoltine sspecies. And we wonder if *Gryllus* in areas with monsoon rains have more variability in instar development than those in California with its more predictable drought periods of a Mediterranean climate?

Variation. **Color:** Variable amount of red on inner rear leg femur. Two of 10 2017 females with tegminal bars.

DNA. Multilocus G147 (S01-28) and G3475 (S17-6) map (Gray *et al.* 2019) with sister taxa *G. saxatilis* (G3484, S17-7, from 14 km E of type locality and the closest population of *G. saxatilis* to the type locality of *G. leei*), G1067 *G. navajo,* and G1340 *G. makhosica*. ITS2 gives (at best) modest separation of *G. leei* from *G. saxatilis* (Fig. 238, p. 236).

Discussion. Singing on arrival at type locality at 18:00 on 18-v-2001 and 19:00 on 20-v-2017, well before sunset. Lava flows in this area from 600 to 15,500 years old (White 1996). The main flow measures, on Google Earth, some 8.5 km wide north to south and 9 km wide east to west. The lava bed is like an island separated from the surrounding flat plains without rocky, suitable habitat for *G. saxatilis.*

There is one other lava flow obligate *Gryllus* in the western US: *G. vulcanus* from New Mexico. But not all lava flows are inhabited by *Gryllus:* at extensive lava flows in Lake Co., SE Oregon (43° 35.5' -121° 1.43'), no *Gryllus* heard 1-vi-1997 despite area looking favorable.

We wonder if the short ovipositor is related to living in lava fields with shallow substrate for oviposition? It would be of interest to know if *G. leei* females oviposit directly into the substrate or can they use pockets of soil and debris within the lava field?

Gryllus makhosica Weissman & Gray, n. sp.

Badland's National Park Field Cricket
Figs 236–238, 251–258, Table 1

'G. #26' of DBW notebooks

Distribution. Known only from Badlands National Park, South Dakota.

Recognition characters and song. A medium sized, slender, always short hind wings, dark colored, long antennae extending well past tip of ovipositor, females with short tegmina and cerci longer than ovipositor in situ. *Song* (Fig. 251, R09-95) a chirp, 3–4 (range 3–5) p/c, 105–185 c/s, PR 16-21. Distinguished from allopatric (nearest populations are ~850 km apart) sister species *G. navajo* from Utah and Arizona by the following: general body color, especially hind femurs, more reddish in *G. navajo* vs. dark in *G. makhosica. G. navajo* lives in sandstone badlands vs. clay badlands for *G. makhosica*. Chirps in *G. makhosica* average 3–4 p/c vs. 4–5 in *G. navajo.* Morphologically, *G. makhosica* has more teeth and longer files on average than *G. navajo* (Fig. 252), more teeth and average longer tegmina (Fig. 253), more teeth but similar male hind femur length (Fig. 254), more teeth and less variable teeth/mm (Fig. 255), while female *G. makhosica* appear to have, on average, longer hind femurs and less variable ovipositor lengths (Fig 256). While there is overlap in all of these metrics for these two species (Table 1, p. 18), *G. makhosica* is not a larger cricket than *G. navajo* as indicated by similar hind femur lengths in males (Fig. 254). Distinguished from allopatric (nearest populations are >520 km apart), rock loving sister species *G. saxatilis* with latter having file with more teeth and longer tegmina, longer cerci and longer ovipositor. Distinguished from allopatric (nearest populations over 1000 km apart), lava inhabiting sister species *G. leei* by *G. makhosica* having non-overlapping and longer files, tegmina length, and ovipositors. Distinguished from allopatric (nearest populations are >1100 km apart) *G. longicercus* by DNA and former having fewer teeth in file, fewer teeth/mm, and non-overlapping ovipositor length and pulse rate (Table 1, p. 18).

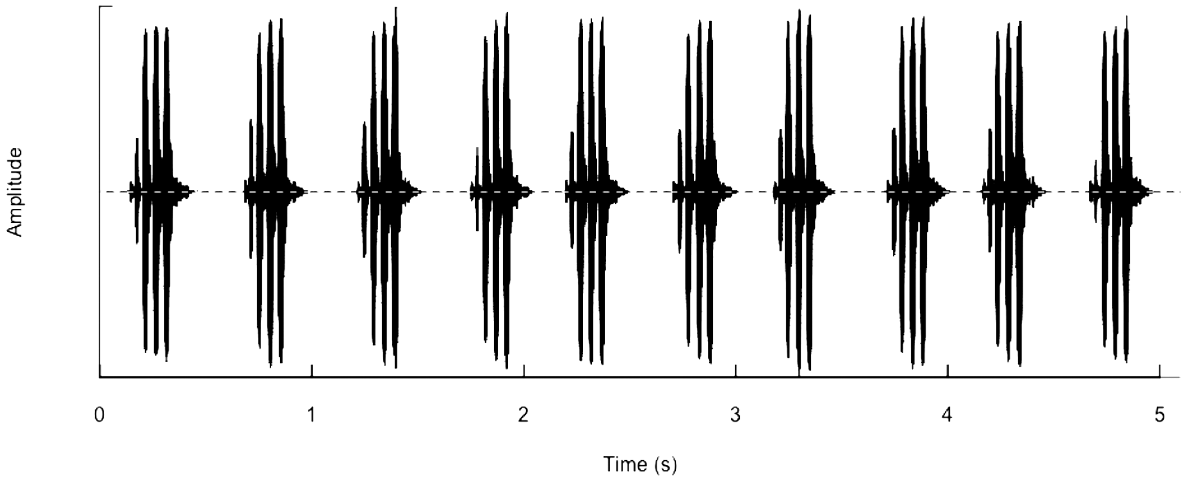

FIGURE 251. Calling song (R09-95) of *G. makhosica* from type locality (S09-89), recorded at 24.5°C.

Holotype. Male (Fig. 257): South Dakota, Jackson Co., Badlands National Park, Cedar Pass Overlook area, 3-vii-2009, 2680', 43° 45' 13.6" -101° 56' 5.1". DB Weissman & DC Lightfoot. S09-89, R09-80, DNA sample G1340. 16S GenBank accession # MK446488; ITS2 GenBank accession # MK441894. BL 20.29, HF 11.89, LC 14.81. Right tegmen removed: 172 teeth, file length 4.0, TL 13.2, TW 5.4. Type deposited in CAS, Entomology Type #19265.

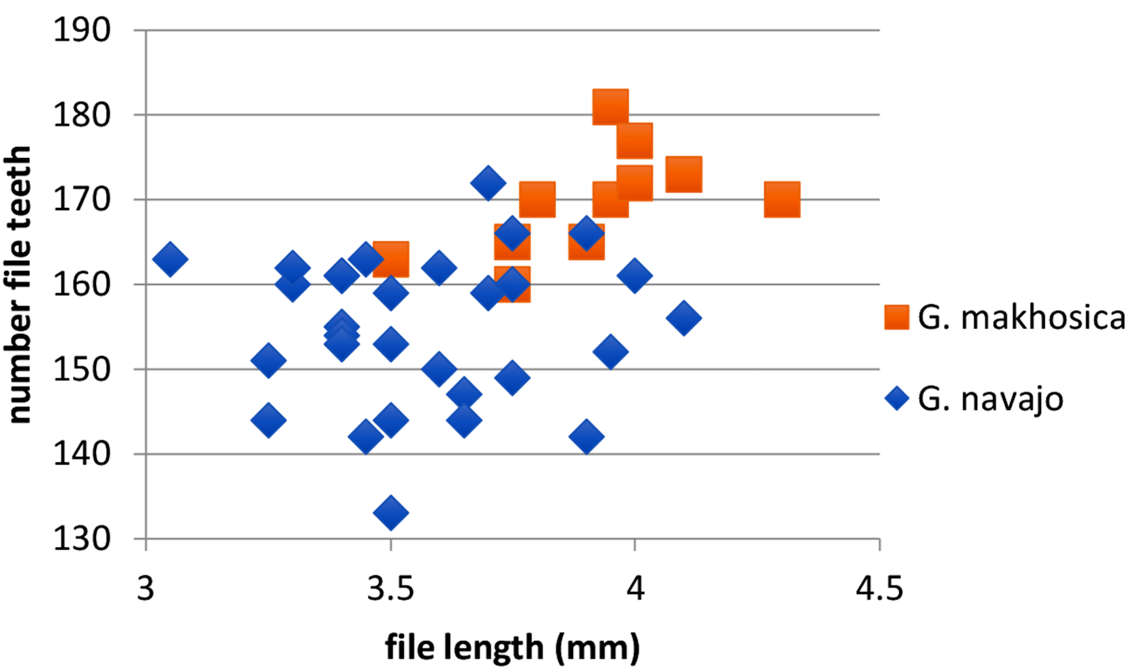

FIGURE 252. Regression file length vs. number file teeth in *G. makhosica* vs. *G. navajo.*

