GRYLLUS CAYENSIS N. SP. (ORTHOPTERA: GRYLLIDAE), A TACITURN WOOD CRICKET EXTIRPATED FROM THE FLORIDA KEYS: SONGS, ECOLOGY AND HYBRIDS

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Abstract

Gryllus cayensis, new species, formerly occurred in tropical hammocks in the Florida Keys but has not been found there since 1972, the initial year of aerial spraying of north Key Largo hammocks for mosquito control. It is now known only from pineland in Everglades National Park. Males of *G. cayensis* make no ordinary calling songs, but some caged males occasionally produce soft 3-4 pulse chirps with a principal frequency of nearly 11 kHz. Males of its sister species, *G. fultoni* (Alexander), which occurs in north Florida, call with loud 2-4 pulse chirps with a principal frequency of about 4.5 kHz.

Key Words: Gryllus cayensis, Gryllus fultoni, calling song, hybridization, phylogeny

RESUMEN

Se describe una nueva especie, *Gryllus cayensis*, la cual solía existir en los "hammocks" tropicales de los Cayos de la Florida, pero que no se ha encontrado allí desde 1972, año en que se inicio la aspersión aérea en el norte de Cayo Largo para el control de mosquitos. Hoy en día solamente en los bosques de pinos del Parque Nacional de los Everglades. Los machos de *G. cayensis* no hacen llamados normales de canciones, pero algunos machos enjaulados ocasionalmente producen chirridos suaves de 3-4 pulsos con una frecuencia principal cercana a los 11kHz. Los machos de una especie hermana, *G. fultoni* (Alexander), la cual ocurre al norte de la Florida, hacen llamados con un fuerte chirrido de 2-4 pulsos con una frecuencia principal de aproximadamente 4.5 kHz.

Most crickets of the genus *Gryllus* are known as field crickets because they occur in fields and other open habitats. However, three of the nine species known from eastern United States live in woods: *G. vernalis* Blatchley, the northern wood cricket; *G. fultoni* (Alexander), the southern wood cricket; and *G. ovisopis* Walker, the taciturn wood cricket. In this paper, I describe a species that occurs in woods in Florida south of Miami. It differs from *G. fultoni*, its closest relative, in morphology, life cycle, song, and mitochondrial DNA. *Gryllus cayensis* and *G. fultoni* produce fertile hybrids in laboratory crosses.

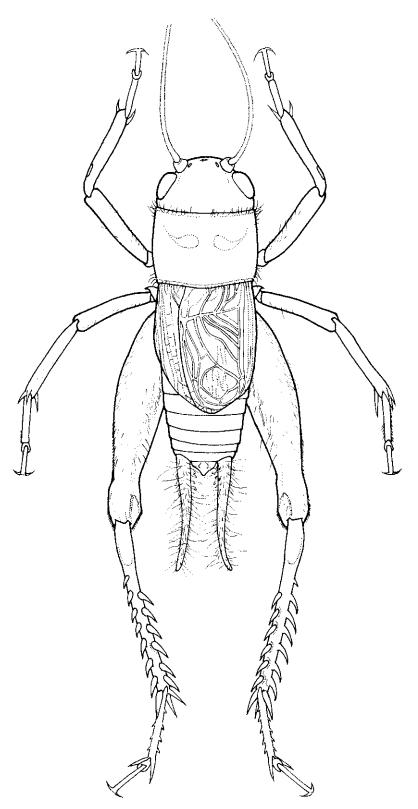
Gryllus cayensis Walker, **New Species** Keys Wood Cricket, Fig. 1

HOLOTYPE.—Male, Florida: Monroe Co., north Key Largo, Sec. 26, T59S, R40E, 23-VIII-Aug. 1958, T. J. Walker, leaf litter in tropical hammock, deposited in Florida State Collection of Arthropods (FSCA). Body black; legs and cerci reddish brown; dorsal field of tegmina brownish black; lateral field paler except at rear. Length of body, 20 mm; pronotal length × width, 4.2 × 5.8; length of tegmen, 7.6; length of hind femur, 13.1. Hind wings about half as long as tegmina.

ALLOTYPE.—Female, same data as holotype. Coloration like holotype but slightly paler. Length of body, 21 mm; pronotal length \times width, 5.0×6.5 ; length of tegmen, 8.5; length of hind femur, 14.3; length of ovipositor, 14.8.

