

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. cojni* and sister species *G. vocalis* specimens.

Discussion. Of the US species discussed in this paper, *G. cojni* 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. cojni* (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. cojni*.

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. cojni* 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. cojni* 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. cojni* 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 *cojni*) 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.

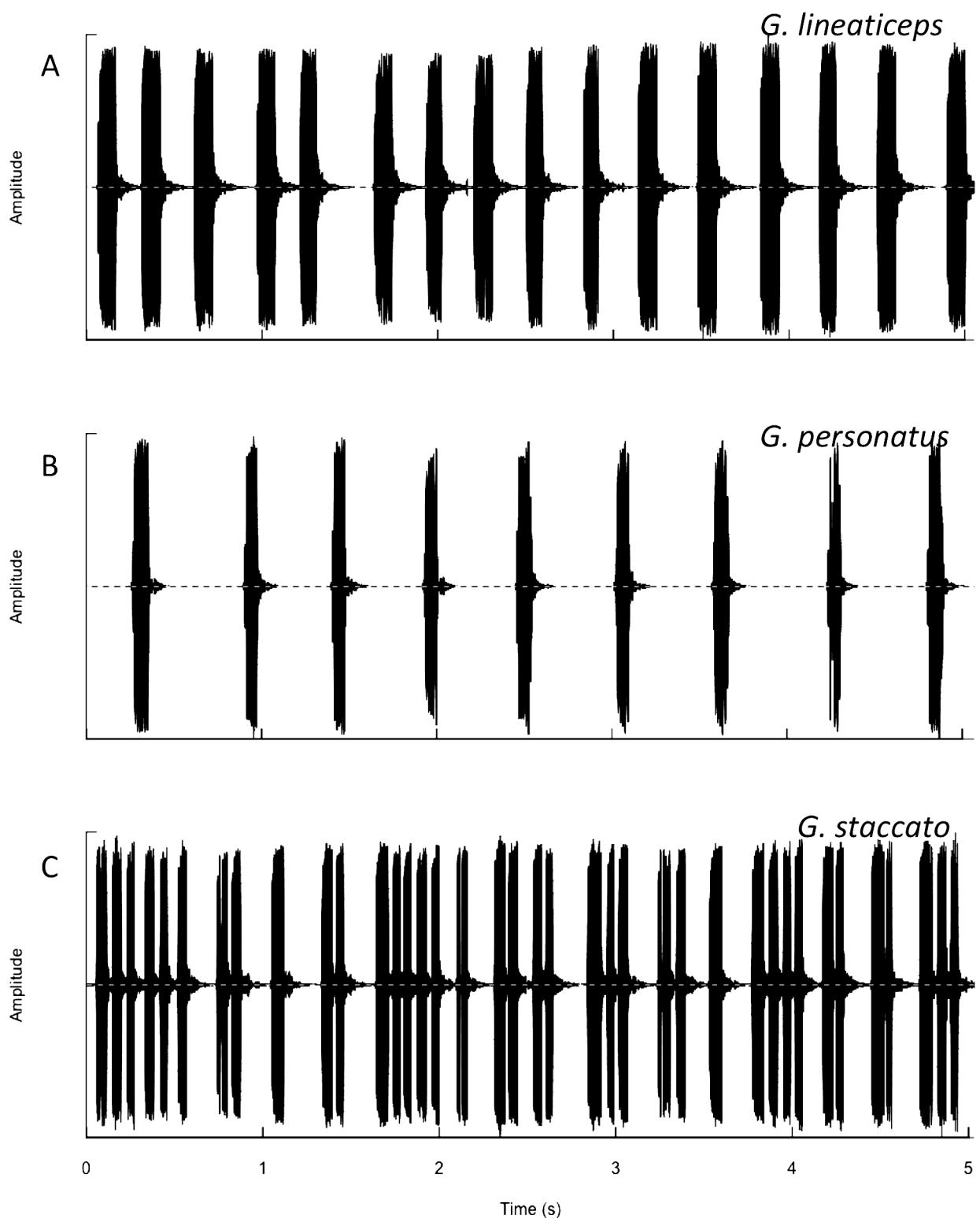


FIGURE 170. Five second waveforms of typical calling songs of (A) *G. lineaticeps*, (B) *G. personatus*, and (C) *G. staccato*. (A) *G. lineaticeps*: (R11-15) Mendocino Co., CA (S11-22), recorded at 24°C; (B) *G. personatus*: (R07-74) from Alpine, TX (S07-41), recorded at 25°C; (C) *G. staccato* (R15-291)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