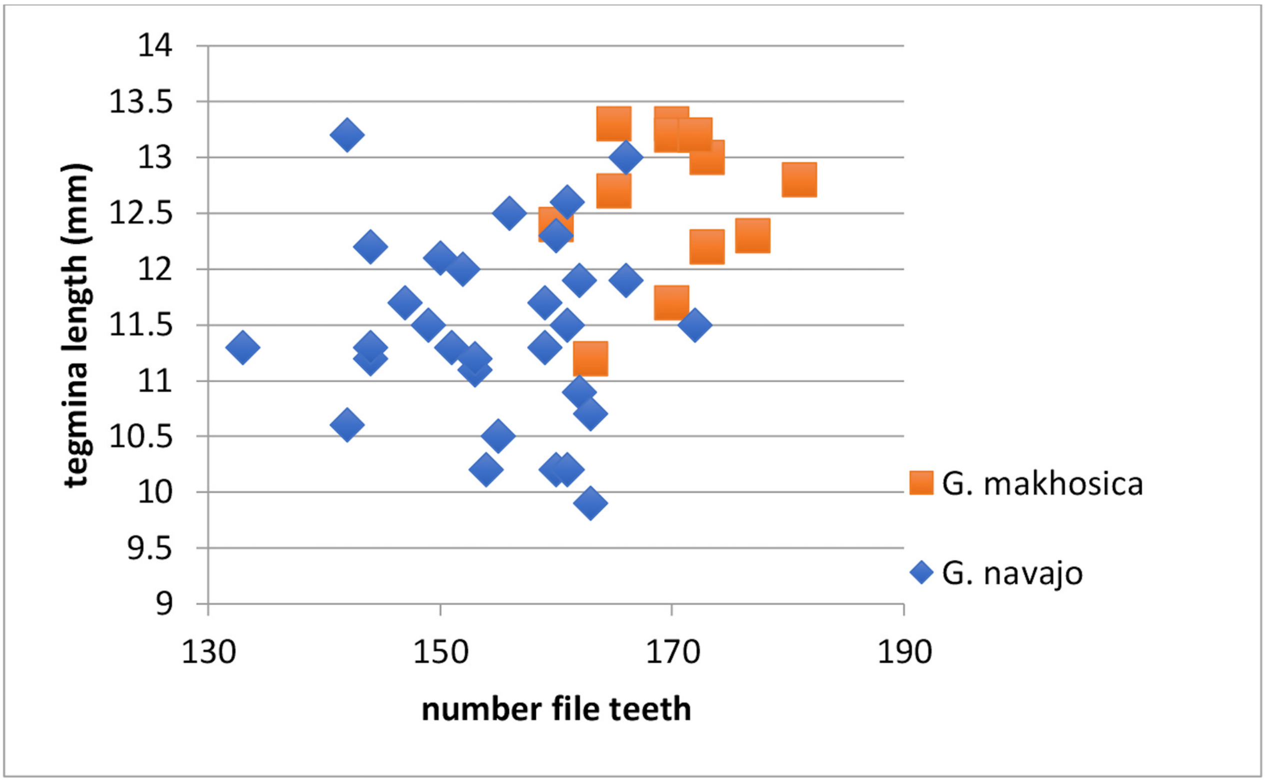

FIGURE 253. Regression number file teeth vs. tegmen length in *G. makhosica* vs. *G. navajo*.

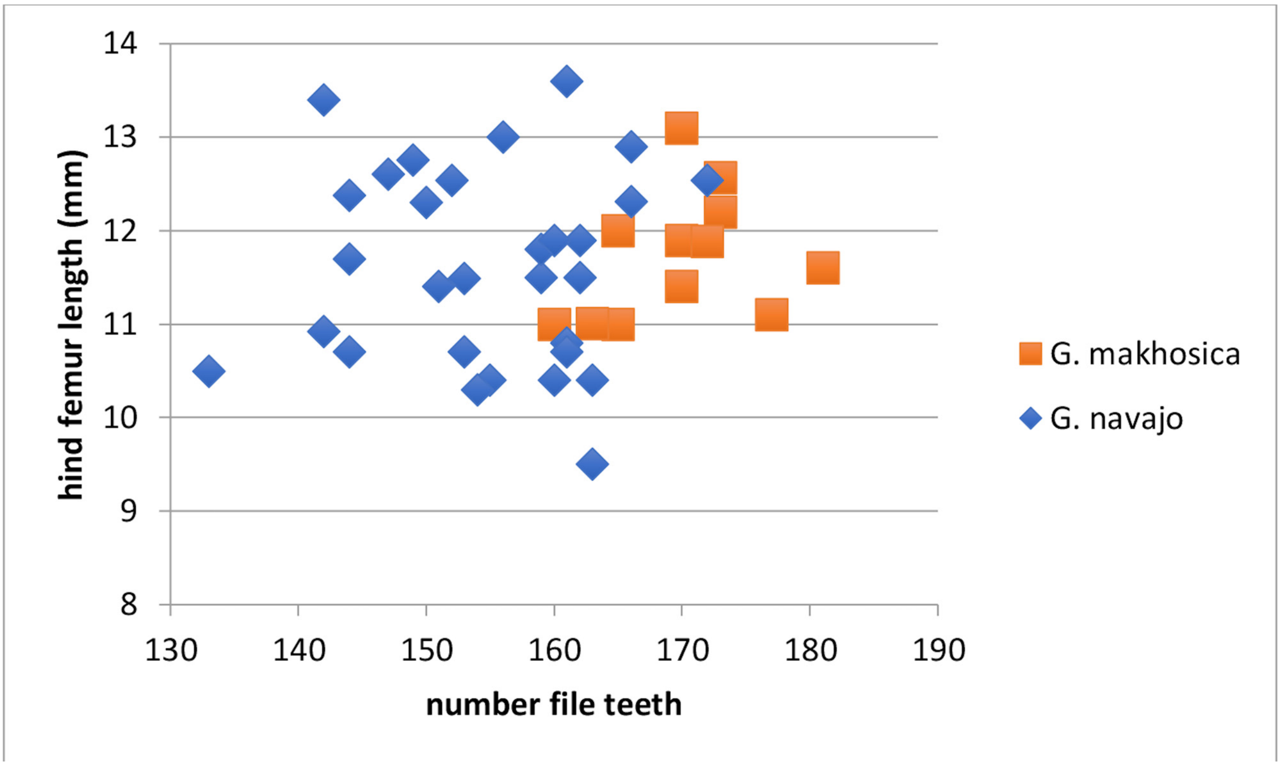

FIGURE 254. Regression number file teeth vs. hind femur length in *G. makhosica* vs. *G. navajo*.

