

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.



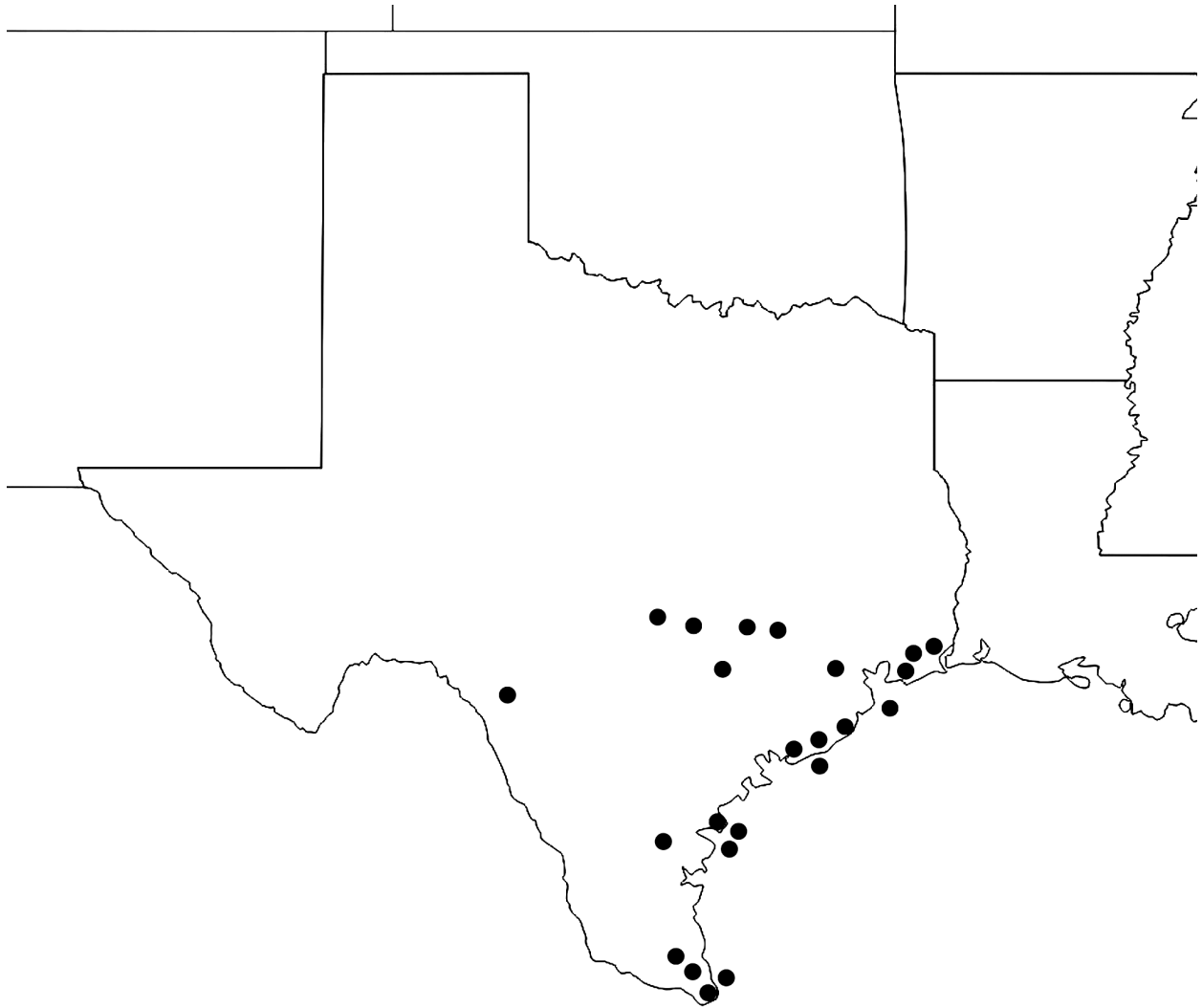
FIGURE 38. Lectotype male, *G. firmus*, specimen and labels.

*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 sum-

mer 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.

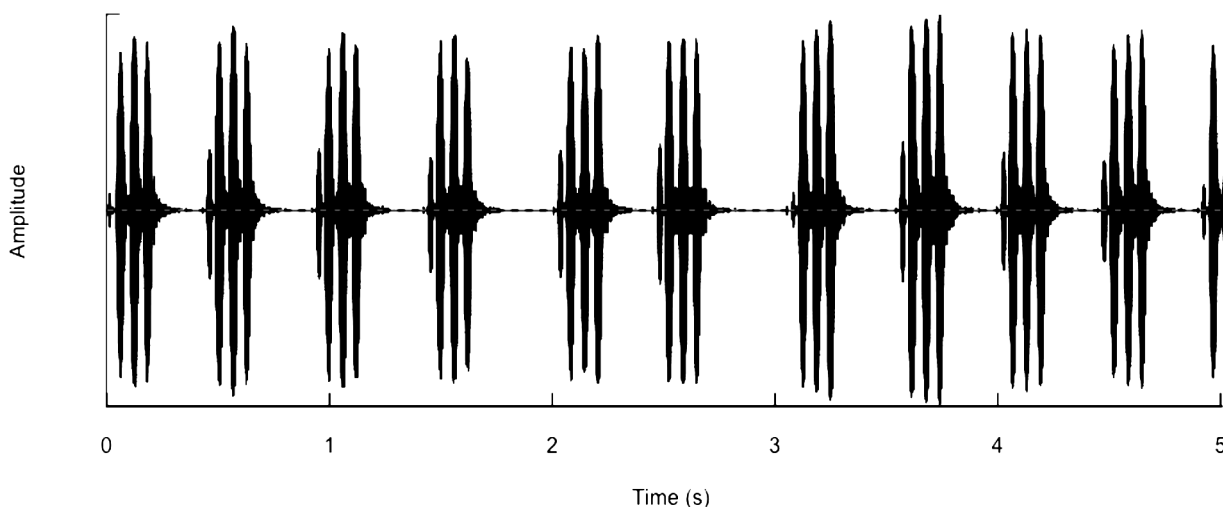


**FIGURE 39.** Populations of *G. firmus* that we studied.

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.