PARATYPES.—122 males [M], 120 females [F]. FSCA: Florida, Monroe Co., Florida Keys, Key Largo, 3 M (1 reared from juvenile), 1 F, same data as holotype; 1 M reared from juvenile, tropical hammock, 9-VIII-1972, T. J. Walker [TJW]; 10 M, 4 F, progeny of previous male and a female with same data; Sugarloaf Key, 1 F reared from juvenile, hammock litter, 24-VI-1964, TJW and R. E. Love; Big Pine Key, 1 F, 9-IV-1948, collector unknown. Dade Co., Everglades National Park, Long Pine Key, pineland, 1 M, 1 F, 19-VIII-1978, TJW; 1 M, 3 F (reared progeny of 1 F coll. 19-VIII-1978); 2 M reared from juveniles, 6 F, 22-23-IX-1980, Robert Sullivan; 31 M, 47 F (reared progeny from 5 F coll. 22-23-IX-1980); 1 M, 2 F, 13-VII-1988, TJW; 72 M, 52 F (reared progeny of 2 F coll. 13-VII-1988). University Michigan Museum of Zoology [UMMZ]: Florida, Dade Co., 6 mi e. Paradise Key [now Royal Palm Hammock], 2 F, pineland, 19-X-1929, T. H. Hubbell.

Six male and six female reared paratypes from those listed above were sent to UMMZ, U. S. National Museum, Philadelphia Academy of Natural Science, and California Academy of Science.



 $\label{thm:cayensis} Fig.~1.~Drawing~of~holotype~male~of~\textit{Gryllus~cayensis}.~Color~photographs~of~living~paratypes~are~accessible~from~the~online~version~of~this~article~at~http://www.fcla.edu/FlaEnt/.$

Identification

Four species of *Gryllus* occur in extreme south Florida: G. assimilis (Fabricius), G. cavensis, G. firmus Scudder, and G. rubens Scudder. G. cavensis is the only one of the four that has any of the following features: reddish brown hind femora, tegmina (measured in situ) shorter than two pronotal lengths, inhabits woods. It is always micropterous, whereas the others are either dimorphic in wing length (G. firmus and G. rubens) or always macropterous (G. assimilis). G. fultoni, a wood cricket occurring north of the range of G. cayensis and similar to it in many respects, has tegmina that are at least twice the length of the pronotum. The stridulatory files of two males from Key Largo had 110 and 100 teeth and were 2.74 and 2.26 mm long respectively. This makes them indistinguishable from the files of *G. fultoni* (Nickle and Walker 1974).

Song

In the field, males of most *Gryllus* species are easy to identify and to locate by their loud, persistent, species-specific calling songs. However, G. cayensis has never been heard to call in the field. Most males in captivity make no sounds when alone, although a few make soft chirps rarely. Only one of five males collected on Key Largo in 1958 was ever heard to stridulate while alone. The soft chirps were tape recorded but the tape was loaned and lost. A male reared from a Key Largo juvenile collected in 1972 was kept for 16 days where it could be monitored for calling during the night and at dawn (my bedroom). It was never heard to stridulate. That male and his consort (also reared) produced eight males that were likewise kept in individual cages in my bedroom. Of four males monitored for 2 weeks, two were never heard, one was heard twice but was too wary to tape, and one produced soft chirps regularly at dawn and was tape recorded. Three of the other males were monitored for 1 week and one was monitored for 4 weeks. None of these was ever heard.

I used CoolEdit 2000 (Syntrillium Software) to analyze the one extant recording of solitary stridulation by *G. cayensis* (Walker Tape Library [WTL] tape 475-2; 22.0°C). Three- and 4-pulsed chirps were produced at a rate of ca. 2.4/s. The pulse rate within the chirps was ca. 33 pulses/s. The principal frequency of the pulses was 10.8 kHz with secondary strong frequencies between 6 and 9 kHz. The chief difference between the rare, soft song of *G. cayensis* and the common, loud song of *G. fultoni* is that the song of the latter species has a principal frequency of ca. 4.5 kHz.

Males of *G. cayensis* from Long Pine Key were also tacitum. Of 24 males reared from females collected 22-23 Sept 1980 and monitored for a

week or more in my bedroom, only one was heard. It occasionally produced soft chirps, but not for a tape recorder.

The only other *Gryllus* known to lack a conventional calling song is *G. ovisopis* (Walker 1974). Like *G. cayensis*, it is flightless and occurs in permanent, woodland habitats. In keeping with their lack of calling, both species have reduced tegmina (tegminal length less than twice that of the pronotum). However, males of *Gryllus insularis* Scudder have tegmina that are approximately as short (ca. 1.9 times the length of the pronotum), yet they produce a typical *Gryllus* calling song (D. B. Weissman, pers. comm.).