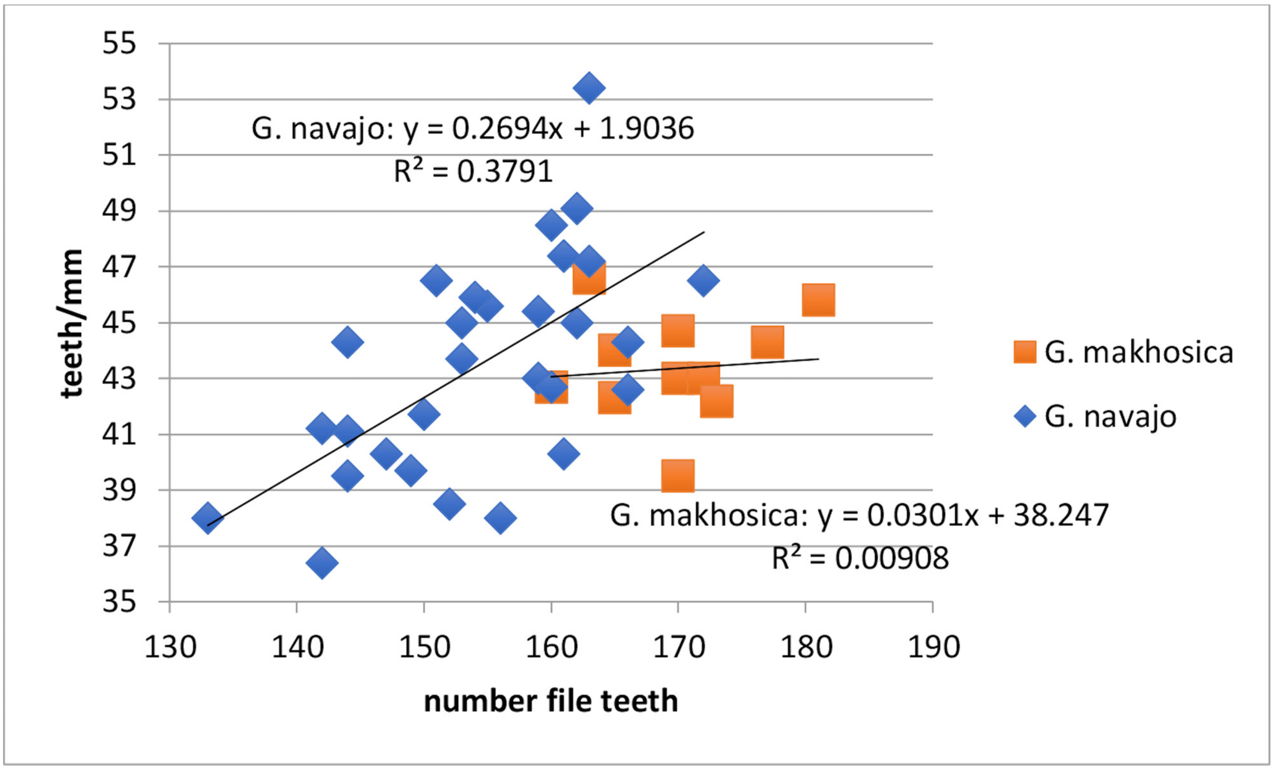

FIGURE 255. Regression number file teeth vs. teeth/mm in *G. makhosica* vs. *G. navajo.*

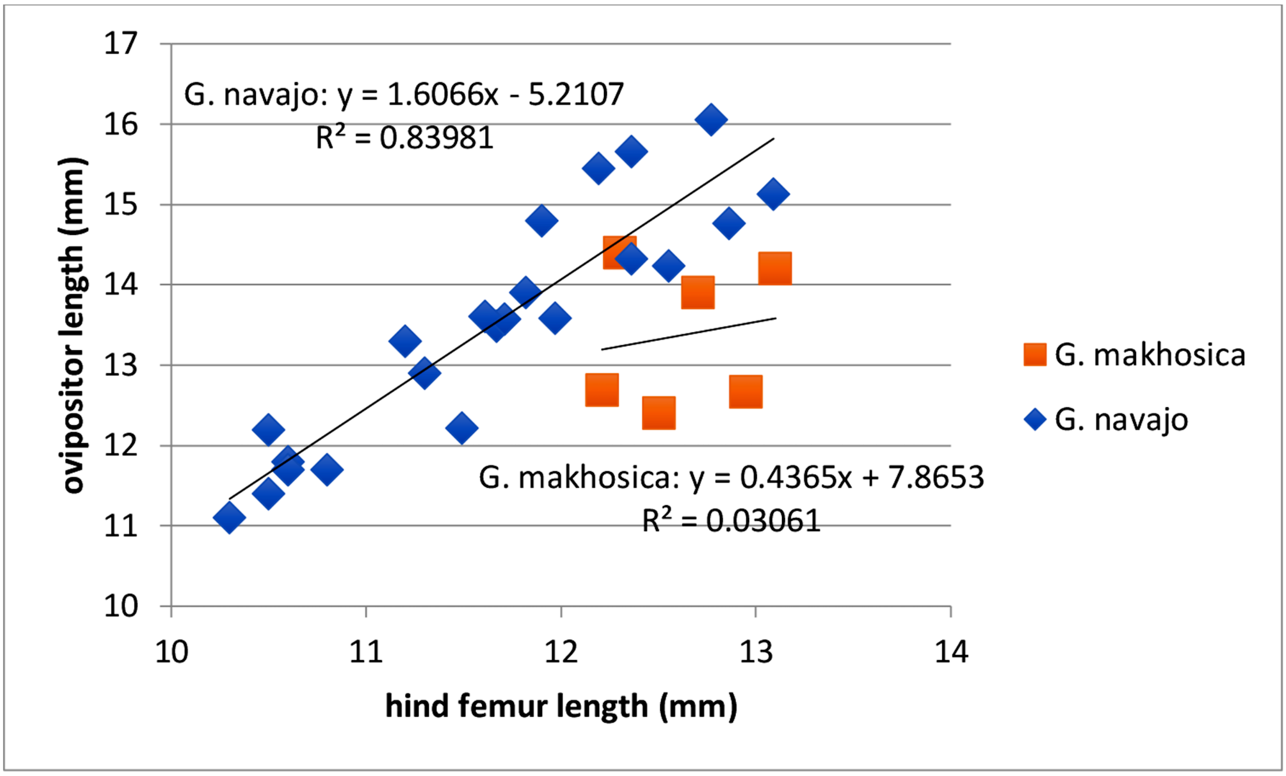

FIGURE 256. Regression hind femur length vs. ovipositor length in *G. makhosica* vs. *G. navajo*.

FIGURE 257. Holotype male *G. makhosica*. Female also from type locality (S09-89).

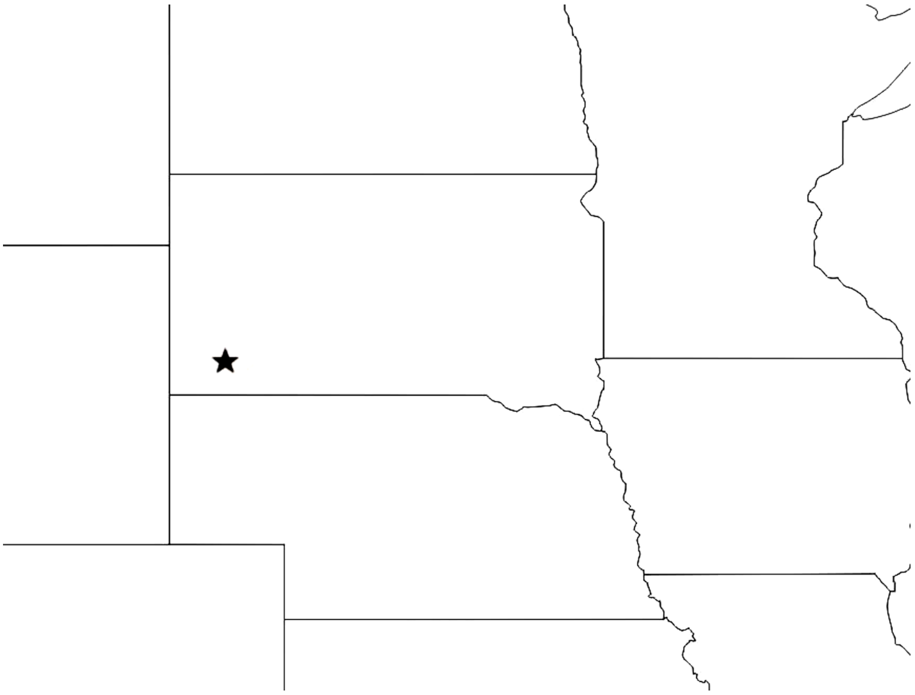

FIGURE 258. Known distribution of *G. makhosica*.