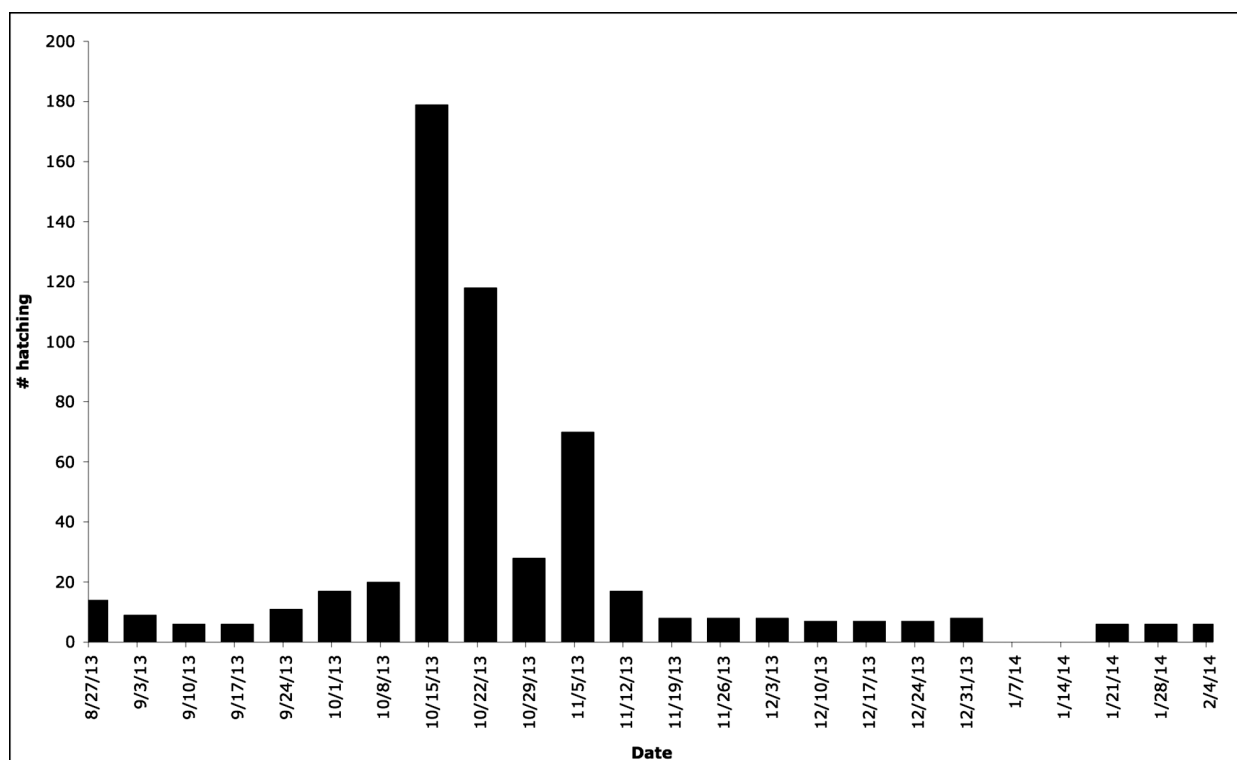
**Variation. Body color:** Coastal individuals, especially females, usually light in color, although 7 of 12 females from Brackettville also light colored, some with head stripes. **Body size:** Inland specimens from Texas are bigger with more teeth and longer ovipositors. Measured immediately after 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♂. 0.5 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. ovisopsis*, *G. pennsylvanicus*, and *G. firmus*, with 1.3% total separation. For ITS2, we show that all Texas populations (*G. ovisopsis* 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.