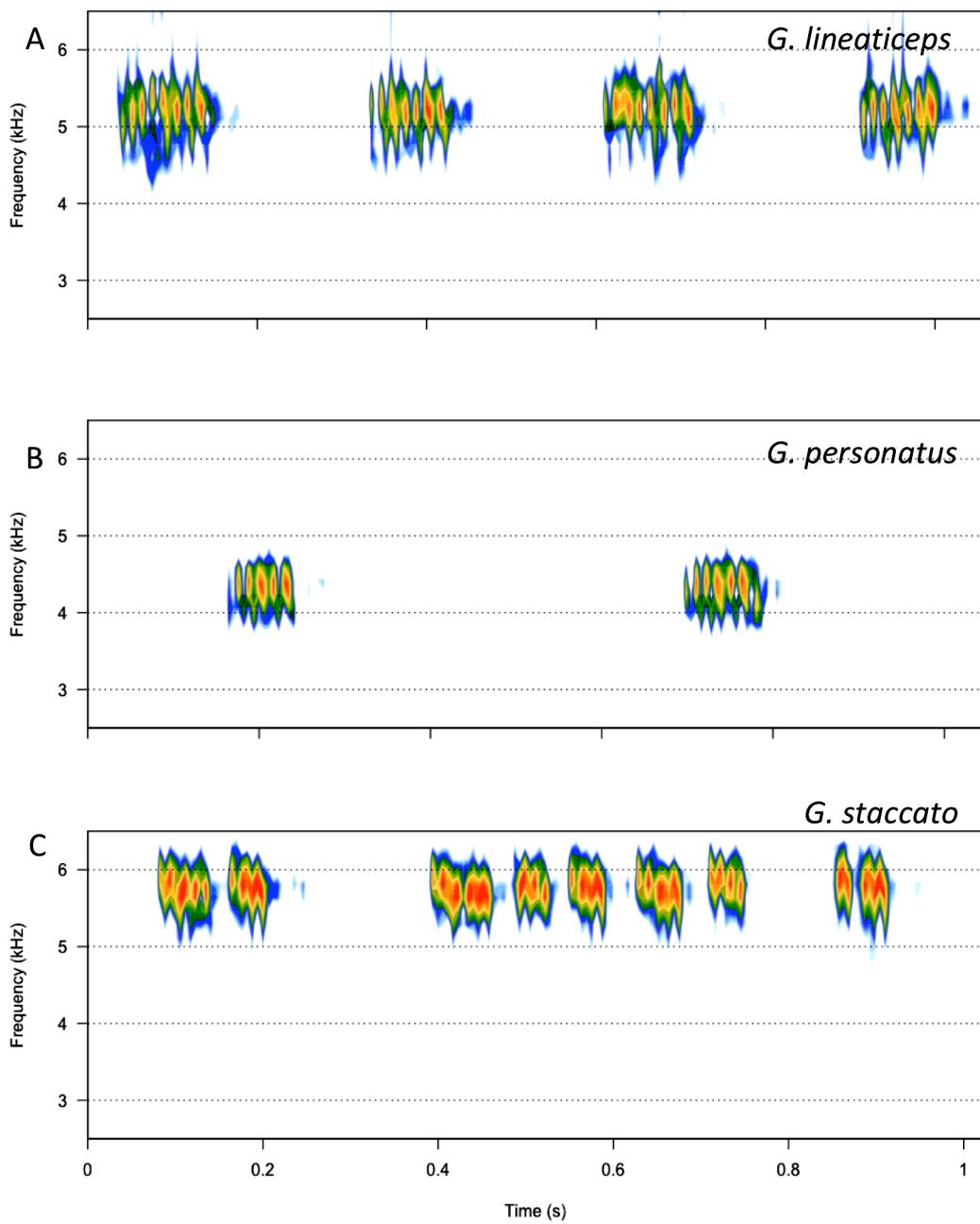


FIGURE 171. One second spectrograms of typical calling songs of (A) *G. lineaticeps*, (B) *G. personatus*, and (C) *G. staccato*, same males as in Fig. 170.

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 al.* (1980).
- 1981 ‘*Gryllus III*’. Rentz & Weissman (1981).
- ‘*Gryllus #3*’ of DBW notebooks.