Paratypes. (Total: 12♂ 6♀). **South Dakota.** Type locality, 29-viii-1989 (S89-75) 4♂ 1♀; 22-vi-1993 (S93-53) 4♂ 3♀; 30-vii-1997 (S97-90) 2♂; 3-vii-2009 (S09-89) 2♂ 2♀.

Derivation of name. "makhosica*"* is Lakota for "badlands" in reference to the cricket's preferred habitat within Badlands National Park, an area inhabited by the Lakota people, and part of a confederation of seven related Sioux tribes.

Geographic range. (Fig. 258). Known only from Badlands National Park, South Dakota, where males sing from holes and crevices in clay badlands.

Habitat. Males sing from large cracks up to 10m above ground level on the face of badland clay cliffs and escarpments. Heard throughout Park in similar environments. Main canyon at Cedar Pass area with grasses, *Atriplex,* and *Sarcobatus.*

Life cycle and seasonal occurrence. One generation/year. Egg diapause not checked but probably absent since adults singing by late June, 1993. Adults known from 22-vi until 29-viii. One late instar male at S89-75, on 29-viii-1989.

Variation. **Hind femur:** vary in color from tan-orange to black.

DNA. Multilocus G1340 (S09-89). Sister species (Gray *et al.* 2019) are widespread *G. saxatilis,* Utah *G. leei,* and Utah and Arizona *G. navajo.*

Discussion. Easy to approach. While *G. makhosica* occurs microsympatrically at the type locality with *G. personatus* (also in clay badlands) and *G. veletis* (in adjacent grassy areas), the latter two species are never found singing much above the canyon floor.

G. makhosica is found no closer than 850 km to the nearest population of *G. navajo* in Utah, and we know of no medium to long cerci, slow chirping similar cricket species, or population, between them. Thus, given morphological and habitat differences discussed above, it seems appropriate to treat them as separate species despite their similar multilocus DNA profiles.

Gryllus navajo Weissman & Gray, n. sp.

Painted Desert Field Cricket
Figs 236–238, 252–256, 259–262, Table 1

'G. #39' in DBW notebooks.

Distribution. Southeastern Utah and northern Arizona.

Recognition characters and song. A slender, medium sized cricket always with short hind wings, frequently with both reddish tegmina and entire hind femur (Fig. 260), very long antennae in some populations (e.g. S07-56) reaching past tip of abdomen in situ. Cerci always longer than hind femur and in certain populations, usually longer than ovipositor tip in situ. *Song* (Fig. 259, R07-61) with 4–5 p/c (range 3–6), 75–180 c/m, PR 16–25. One of morphologically similar, never sympatric western US *Gryllus* spp. including *G. makhosica, G. saxatilis*, and *G. leei*. Distinguished from DNA similar but allopatric sister species *G. makhosica* from South Dakota by the following (and see Discussion, and comparative regressions, under *G. makhosica*, p. 251): general body color, especially hind femurs, more reddish in *G. navajo* vs. dark in *G. makhosica,* pronotum shinier in *G. navajo*; *G. navajo* lives in sandstone badlands vs. clay badlands for *G. makhosica*. Chirps in *G. makhosica* average 3–4 p/c vs. 4–5 in *G. navajo.* Elsewhere, under *G. makhosica*, we make several physical comparisons, employing regression analysis, between file teeth number, length of file, teeth/mm, tegmina length, hind femur length, and ovipositor length. While there is overlap in all of these metrics for these two species, their nearest populations are separated by some 850 km. Distinguished from sister species *G. saxatilis* whose cerci almost never longer than ovipositor and rarely (except at Checkerboard Mesa, Zion National Park) in open sandstone habitats and usually associated with rocks. Distinguished from Utah sister species *G. leei* which inhabits lava flows, has a shorter ovipositor and is separated by the Pahvant Mt. Range and Sevier Plateau of central Utah from *G. navajo*. Distinguished (Table 1, p. 18) from *G. longicercus* by *G. navajo* having fewer teeth in file, shorter cerci length, higher pulse rate, and different DNA (Gray *et al.* 2019).

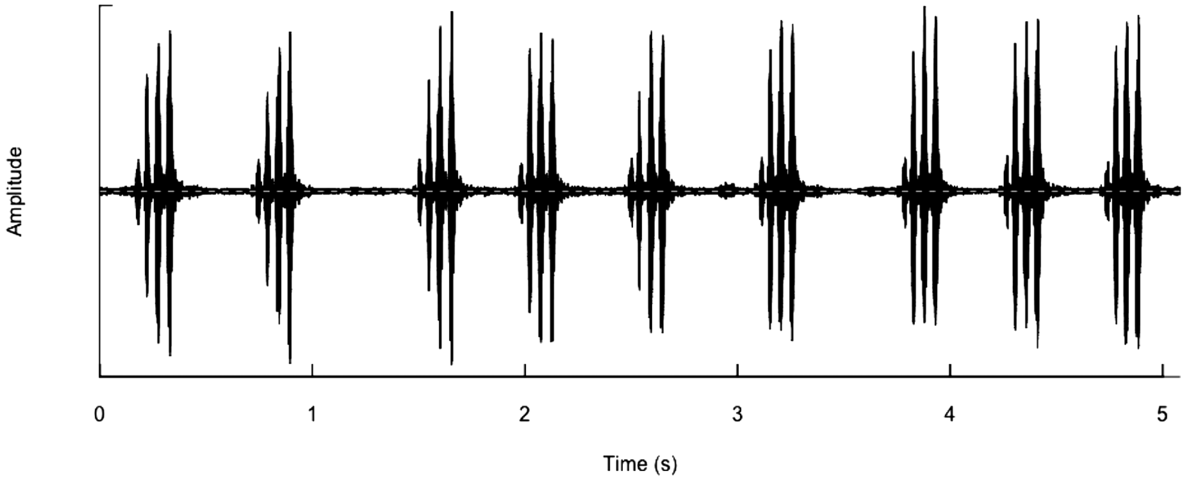

FIGURE 259. Calling song (R07-61) of *G. navajo* from Coconino Co., AZ (S07-56), recorded at 25°C.

Holotype. Male (Fig. 260). USA, **Utah.** *Emery Co.,* 6.5 m W of Hwy 24 and 1.3 m W turnoff for Goblin Valley State Park, 5400’, S92-108, R92-180, BL 17.67, HF 10.3, LC 10.2. Right tegmen removed, 154 teeth, FL 3.4, TL 10.2, TW 4.3. Type deposited in CAS, Entomology Type #19268.

Paratypes. (Total: 43♂ 35♀). **Arizona.** *Coconino Co.,* 49 m E Flagstaff on Hwy 99 ~6.85 road m NW I40, mile post 59.5, 4838’, 35° 08.548’ -110° 53.535’, 8-viii-1991, (S91-89) 8♂ 11♀; 12-vi-1996 (S96-64) 2♂ 1♀; 14-vi-2007 (S07-56) 13♂ 13♀. Moenkopi Dune area on Hwy 264 3.1 m SE Tuba City, 4680’, 6-viii-1991 (S91-82) 7♂ 1♀; 7-ix-1999 (S99-111) 1♂. **Utah.** Type locality, 1-viii-1992 (S92-108) 7♂; 11-vi-1996 (S96-58) 3♂ 9♀. *Wayne Co.,* Hwy 24 3 m NE Hanksville, 11-vi-1996 (S96-60) 2♂.

Other collections, not counted as paratypes. **Utah.** *Emery Co.,* Goblin Valley State Park, campground, 5000’, 18-v-2016, 10♂ 19♀. Black Dragon Canyon, 4350’, 24-v-2017, 32♂ 8♀. *San Juan Co.*, Oljato-Monument Valley, Douglas Mesa Rd. (County Road 419) 6 m N Utah—Arizona border, 5575’, 26-v-2017, 10♂ 3♀.