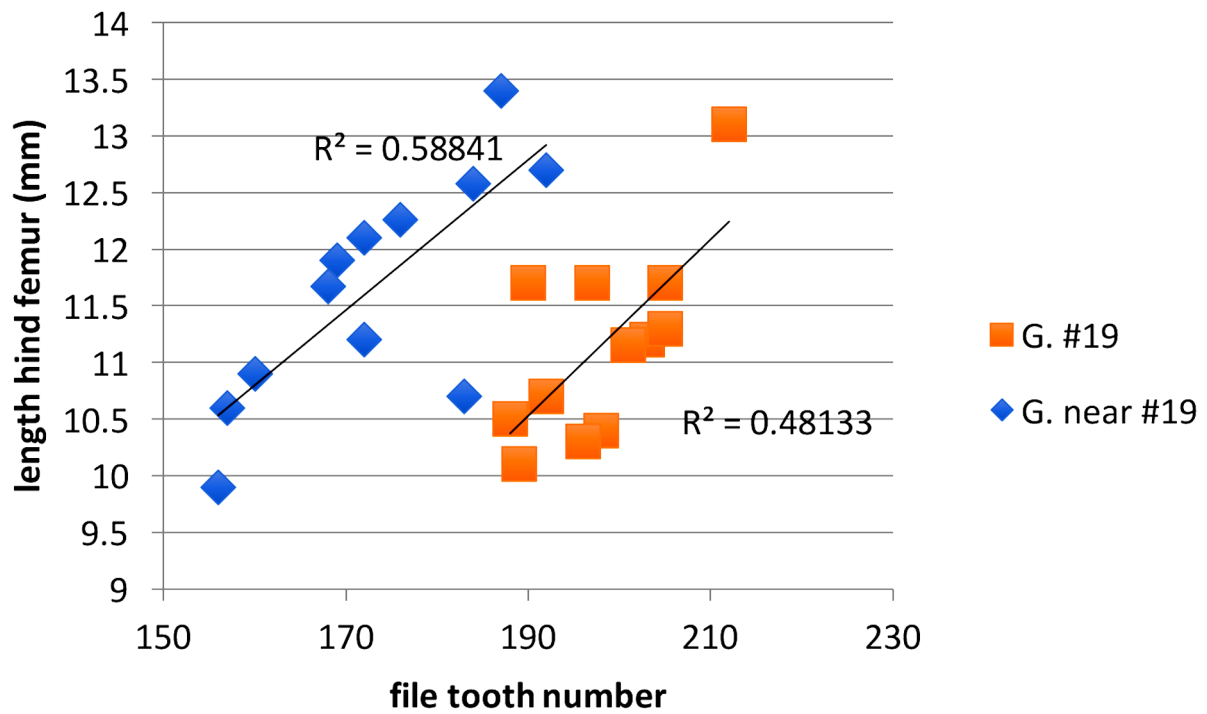


FIGURE 43. Regression file tooth number vs. length hind femur in ‘G. #19’ vs. ‘G. near #19.’

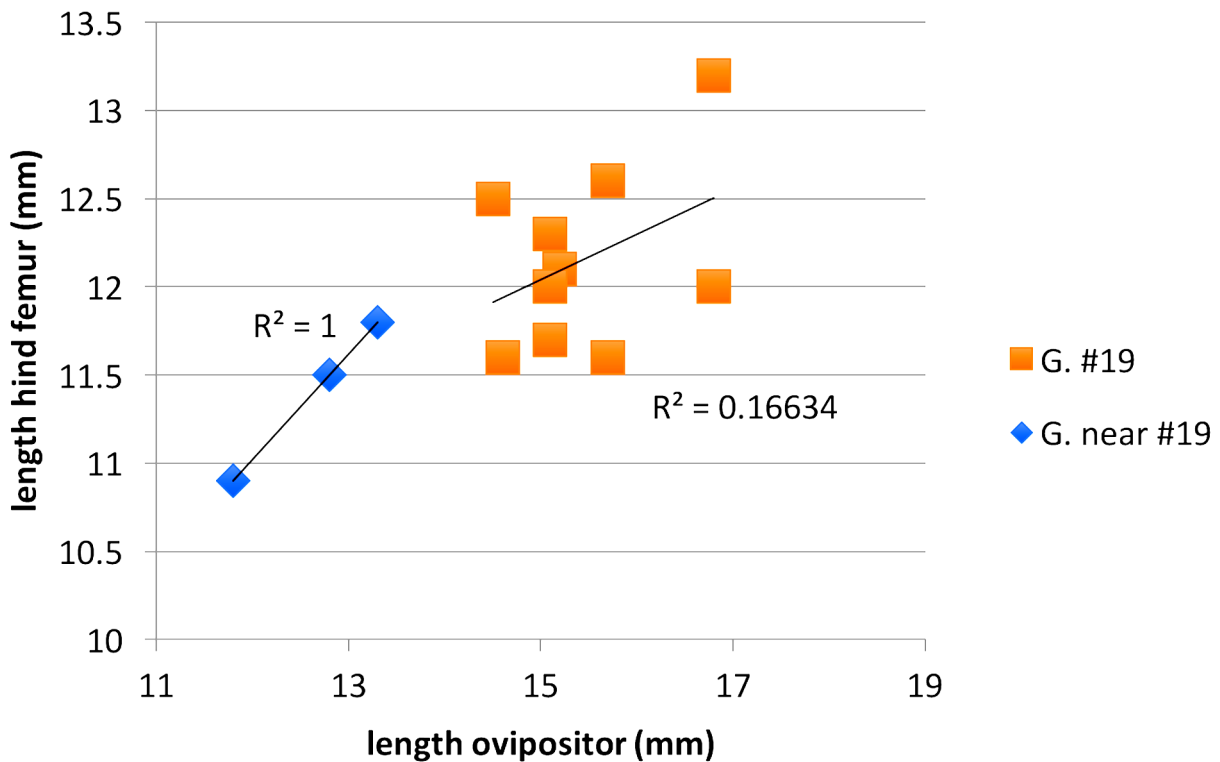


FIGURE 44. Regression length ovipositor vs. length hind femur in ‘G. #19’ vs. ‘G. near #19.’

(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 13<sup>th</sup>, 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 1 female (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.