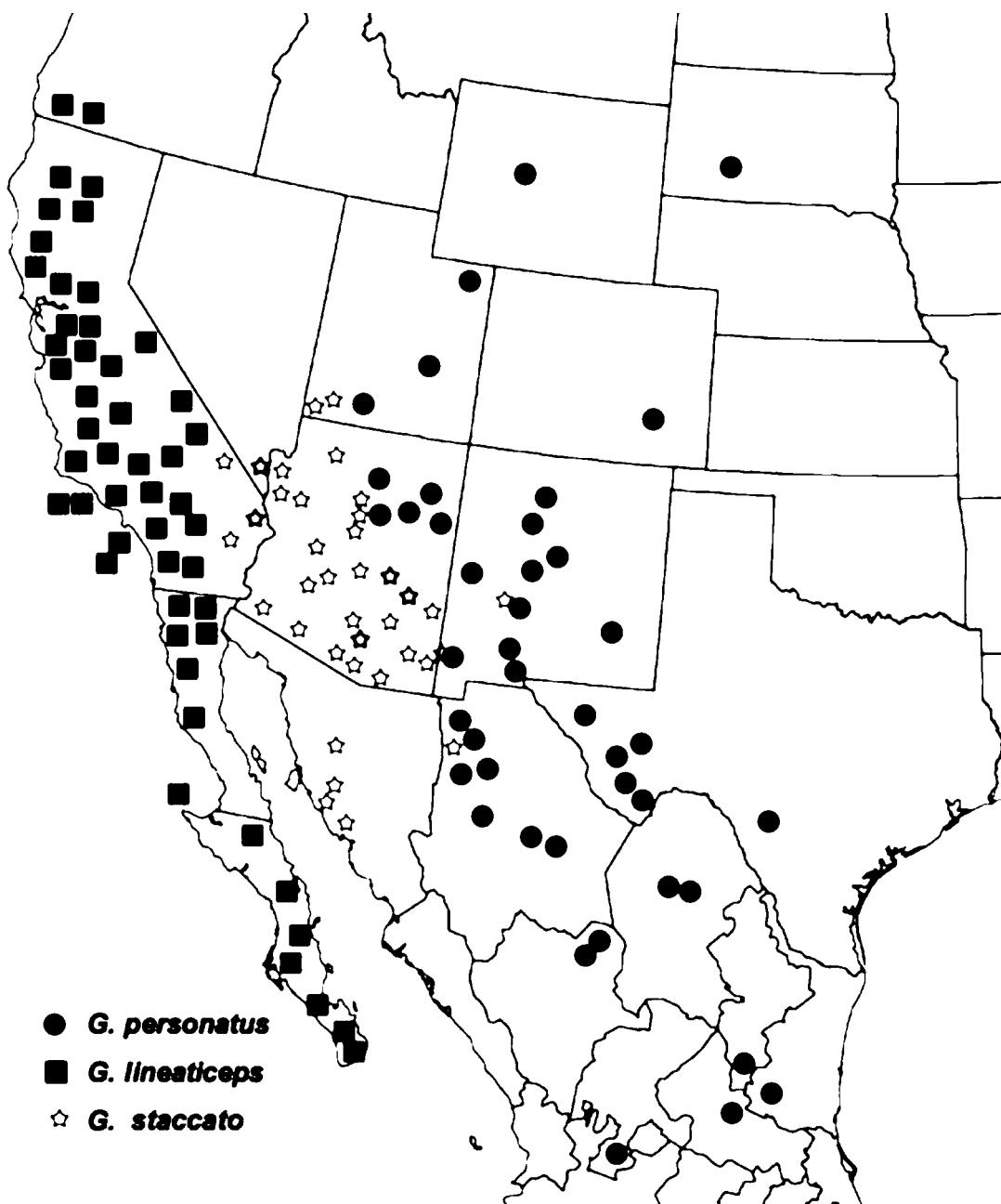


FIGURE 172. Known distribution (from Gray *et al.* 2016b) showing, basically, allopatric localities of the three Lineaticeps Group taxa.

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).