Derivation of name. Named for the Native Americans (Diné) of the Navajo Nation who inhabit this area.

Geographic range. (Fig. 261) Southeastern Utah and northern Arizona, associated with Painted Desert red sandstone outcrops and escarpments and occasionally rocky outcrop areas, as at type locality.

Habitat. Singing from cracks in sandstone cliffs at Moenkopi Dunes (S91-82), near Hanksville (S96-60), and at 79 km E Flagstaff (S07-56) and occasionally in valley floors. Many more males walking around at Goblin Valley (S96-58) and 79 km E Flagstaff (S07-56) than singing: at S07-56, for every male heard singing, we collected 5 males (and many females) at a long oatmeal trail laid in the open, vegetated, sandy valley floor away from the sandstone escarpments. At Goblin Valley, it appears that the crickets live within cracks in the mudstone/sandstone escarpments during the day, and then descend to forage on the valley floor at night; adult males call both from cracks in the escarpments and from the valley floor (often from under the meager plant cover), whereas females and nymphs more likely encountered on the valley floor (DAG observations 14-vi-1999, 9-viii-2005, 18-v-2016, 25-v-2017, 20-22-v-2018).

FIGURE 260. Holotype male of *G. navajo.*

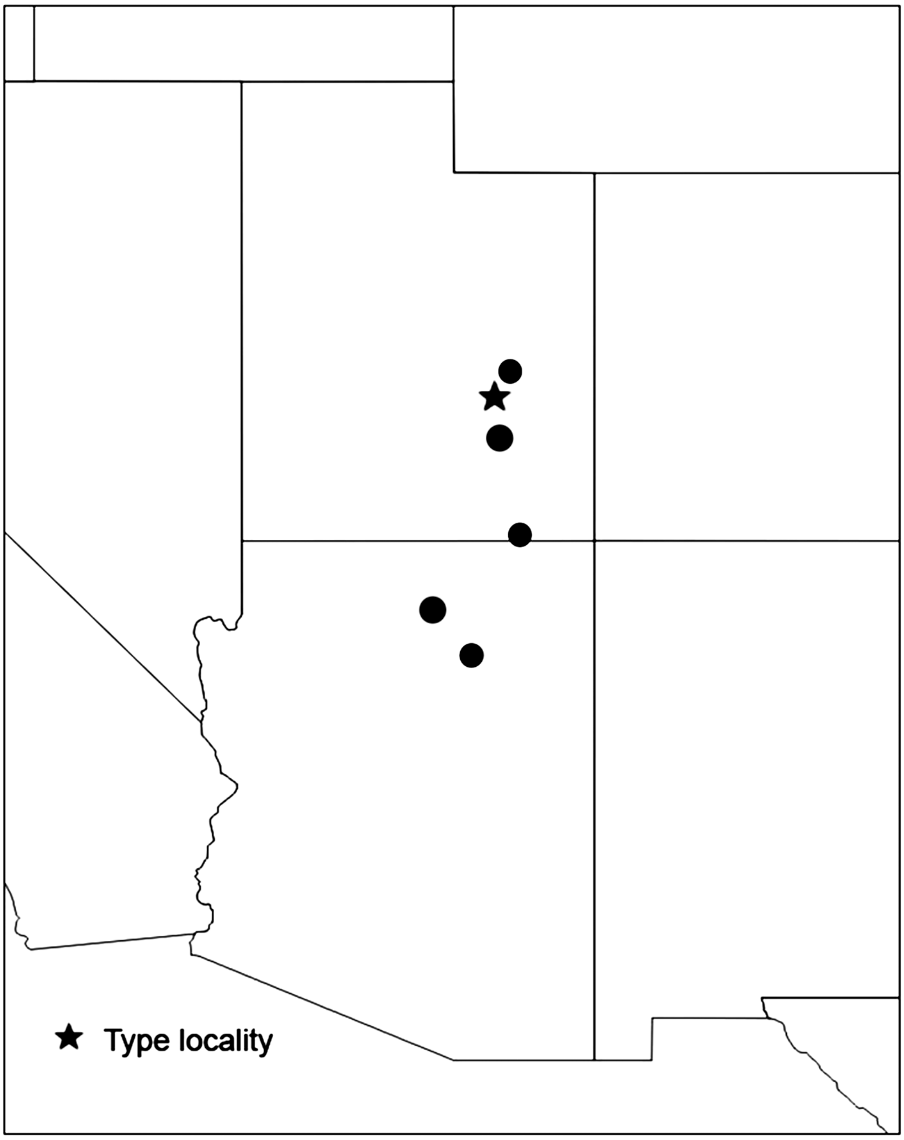

FIGURE 261. Known distribution of *G. navajo.*

Life cycle and seasonal occurrence. No egg diapause Moenkopi Dunes (S91-82); Goblin Valley (May collections, 2016-2018); capable of multiple generations per year under lab conditions, but situation in the field less clear. Adults known from mid-May through early September with nymphs also collected during June through August visits. For instance, collections in May at Goblin Valley were mostly of adults: (18-v-2016) 9 adult males, 19 adult females, 1 nymph male; (26-v-2017) 54 adult males, 36 adult females, 1 nymph female and 1 nymph male, whereas collections in August (1-viii-1992 and 9-viii-2005), only many early to mid-instars seen. It is not clear to us if these August nymphs represent what will become a second generation, or if those nymphs will be the ones that overwinter until spring. Given that the average high/low temperature in September and October is 30.6/10.0°C and 22.2/2.8°C, respectively (https://weather.com/weather/monthly/l/Goblin+Valley+State+Park+UT+USUT0091:1:US), we suspect that these August nymphs overwinter rather than become an adult second generation.

Variation. **Color:** Individuals vary from solid red (Fig. 262, Moenkopi Dunes, S91-82) to almost solid black except for the hind femurs, which are usually reddish. Most females with tegminal bars. **Head:** varies from red to black, many times with a black face and a reddish top of head. **Cerci length:** 17 of 24 females from the 3 collection dates at 79 km E Flagstaff have their cerci longer than the ovipositor tip in situ. In all other collections, the female cerci in situ are slightly shorter than the ovipositor tip.

DNA. Multilocus 2016-040 (type locality, Goblin Valley State Park, campground) and G1067 (79 km E Flagstaff, S07-56) sister species (Gray *et al.* 2019) with widespread *G. saxatilis,* Utah lava *G. leei,* and South Dakota Badlands *G. makhosica.*

FIGURE 262. Color variation in *G. navajo.* Viewing left to right: holotype male from Goblin Valley, UT (S92-108); male from Coconino Co., AZ (S07-56); female (with spermatophore) from Coconino Co., AZ (S91-89); and red male from Moenkopi Dunes, AZ (S91-82).

Discussion. The question arises if *G. navajo* could just be an edaphic color form of some *Gryllus,* especially *G. saxatilis* or *G. makhosica,* that is darker when living away from red sandstone? We think not, especially when one considers the unique behavior displayed by this species at the type locality and E Flagstaff (S07-56)—their high density and the tendency of both sexes to walk around away from cover is unusual in *Gryllus* and certainly unknown for any similar western taxon discussed under "Recognition characters" (but note *G. lightfooti* does this in some dense populations, e.g. Maricopa Co., AZ, 33.97995, -111.87249, 8-viii-2016). Lab cultures continue to produce variably reddish individuals and do not simply result in dark *G. saxatilis*-like coloration. Genetic structure of cricket populations in and around the Colorado Plateau is being examined by E. Collosi *et al.* using RAD-seq SNP data, and should help clarify the situation with respect to *G. navajo* and *G. saxatilis*.