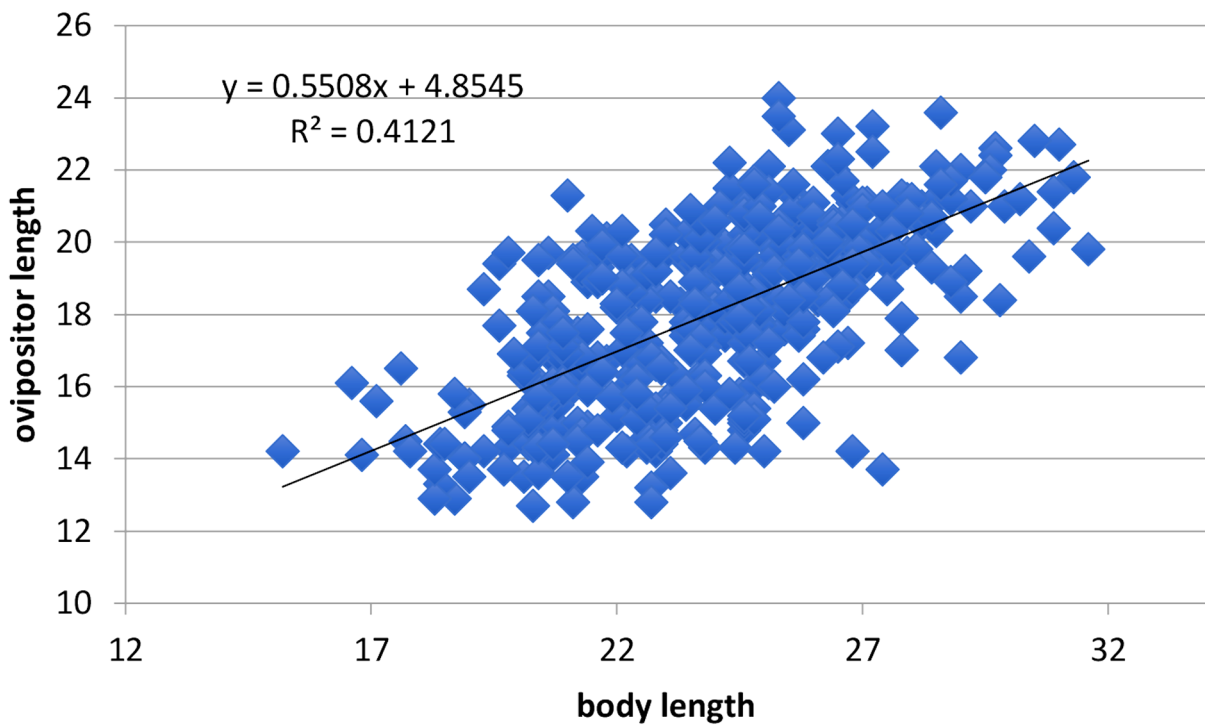
We now discuss the various comparisons that we made between 'pure' populations of *G. firmus* and *G. pennsylvanicus* in areas of the US west of the Mississippi River and compare our results with what has been previously documented in the above cited publications. Unfortunately, we have also not found 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](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,  $R^2=0.68434$ ).

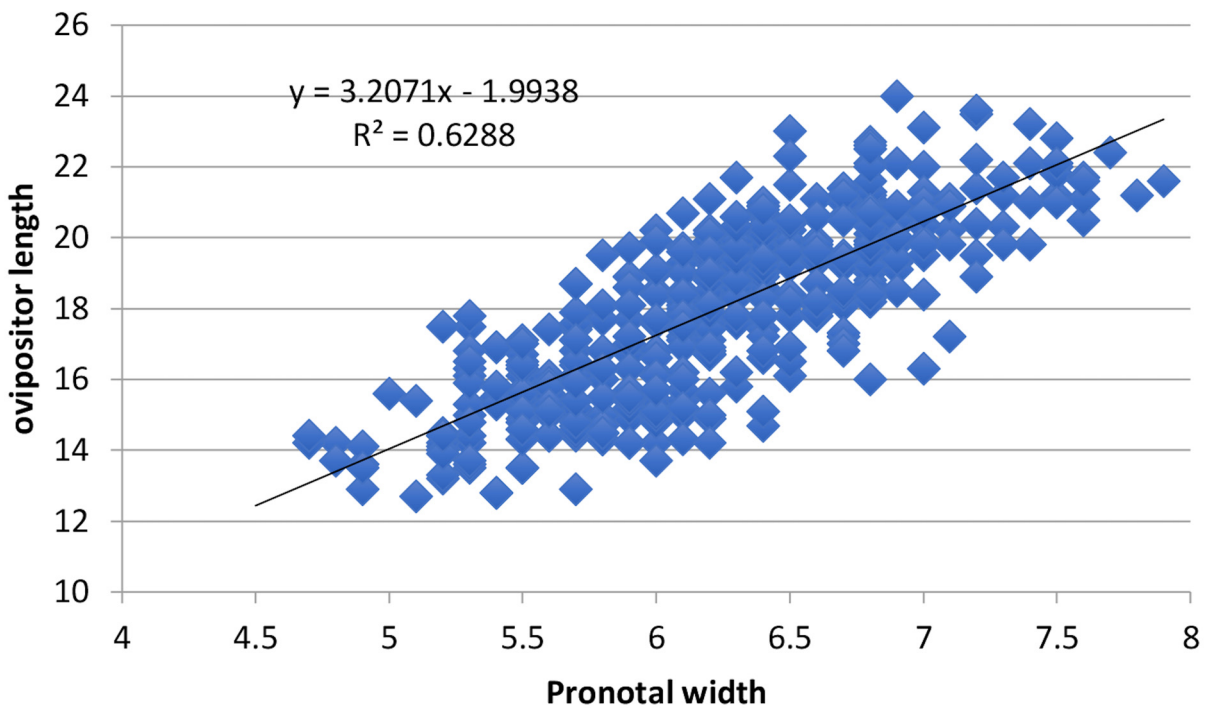
The three regressions clearly display no separation between the two taxa, and merely show that larger female crickets, measured in several different ways, have longer ovipositors. In this instance, the lack of separation of taxa is not a surprise as the majority of the individuals were sampled from 'admixed' 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  $F_{1,158} = 229.83$ ,  $P < 2e-16$ ; Species  $F_{1,158} = 60.85$ ,  $P < 7.8e-13$ ).