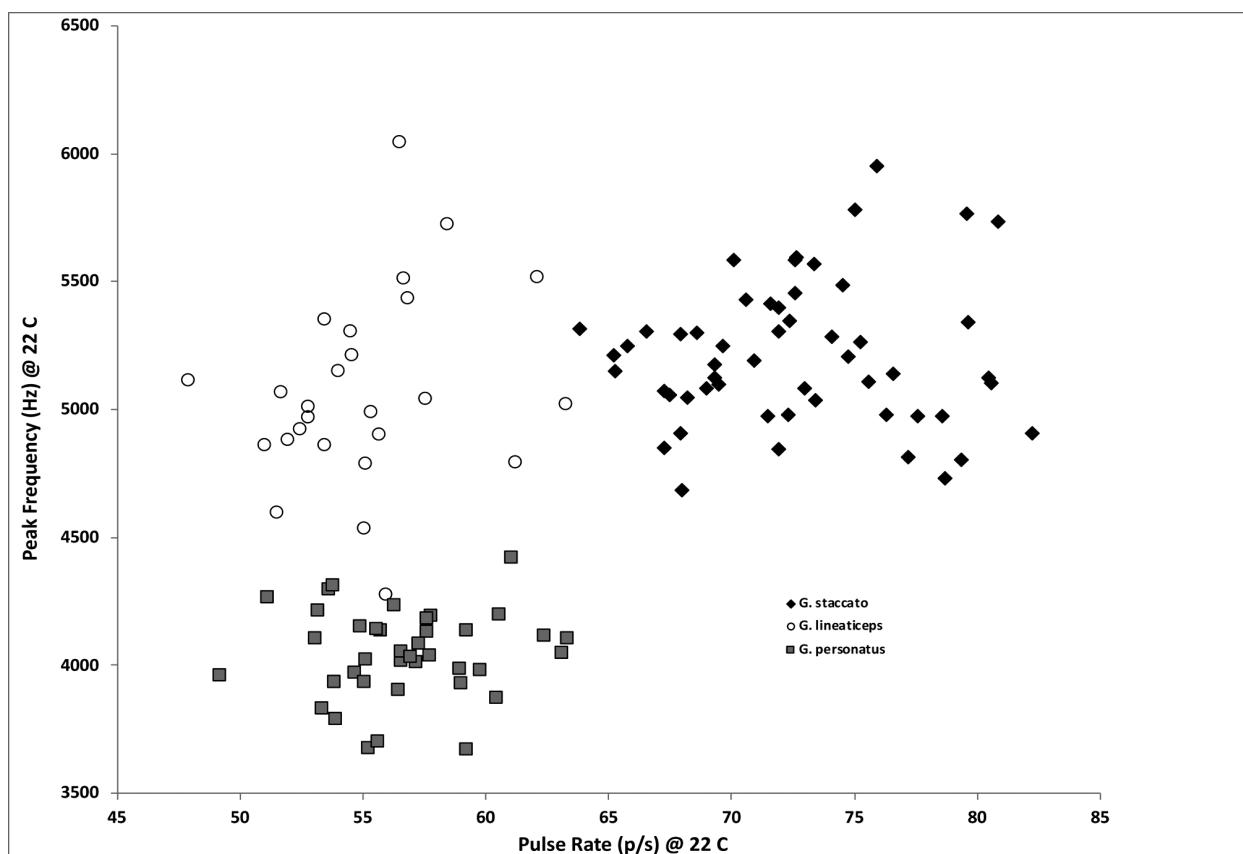


FIGURE 173. Separation of species within the Lineaticeps Group by song (from Gray *et al.* 2016b). Most points represent lab-reared individuals; therefore, it is possible that field-caught individuals (see Table 1, p. 18) would show somewhat less clear separation given known effects of developmental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