G. navajo were poor singers in the field E Flagstaff (S07-56), and we have found that in some other *Gryllus* species, when at high densities, males do not need to sing much to attract females since both sexes are mobile and would easily find each other with random walkabouts (and maybe assisted by their long antennae?). Once back in the laboratory, these males sang well. In contrast, male *G. navajo* singing well in the field at Moenkopi Dunes (S91-82) and Goblin Valley (S96-58), sang poorly once in the laboratory: of 7 males collected 6-viii-1991 at Moenkopi, the first male was recorded 31-viii; for the 3 Goblin Valley males collected 11-vi-1996, the first male was recorded 5-vii. On the other hand, adult males collected in May, 2017, were relatively easy to record (N=112 males from several localities). Such variable, taciturn behavior may also reflect past, high tachinid parasitism, although despite our multiple collecting trips, we have never collected a single tachinid-parasitized *G. navajo*!

Lots of red mites on both sexes E Flagstaff (S91-89 and S07-56) on two visits.

Species/topics that need further investigations

1. How many generations a year do *Gryllus* living in the Southwestern US have? What is the influence of rainfall on this potential generation number and for how long are eggs viable after being laid in dry substrate?

2. How precise is female song recognition/preference in *Gryllus* species with very variable calling songs, e.g. *G. staccato* (with variable pulses/chirp) and *G. cohni* (with variable pulses/trill)? If females are relatively indiscriminate given the within-species variation in male song, does that increase the likelihood of mistaken female phonotaxis to non-conspecific song?

3. Do second generation individuals of *G. veletis*, *G. veletisoides*, *G. fultoni*, and *G. firmus* contribute to populations in subsequent years?

4. For sister species *G. armatus* and *G. integer*, what is happening, or has happened, between them in the Four Corners area where individuals have *G. integer* DNA but sing like *G. armatus*?

5. For *G. cohni*, what explains the biogeographically disjunct populations in the Cape area of Baja California Sur versus those in southern Arizona and on the Mexico mainland? Are they really all conspecific as treated here?

6. In the Pennsylvanicus Group: Are the *G. firmus* populations in Florida and Texas really conspecific as treated here? What is the evolutionary history of Texas *G. firmus* and *G. pennsylvanicus* in the western US? To what extent, and how, is reproductive isolation between them maintained? How does this compare to the results of similar studies from the eastern United States?

7. For *G. montis*, what is the evolutionary history of the 4 genetic clades? How many species are involved? To what extent have the Southwestern species of montane (*G. montis*) and sub-montane (*G. veletis, G. lightfooti*, *G. longicercus*) hybridized? Under some reconstructions, Clades 1-3 could be a monophyletic group of three lineages, but Clade 4 is always distinct, so convergent and/or parallel evolution seems likely in the Group. Why? To what extent does this reflect selection versus simply shared history?

8. Are *G. rubens* and *G. texensis* hybridizing in the Tulsa, Oklahoma, area where the two taxa separate poorly by pulse rate?

9. How has evolutionary diversification operated in the Saxatilis Group? Are the narrower endemic species (*G. leei*, *G. makhosica*, *G. navajo*) derived from a widespread proto-*saxatilis* ancestor? To what extent has gene flow between *G. saxatilis* and each of the narrower endemic species shaped their genomes and impacted adaptation to particular soils/substrates? What are the evolutionary histories of the genetically similar ‘G. mohave’, ‘G. mormoni’, and ‘G. tulare’ lineages, and should they be considered species?

10. How has evolutionary diversification operated in the Veletis Group? Are *G. planeta* and/or Clade 1 of *G. montis* derived from the more widespread *G. veletis*? To what extent is reproductive isolation maintained, and how, between *G. planeta* and *G. veletis*, when sympatric? What is the evolutionary history of the two *G. veletis* ITS2 groupings—those individuals in NV, NM, TX, and OK vs. those from IN, IL, and UT?

11. How does adaptation to living on lava progress? Are there commonalities between *G. leei* and *G. vulcanus* despite them not being closely related? For *G. vulcanus*, what is the relationship of the two known populations given their separation of ~210 km with no suitable intervening habitat?

We hope that this work, as well as the multilocus phylogeny companion paper (Gray *et al.* 2019) will facilitate many such further investigations.

Conservation Considerations

While several species of US *Gryllus* have limited distributions, all, fortunately, occur in areas that are already formally protected (*G. chisosensis, G. cayensis, G. vulcanus, G. sotol, G. makhosica*) or de facto protected by a nearby astronomical facility (*G. planeta)* or the inability to build on lava flows (*G. leei)*.

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APPENDIX A. GenBank accession numbers for representative samples.

Species	ID	16S	ITS2
Gryllus alexanderi	G450	MK446423	
Gryllus alexanderi	G451	MK446424	MK441843
Gryllus armatus	2003-214	MK446428	
Gryllus armatus	G1918	MK446425	
Gryllus armatus	G2172	MK446427	
Gryllus armatus	G3439		MK441844
Gryllus armatus	G3440		MK441845
Gryllus armatus	G3441		MK441846
Gryllus armatus	G649	MK446426	
Gryllus assimilis *	G1901	MK446430	MK441847
Gryllus assimilis	G3367		MK441849
Gryllus assimilis	G3373	MK446429	MK441848
Gryllus assimilis	WG1	MK446431	
Gryllus bimaculatus	G2151	MK446421	
Gryllus bimaculatus	G2239	MK446422	
Gryllus bimaculatus	WG23	MK446420	MK441842
Gryllus brevicaudus	G1310	MK446436	
Gryllus brevicaudus	G1324	MK446435	
Gryllus brevicaudus	G3354		MK441852
Gryllus brevicaudus	G3393	MK446434	MK441851
Gryllus brevicaudus	G4	MK446432	
Gryllus brevicaudus	G5		MK441850
Gryllus brevicaudus	WG9	MK446433	
Gryllus bryanti	GBM01	MK446437	MK441853
Gryllus bryanti	GBM03	MK446438	MK441854
Gryllus bryanti	GBM05	MK446439	MK441855
Gryllus bryanti	GBM09	MK446440	
Gryllus campestris	2009-018	MK446419	MK441841
Gryllus cayensis	TJW1	MK446448	
Gryllus cayensis	TJW11	MK446447	
Gryllus cayensis	TJW12	MK446449	
Gryllus cayensis	TJW13	MK446450	
Gryllus cayensis	TJW3	MK446446	
Gryllus cayensis	TJW5	MK446441	
Gryllus cayensis	TJW6	MK446442	
Gryllus cayensis	TJW7	MK446443	
Gryllus cayensis	TJW8	MK446445	
Gryllus cayensis	TJW9	MK446444	
Gryllus chisosensis	G1192	MK446451	MK441857
Gryllus chisosensis	G3399	MK446452	MK441858
Gryllus chisosensis	G3400	MK446453	MK441856
Gryllus cohni	2003-294	MK446454	
Gryllus cohni	2006-248	MK446455	
Gryllus cohni	G101	MK446458	
Gryllus cohni	G102	MK446459	MK441859
Gryllus cohni	G1504	MK446456	
Gryllus cohni	G1505	MK446457	

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APPENDIX A. (Continued)