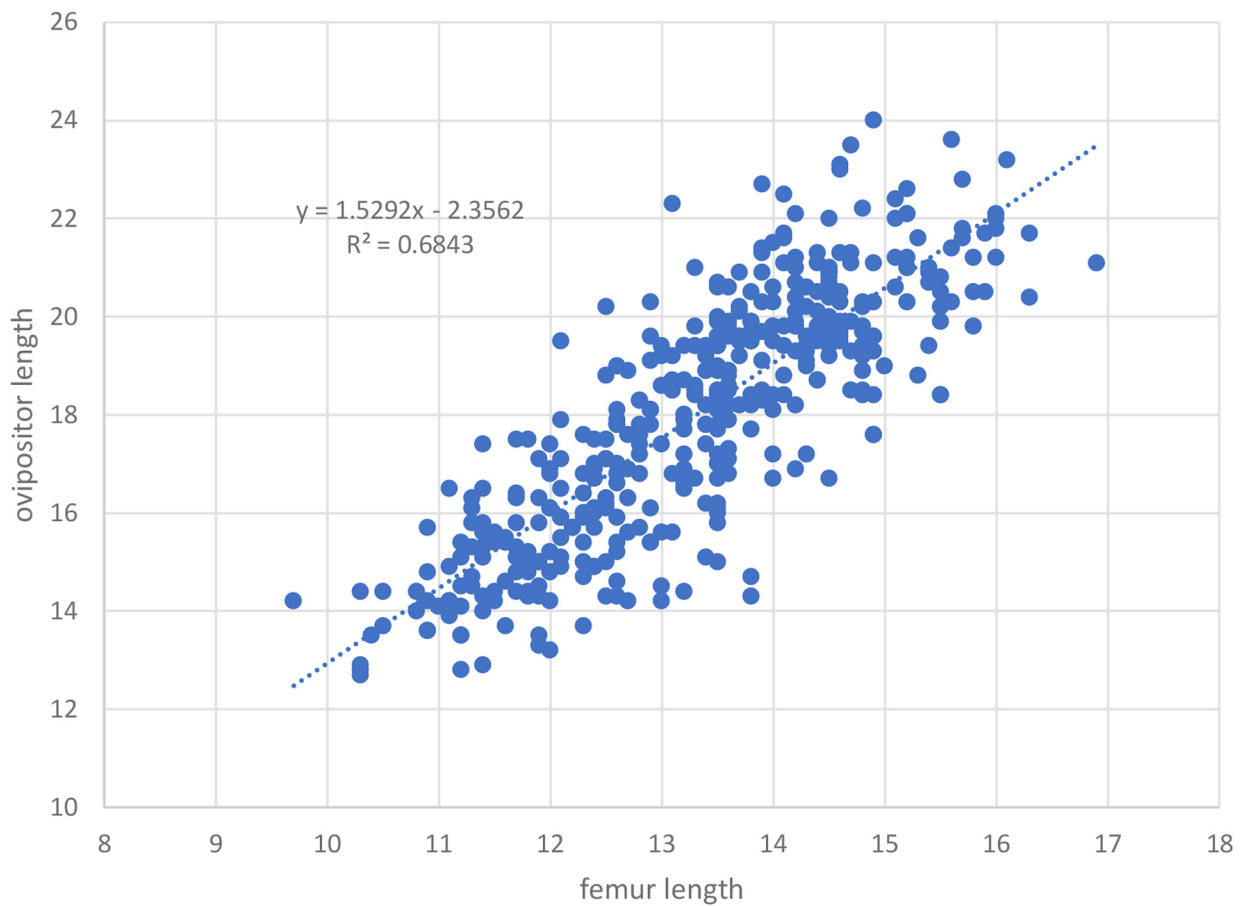
This seems promising, however the difference is clearly not diagnostic and, remarkably, for these western samples, *G. pennsylvanicus* have longer ovipositors for a given body size than do TX *G. firmus*, which is opposite the pattern observed by other authors studying populations farther east. Note 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,  $R^2=0.80151$ ).