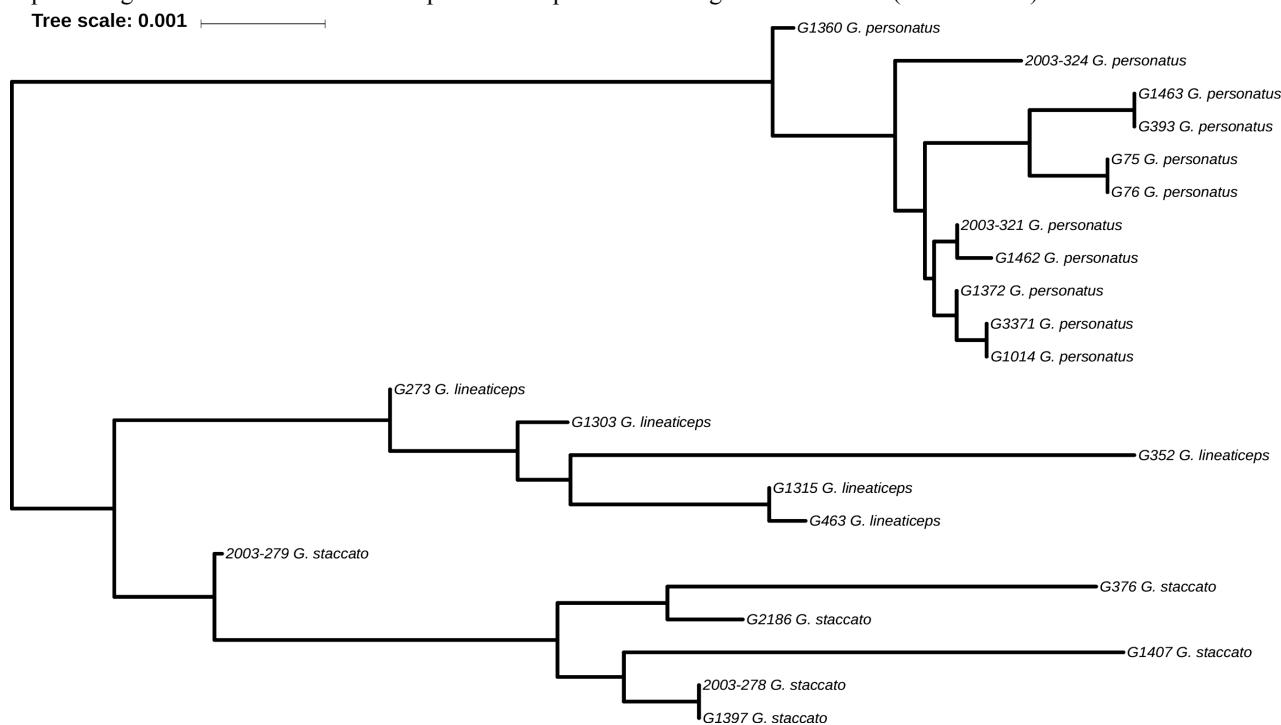


FIGURE 174. ITS2 gene tree. Collection stop numbers for *G. lineaticeps* samples: S00-15, Guadalupe Island, Mexico (G273); S04-64 (G352); S05-39 (G463); S09-28 (G1303); S09-37 (G1315). Collection stop numbers for *G. personatus* samples: S99-84, Durango, Mexico (G393); S03-127, from Coahuila, Mexico (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.