Species	ID	16S	ITS2
Gryllus cohni	G3217	MK446460	MK441861
Gryllus cohni	G3248	MK446461	MK441860
Gryllus firmus	G1073		MK441870
Gryllus firmus	G1074	MK446605	MK441873
Gryllus firmus	G1186	MK446606	MK441871
Gryllus firmus	G1915	MK446602	MK441872
Gryllus firmus	G1916	MK446607	
Gryllus firmus	G1917	MK446603	
Gryllus firmus	G1920	MK446575	MK441865
Gryllus firmus	G1922	MK446600	MK441866
Gryllus firmus	G2029	MK446604	MK441867
Gryllus firmus	G2034		MK441868
Gryllus firmus	G2136	MK446601	
Gryllus firmus	G2165		MK441869
Gryllus firmus	G60	MK446572	MK441862
Gryllus firmus	G61	MK446573	MK441863
Gryllus firmus	G62	MK446574	MK441864
Gryllus fultoni	G1138	MK446466	
Gryllus fultoni	G1704	MK446467	
Gryllus fultoni	G1712	MK446464	
Gryllus fultoni	G32	MK446462	MK441874
Gryllus fultoni	G34	MK446463	MK441875
Gryllus fultoni	G35	MK446465	MK441876
Gryllus integer	2003-041	MK446476	
Gryllus integer	2003-042	MK446477	
Gryllus integer	G1441	MK446472	
Gryllus integer	G2113	MK446470	
Gryllus integer	G2115	MK446473	
Gryllus integer	G2138	MK446474	
Gryllus integer	G2431	MK446475	
Gryllus integer	G245	MK446478	
Gryllus integer	G246	MK446479	
Gryllus integer	G58	MK446471	
Gryllus integer	G623		MK441877
Gryllus integer	G624	MK446468	MK441878
Gryllus integer	G625	MK446469	
Gryllus leei	G146	MK446480	MK441879
Gryllus leei	G147	MK446481	
Gryllus leei	G3470		MK441880
Gryllus leei	G3475		MK441881
Gryllus leei	G3487		MK441882
Gryllus lightfooti	G1179	MK446525	
Gryllus lightfooti	G3061	MK446528	
Gryllus lightfooti	G3435	MK446526	MK441883
Gryllus lightfooti	G3436	MK446485	
Gryllus lightfooti	G3438		MK441884

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APPENDIX A. (Continued)

Species	ID	16S	ITS2
Gryllus lightfooti	G3445	MK446482	
Gryllus lightfooti	G3448	MK446486	
Gryllus lightfooti	G3450	MK446527	MK441885
Gryllus lightfooti	G3451	MK446524	
Gryllus lineaticeps *	G1303		MK441888
Gryllus lineaticeps	G1315		MK441887
Gryllus lineaticeps	G2028	MK446534	
Gryllus lineaticeps	G273		MK441886
Gryllus lineaticeps	G371	MK446533	
Gryllus locorojo *	G2217		MK441889
Gryllus longicercus	G2175	MK446537	MK441892
Gryllus longicercus	G2176	MK446535	MK441893
Gryllus longicercus	G2177	MK446536	
Gryllus longicercus	G2182	MK446538	
Gryllus longicercus	G2183	MK446539	
Gryllus longicercus	G3390		MK441890
Gryllus longicercus	G3392		MK441891
Gryllus makhosica	G1340	MK446488	MK441894
Gryllus makhosica	G1363	MK446487	MK441895
Gryllus montis	2005-004	MK446564	
Gryllus montis	2012-222	MK446562	
Gryllus montis	G1046	MK446567	MK441903
Gryllus montis	G1047	MK446566	MK441904
Gryllus montis	G1048		MK441905
Gryllus montis	G1353	MK446540	MK441901
Gryllus montis	G2273	MK446565	MK441902
Gryllus montis	G2462	MK446547	MK441896
Gryllus montis	G2464	MK446560	MK441897
Gryllus montis	G2466	MK446548	MK441898
Gryllus montis	G2472		MK441900
Gryllus montis	G2475	MK446561	MK441899
Gryllus montis	G2499	MK446563	
Gryllus multipulsator *	G1414	MK446568	
Gryllus multipulsator	G577		MK441906
Gryllus multipulsator	G248	JX269054.1	
Gryllus multipulsator	G251	JX269055.1	
Gryllus navajo	2005-202	MK446569	
Gryllus navajo	2005-204	MK446570	
Gryllus navajo	2016-050	MK446571	MK441909
Gryllus navajo	G1124	MK446489	MK441907
Gryllus navajo	G1198	MK446490	MK441908
Gryllus navajo	G1215	MK446491	
Gryllus ovisopis	2012-012	MK446609	
Gryllus ovisopis	2012-013	MK446610	
Gryllus ovisopis	WG5	MK446608	
Gryllus pennsylvanicus	G1239	MK446579	

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APPENDIX A. (Continued)

Species	ID	16S	ITS2
Gryllus pennsylvanicus	G1242	MK446580	
Gryllus pennsylvanicus	G1275	MK446597	
Gryllus pennsylvanicus	G138	MK446598	
Gryllus pennsylvanicus	G139	MK446599	
Gryllus pennsylvanicus	G1429	MK446590	
Gryllus pennsylvanicus	G1435	MK446591	
Gryllus pennsylvanicus	G2208	MK446581	MK441912
Gryllus pennsylvanicus	G2209	MK446582	
Gryllus pennsylvanicus	G266	MK446588	
Gryllus pennsylvanicus	G267	MK446589	
Gryllus pennsylvanicus	G351	MK446592	
Gryllus pennsylvanicus	G365	MK446593	
Gryllus pennsylvanicus	G368	MK446594	
Gryllus pennsylvanicus	G40	MK446596	
Gryllus pennsylvanicus	G420	MK446576	
Gryllus pennsylvanicus	G492	MK446577	
Gryllus pennsylvanicus	G493	MK446578	
Gryllus pennsylvanicus	G643	MK446595	
Gryllus pennsylvanicus	G645	MK446583	
Gryllus pennsylvanicus	G709	MK446584	MK441910
Gryllus pennsylvanicus	G710	MK446585	MK441911
Gryllus pennsylvanicus	UTM1	MK446586	
Gryllus pennsylvanicus	UTM3	MK446587	
Gryllus personatus *	G1014		MK441913
Gryllus personatus	G1360		MK441914
Gryllus personatus	G3371		MK441915
Gryllus planeta	G3088	MK446611	MK441916
Gryllus planeta	G3094	MK446612	MK441917
Gryllus planeta	G3114	MK446549	MK441918
Gryllus regularis	G1098	MK446613	
Gryllus regularis	G1100	MK446614	
Gryllus regularis	G1101	MK446615	MK441919
Gryllus regularis	G3154		MK441920
Gryllus regularis	G3280		MK441921
Gryllus rubens	F122		MK441922
Gryllus rubens	G144	MK446618	
Gryllus rubens	G2019	MK446617	
Gryllus rubens	G235	MK446616	
Gryllus saxatilis	2003-004	MK446498	
Gryllus saxatilis	2012-076	MK446501	
Gryllus saxatilis	2014-007	MK446497	
Gryllus saxatilis	G1264	MK446503	
Gryllus saxatilis	G1295	MK446623	
Gryllus saxatilis	G1299		MK441934
Gryllus saxatilis	G1300	MK446622	
Gryllus saxatilis	G1301	MK446499	MK441929

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APPENDIX A. (Continued)

Species	ID	16S	ITS2
Gryllus saxatilis	G1306	MK446500	
Gryllus saxatilis	G1328	MK446492	MK441923
Gryllus saxatilis	G1430	MK446504	
Gryllus saxatilis	G1432	MK446502	
Gryllus saxatilis	G2105	MK446493	
Gryllus saxatilis	G2106	MK446494	
Gryllus saxatilis	G2705	MK446495	MK441926
Gryllus saxatilis	G2706		MK441927
Gryllus saxatilis	G2707	MK446496	
Gryllus saxatilis	G2717	MK446627	
Gryllus saxatilis	G2718	MK446628	MK441937
Gryllus saxatilis	G2798	MK446625	
Gryllus saxatilis	G3176	MK446626	MK441936
Gryllus saxatilis	G3180		MK441935
Gryllus saxatilis	G3184	MK446484	MK441924
Gryllus saxatilis	G3190	MK446483	MK441925
Gryllus saxatilis	G3426	MK446619	
Gryllus saxatilis	G3427	MK446620	
Gryllus saxatilis	G3429		MK441928
Gryllus saxatilis	G3431		MK441931
Gryllus saxatilis	G3434		MK441930
Gryllus saxatilis	G3449	MK446621	
Gryllus saxatilis	G452	MK446624	MK441932
Gryllus saxatilis	G453		MK441933
Gryllus sotol	G3493		MN136862
Gryllus sotol	G3505		MK441938
Gryllus sotol	G3508		MK441939
Gryllus sotol	G3509		MK441941
Gryllus sotol	G3511		MK441940
Gryllus staccato *	G1410	MN136664	
Gryllus staccato	G1397		MK441942
Gryllus staccato	G1407		MK441943
Gryllus texensis	d102	MK446518	MK441944
Gryllus texensis	d1042	MK446511	MK441945
Gryllus texensis	d1100	MK446508	
Gryllus texensis	d57	MK446513	
Gryllus texensis	d679	MK446512	
Gryllus texensis	d686	MK446507	
Gryllus texensis	G1000	MK446517	
Gryllus texensis	G1001	MK446520	
Gryllus texensis	G1002	MK446521	
Gryllus texensis	G1004	MK446523	
Gryllus texensis	G1333	MK446519	
Gryllus texensis	G1343	MK446516	
Gryllus texensis	G1344	MK446515	
Gryllus texensis	G1347	MK446514	