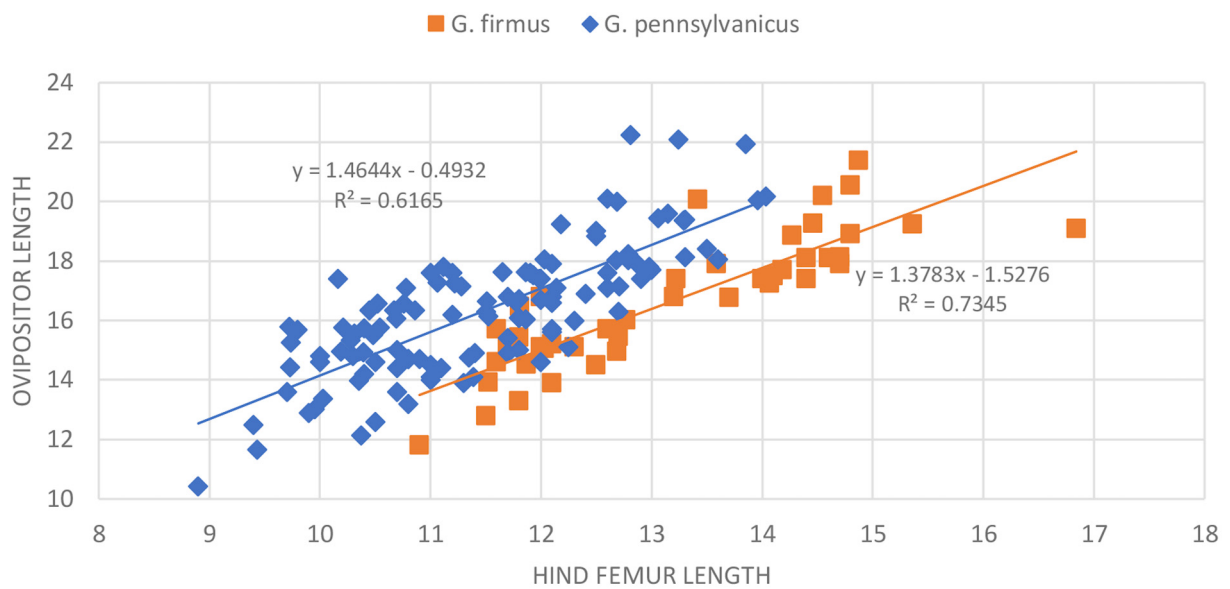
**FIGURE 45.** Regression body length vs. ovipositor length using combined data for *G. firmus* and *G. pennsylvanicus* from Larson *et al.* (2013).



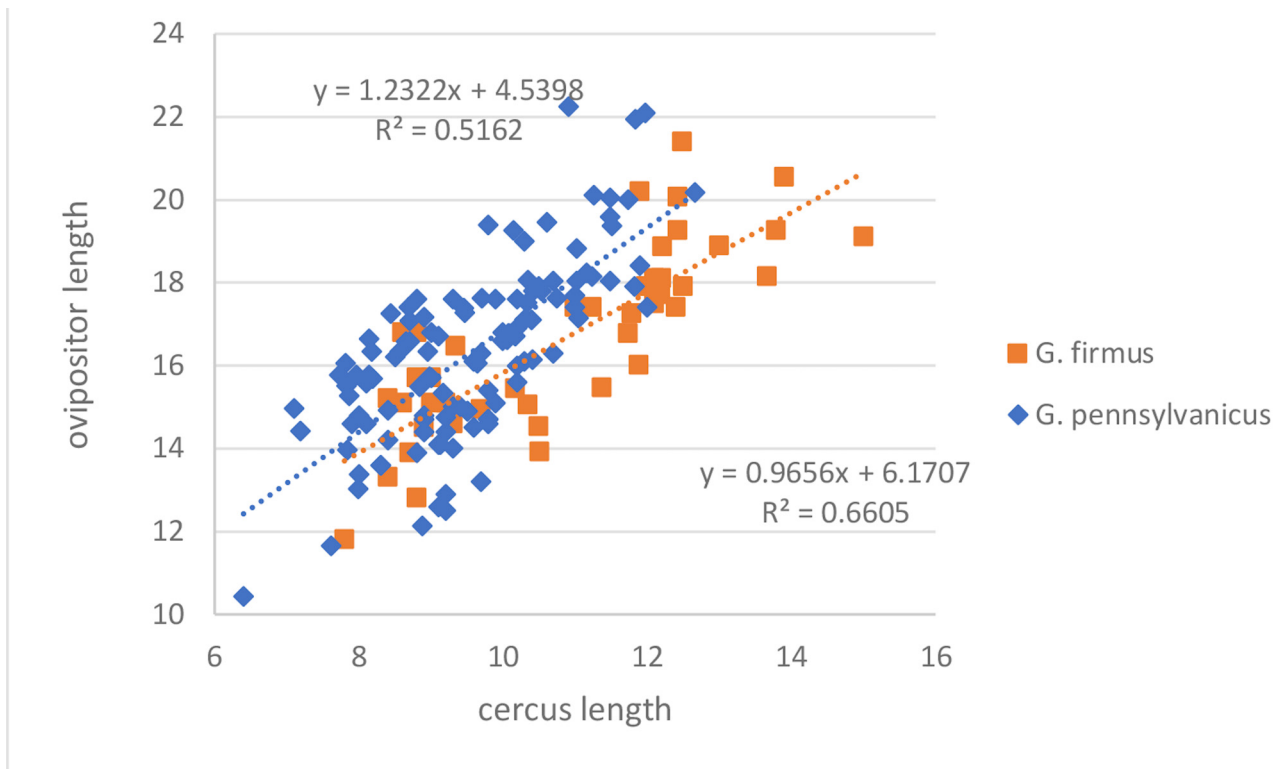
**FIGURE 46.** Regression pronotal width vs. ovipositor length using combined data for *G. firmus* and *G. pennsylvanicus* from Larson *et al.* (2013).