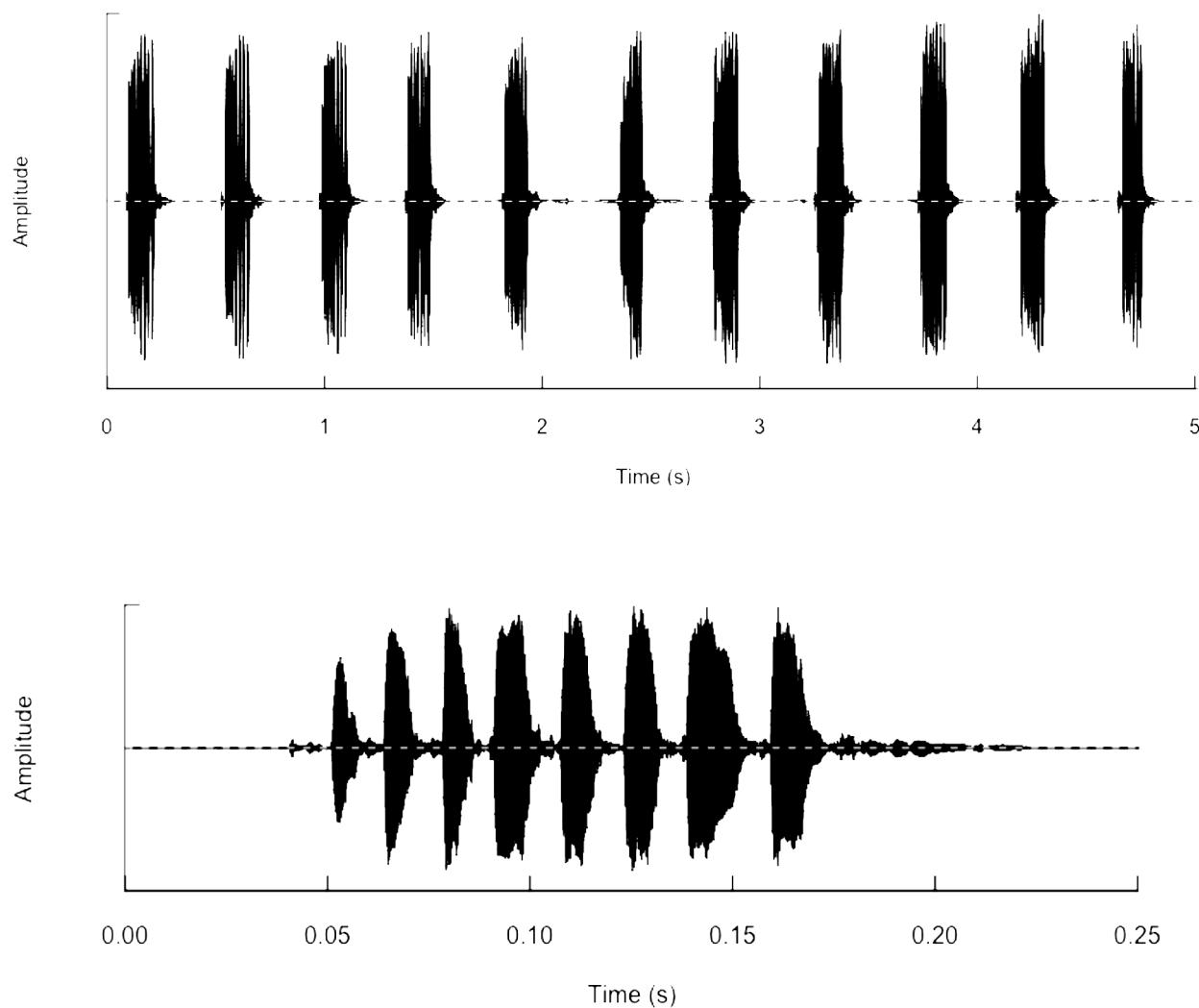


FIGURE 176. Calling song (R11-15) of *G. lineaticeps* from Mendocino Co., CA (S11-22), recorded at 25°C; lower panel shows structure of a single chirp.

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 (un-

publ.) 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.