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APPENDIX A. (Continued)

Species	ID	16S	ITS2
Gryllus texensis	G1921	MK446522	
Gryllus texensis	G2432	MK446509	
Gryllus texensis	G2433	MK446510	
Gryllus texensis	G2434	MK446505	
Gryllus texensis	G2435	MK446506	
Gryllus texensis	G3404		MK441946
Gryllus thinos	G1163		MK441948
Gryllus thinos	G2016	MK446633	
Gryllus thinos	G2018	MK446632	
Gryllus thinos	G2022		MK441947
Gryllus thinos	G2022	MK446634	
Gryllus thinos	G2629	MK446629	
Gryllus thinos	G2636	MK446630	
Gryllus thinos	G2638	MK446631	
Gryllus transpecos	G1175	MN136663	
Gryllus transpecos	G3056	MK446529	
Gryllus transpecos	G3059	MK446639	MK441952
Gryllus transpecos	G3060	MK446638	MK441955
Gryllus transpecos	G3062	MK446531	MK441949
Gryllus transpecos	G3065	MK446640	MK441953
Gryllus transpecos	G3066	MK446532	
Gryllus transpecos	G3067	MK446530	MK441950
Gryllus transpecos	G3069	MK446641	MK441954
Gryllus transpecos	G3355	MK446635	
Gryllus transpecos	G3370	MK446636	
Gryllus transpecos	G3380	MK446637	MK441951
Gryllus veintinueve	2015-055		MK441956
Gryllus veintinueve	G1139		MK441959
Gryllus veintinueve	G1211		MK441958
Gryllus veintinueve	G1330	MK446642	
Gryllus veintinueve	G1331	MK446643	
Gryllus veintinueve	G1451	MK446644	MK441957
Gryllus veintinueve	G1453	MK446645	
Gryllus veletis	2003-029	MK446661	
Gryllus veletis	2003-030	MK446662	
Gryllus veletis	2003-178	MK446553	
Gryllus veletis	G1006	MK446558	
Gryllus veletis	G1015	MK446559	
Gryllus veletis	G1016	MK446555	
Gryllus veletis	G1017	MK446556	
Gryllus veletis	G1019	MK446557	
Gryllus veletis	G1039	MK446551	
Gryllus veletis	G1276	MK446653	
Gryllus veletis	G1335	MK446659	
Gryllus veletis	G1337	MK446660	
Gryllus veletis	G1345	MK446550	

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APPENDIX A. (Continued)

Species	ID	16S	ITS2
Gryllus veletis	G1346	MK446658	
Gryllus veletis	G156	MK446663	
Gryllus veletis	G1567	MK446552	
Gryllus veletis	G157	MK446554	
Gryllus veletis	G1713	MK446646	
Gryllus veletis	G1714	MK446647	
Gryllus veletis	G1715	MK446648	
Gryllus veletis	G2639	MK446651	
Gryllus veletis	G2652	MK446652	
Gryllus veletis	G2895		MK441971
Gryllus veletis	G2896		MK441972
Gryllus veletis	G2899		MK441966
Gryllus veletis	G29	MK446649	
Gryllus veletis	G2912	MK446655	
Gryllus veletis	G2919	MK446656	
Gryllus veletis	G2927		MK441963
Gryllus veletis	G2936		MK441969
Gryllus veletis	G2944	MK446657	
Gryllus veletis	G2963		MK441967
Gryllus veletis	G2968		MK441970
Gryllus veletis	G2983		MK441968
Gryllus veletis	G30	MK446654	MK441965
Gryllus veletis	G3131		MK441960
Gryllus veletis	G3134		MK441961
Gryllus veletis	G3304		MK441962
Gryllus veletis	G39	MK446650	MK441964
Gryllus veletisoides	G566	MN136662	MN136861
Gryllus veletisoides	2005-058	MK446675	
Gryllus veletisoides	G1219	MK446671	
Gryllus veletisoides	G1876	MK446666	
Gryllus veletisoides	G2252	MK446676	
Gryllus veletisoides	G2504	MK446674	
Gryllus veletisoides	G292	MK446670	
Gryllus veletisoides	G3167		MK441973
Gryllus veletisoides	G494	MK446668	
Gryllus veletisoides	G538	MK446677	
Gryllus veletisoides	G539	MK446678	
Gryllus veletisoides	G540	MK446679	MK441975
Gryllus veletisoides	G541	MK446680	MK441974
Gryllus veletisoides	G565	MK446672	
Gryllus veletisoides	G568	MK446673	
Gryllus veletisoides	G581	MK446669	
Gryllus veletisoides	G586	MK446667	
Gryllus veletisoides	G601	MK446664	
Gryllus veletisoides	G602	MK446665	
Gryllus vernalis	G1739		MK441976

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APPENDIX A. (Continued)

Species	ID	16S	ITS2
Gryllus vernalis	G1740	MK446683	
Gryllus vernalis	G26	MK446681	
Gryllus vernalis	G27	MK446682	MK441979
Gryllus vernalis	G2754	MK446684	
Gryllus vernalis	G2755	MK446685	
Gryllus vernalis	G31	MK446686	MK441978
Gryllus vernalis	G33	MK446687	MK441977
Gryllus vernalis	G440	MK446688	
Gryllus vocalis	2007-172	MK446711	
Gryllus vocalis	2007-175	MK446708	
Gryllus vocalis	2016-043		MK441984
Gryllus vocalis	G1409	MK446695	
Gryllus vocalis	G1422	MK446691	
Gryllus vocalis	G1465	MK446699	
Gryllus vocalis	G1873	MK446701	
Gryllus vocalis	G204	MK446712	
Gryllus vocalis	G205	MK446702	
Gryllus vocalis	G206	MK446713	
Gryllus vocalis	G2244	MK446714	
Gryllus vocalis	G2265	MK446700	
Gryllus vocalis	G2477	MK446696	
Gryllus vocalis	G2479	MK446693	
Gryllus vocalis	G2481	MK446694	
Gryllus vocalis	G2543	MK446692	
Gryllus vocalis	G2596	MK446703	
Gryllus vocalis	G2735	MK446697	
Gryllus vocalis	G3219	MK446698	MK441982
Gryllus vocalis	G3335	MK446689	MK441980
Gryllus vocalis	G3337	MK446690	MK441981
Gryllus vocalis	G487		MK441983
Gryllus vocalis	G531	MK446704	
Gryllus vocalis	G532	MK446705	
Gryllus vocalis	G536	MK446706	
Gryllus vocalis	G563	MK446707	
Gryllus vocalis	WG10	MK446709	
Gryllus vocalis	WG12	MK446710	
Gryllus vulcanus	2016-025		MK441987
Gryllus vulcanus	G1030	MK446543	
Gryllus vulcanus	G1031	MK446544	
Gryllus vulcanus	G1032	MK446545	MK441985
Gryllus vulcanus	G1033	MK446717	MK441988
Gryllus vulcanus	G1034	MK446546	
Gryllus vulcanus	G1050	MK446715	MK441989
Gryllus vulcanus	G1146	MK446541	MK441986
Gryllus vulcanus	G1156	MK446542	
Gryllus vulcanus	G1196	MK446716	

* Additional samples are available on GenBank from Gray *et al*. 2016; Weissman *et al*. 2012; Weissman *et al*. 2009.