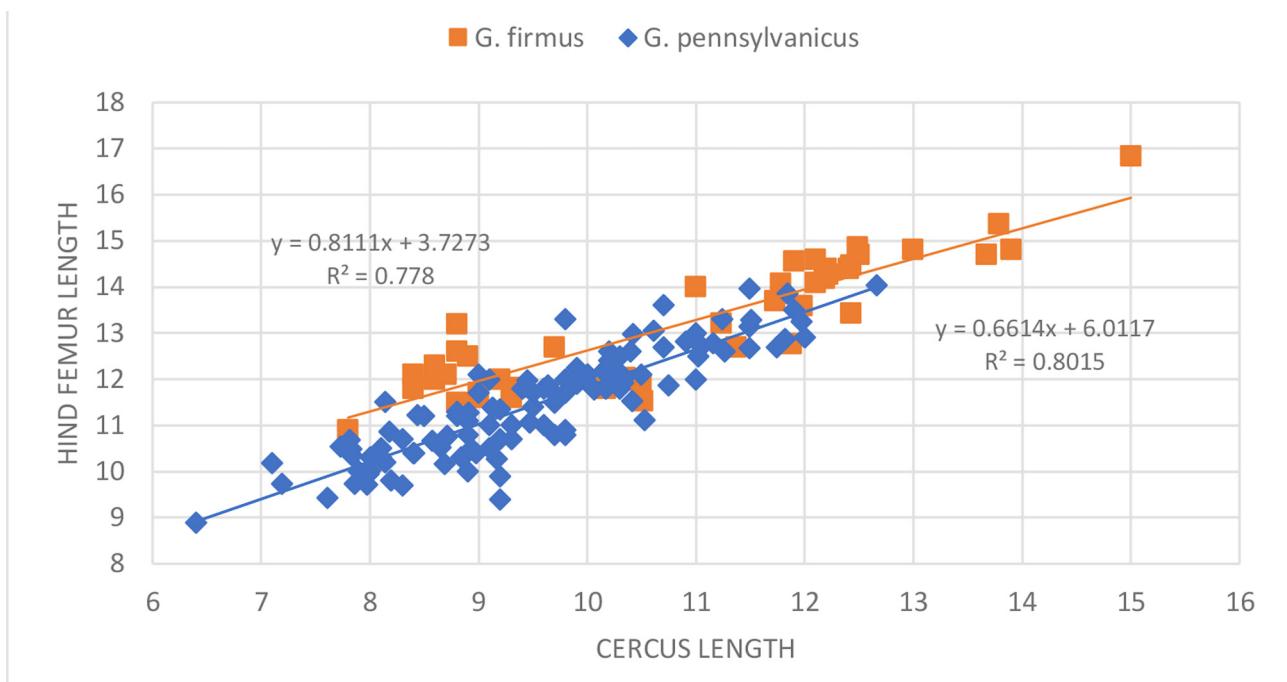
**FIGURE 47.** Regression hind femur length vs. ovipositor length using combined data for *G. firmus* and *G. pennsylvanicus* from Larson *et al.* (2013).



**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*.



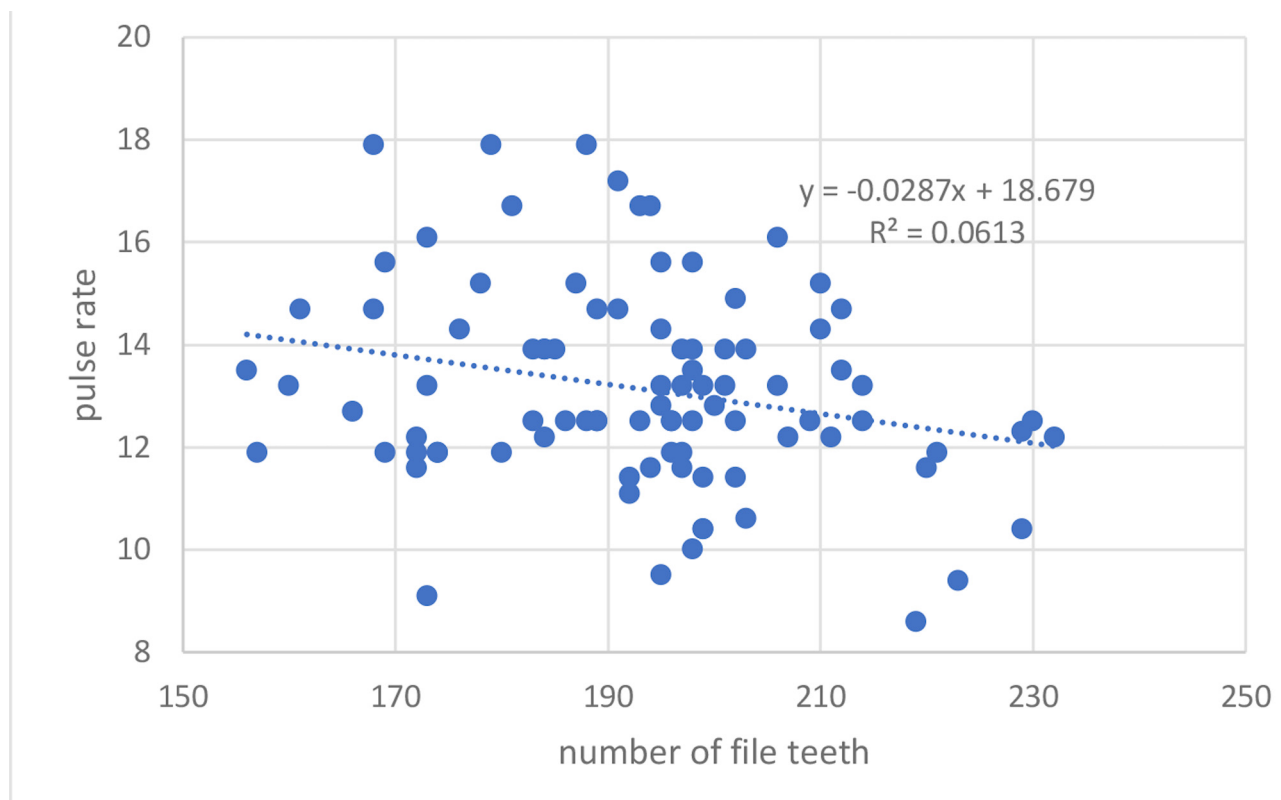
**FIGURE 50.** Regression cercus length vs. hind femur length in *G. firmus* vs. *G. pennsylvanicus*.