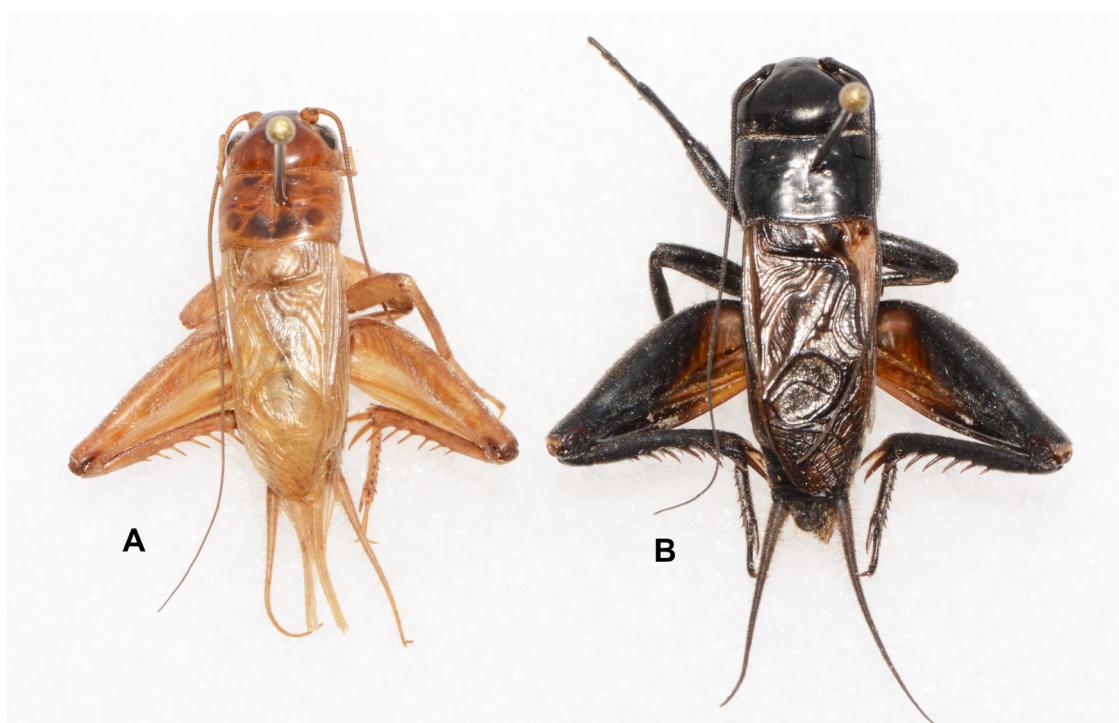


FIGURE 177. Color variation in *G. lineaticeps*: Reddish male (A) and female (C) from Madera Co., CA (S15-91); black male (B) from Tuolumne Co., CA (S10-13).

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).

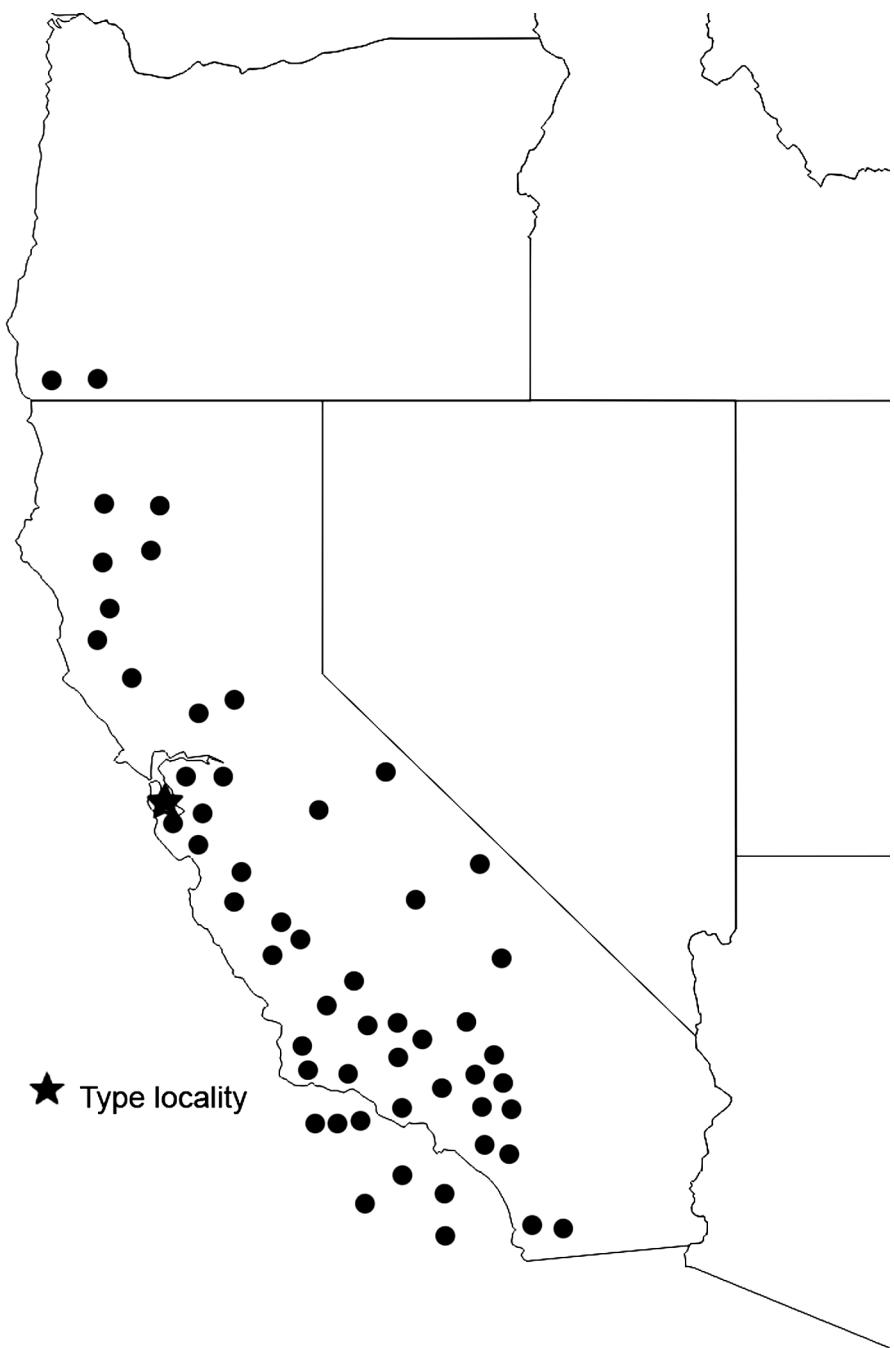


FIGURE 178. Known US distribution of *G. lineaticeps*.

***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, fastigium 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.