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?

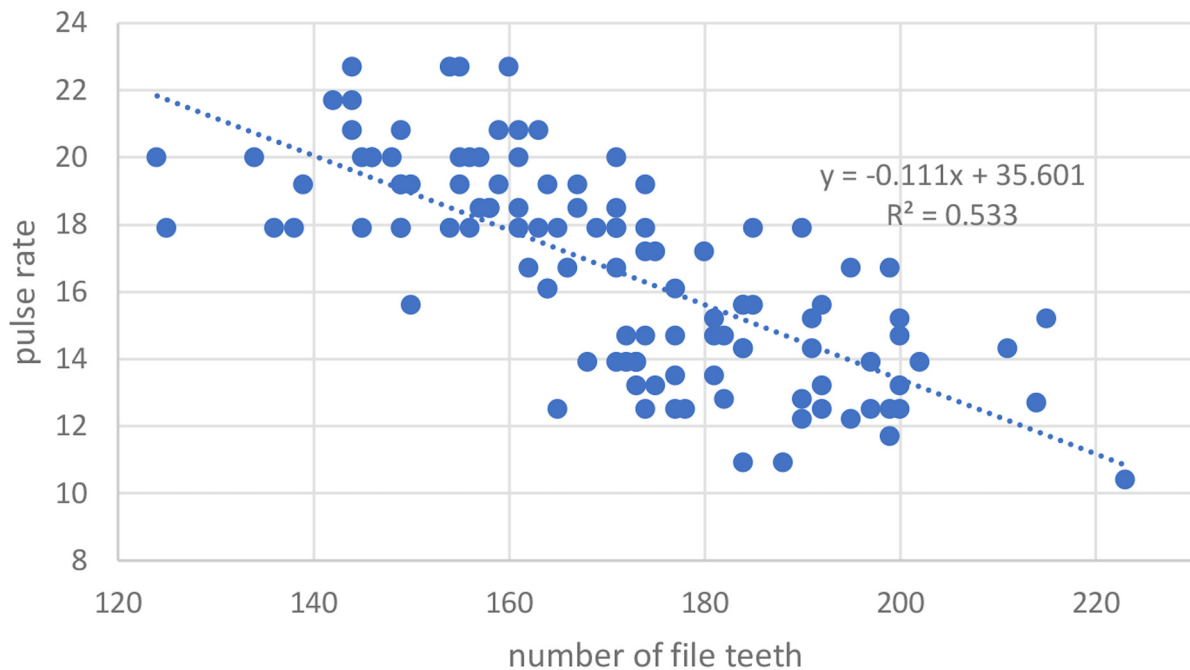


**FIGURE 51.** Regression number of file teeth vs. pulse rate in *G. firmus*.

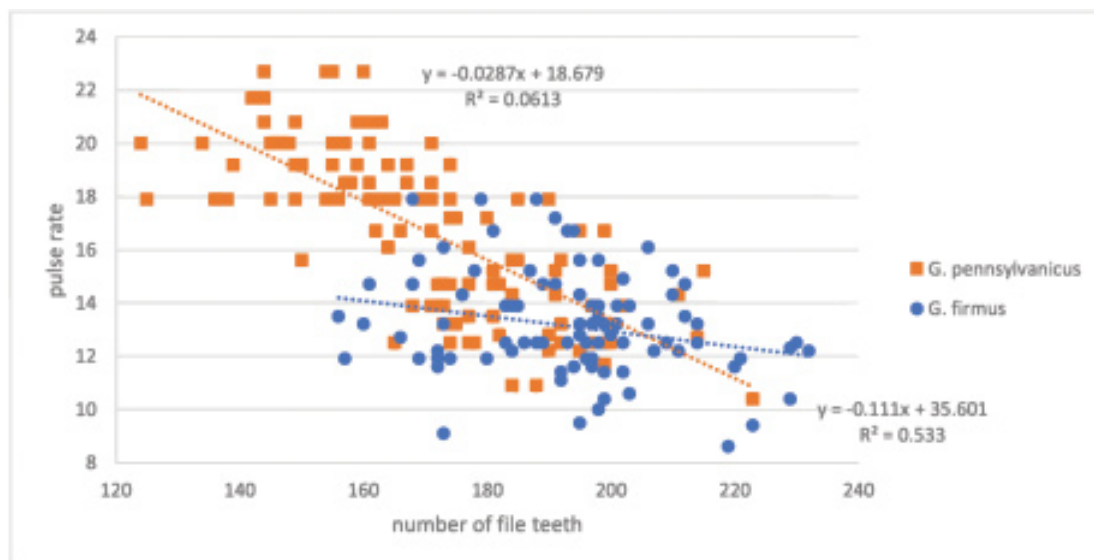
**2. File tooth number and pulse rate:** Harrison & Arnold (1982) state that *G. firmus* has more file teeth than *G. pennsylvanicus* and that the pulse rates differ between the species but with overlap. We find file tooth numbers to be useful in coastal Texas, as they are in Florida (Nickle & Walker 1975), because they separate TX *G. firmus* from all other sympatric congeners, 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 ( $F_{1,202} = 164.06$ ,  $P < 2e-16$ ), pulse rate ( $F_{1,202} = 61.90$ ,  $P < 2.15e-13$ ), and their interaction (teeth\*species,  $F_{1,202} = 64.92$ ,  $P < 6.7e-14$ ). 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](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.