An aspect of calling that is not generally appreciated is that songs carry poorly between sender and receiver if both are at ground level. Michelsen (1985) calculated that [field] crickets might be able to hear each other on the ground only at distances less than 1 to 2 m. On the other hand, if sender or receiver (or both) is above ground level, transmission is much improved. Thus a cricket flying above a calling male can hear its call at a much greater distance than can a ground-level cricket. That flying crickets hear and respond to songs coming from the ground can be demonstrated with sound-baited traps that catch only flying crickets. For example, thousands of Gryllus rubens Scudder and hundreds of Gryllus firmus Scudder flew into 1.4 m diameter funnels baited with broadcasts of synthetic calls (Walker 1986). The only way that a male can broadcast to distant, ground-level females is to call from a perch. Males of the two large, groundliving, woods-inhabiting, non-taciturn crickets in north Florida often do just that. Gryllus fultoni and Anurogryllus arboreus Walker males often call from 0.5 to 2 m above ground level by ascending tree trunks (Paul and Walker 1979). Females of these two species are always flightless. A disadvantage of calling from tree trunks is greater exposure to acoustically orienting predators (Walker 1964). In fact a disadvantage of calling from anywhere is that some predators and parasitoids find prey by homing on their calling songs (Burk 1982; Walker 1993). Loss or reduction of calling should be most likely in crickets that are flightless, live in permanent, dense populations, and are plagued by acoustically orienting predators and parasitoids. G. cayensis probably met at least the first two of these criteria when it lost its long-range calling song and reduced its solitary stridulations.

Although males of *G. cayensis* seldom stridulate while alone, they readily produce courtship songs when they encounter a female. The reared 1972 Key Largo male that remained silent for 16 days in my bedroom, almost immediately used song to court an introduced female. This was recorded (WTL 475-1; 26.2°C) and found to consist of groups of 3 to 10 pulses often followed by a tick.

The pulse rate within the groups was ca. 57 pulses/s, and the group rate was ca. 5/s. The strongest frequency of the pulses was 5.6 kHz and of the ticks, 15.8 kHz.

Ten-second samples of the courtship and calling songs (WTL 475-1 and 2) were digitized and saved as .wav files. These are accessible from the online version of this article at http://www.fcla.edu/FlaEnt/.

Distribution, Ecology, and Seasonal Life Cycle

G. cayensis is known only from tropical hammocks in the Florida Keys and from pinelands south of N lat 25.4° in Dade Co., Florida. The southernmost Florida records for G. fultoni are Marion and Volusia Counties; for G. ovisopis, Lake Placid and Punta Gorda. Thus G. cayensis is geographically isolated by more than 350 km from G. fultoni and by more than 200 km from G. ovisopis.

The seasonal life cycle of G. cayensis has not been studied in the field, but laboratory rearing, weather records, and collecting records provide clues. In the laboratory at 25°C and 16L:8D photoperiod, development from egg to adult requires about 6 months. Eggs of field-collected adults hatched in about 4 weeks under these conditions. There was never delayed hatch as with the eggs of Gryllus species that produce all diapause eggs or mixtures of diapause and nondiapause eggs (Walker 1980). Average temperatures at Key West and Miami are above 25°C from May through October and below 25°C from November through April (USDC 1933, 1960). Adults of G. cayensis have been collected in April, July, August, and September; late juveniles in June, July, August, and September; and one early juvenile was collected in August. (Juveniles were reared to adults prior to identification.)

These temperatures and collecting records do not preclude G. cavensis from breeding continuously, with all stages occurring at all times. However, the Keys and adjacent mainland Florida have a winter and spring dry season that lasts from November through April. On average, less than 25% of the yearly rainfall occurs during this six-month period (Homestead, Flamingo, and Long Key stations; USDC 1960). During the hot days of April and early May, before the rains start, drought often becomes severe and Gryllus hatchlings would probably not survive. If the dry season prevents continuous breeding, large nymphs or diapausing adults would be the expected late dry-season stages, because they have the most favorable surface-to-volume ratios. These could become reproductively active adults in anticipation of, or in response to, the start of summer rains. The progeny of these adults would become adults in late summer, which, in turn, would lay eggs that would produce the large nymphs or diapausing adults required to survive the dry season. Eggs laid in the dry season would either not hatch or produce nymphs that would desiccate.

Rearing and Experimental Crosses

Because the Keys were distant and specimens of *G. cayensis* were difficult to collect, I brought live specimens to Gainesville for further study and for increase through rearing.

Some 85% of the paratypes of *G. cayensis* are reared progeny of females collected as they fed at trails of oatmeal laid in the pineland of Long Pine Key. In 1978, 1980, and 1988, I obtained a total of 206 adults from eight field-collected females.

On 9 Aug 1972, I captured two mid-sized juveniles at oatmeal trails in hammocks on Key Largo. I reared the two under an open shelter in Gainesville and obtained an adult male and female by 26 September. The pair mated by 1 October and the first eggs hatched 5 Nov 1972. The female was deprived of her consort on 29 Oct (for pinning) but continued to lay fertile eggs until she died in mid-December. Throughout her oviposition, I attempted to rear cohorts of her progeny in the field and in the laboratory at 25°C and 16L:8D photoperiod. Under field conditions, none of 200 juveniles survived beyond the first few stadia. Juveniles that hatched in the field in early or mid-November died in about one month; early juveniles transferred to the field from the laboratory in mid-December and mid-January lasted longer but none reached the middle stadia and none survived as long as three months. When many juveniles died at once in the jars in the field, they appeared to succumb to a white mold. Under laboratory conditions, about 400 early juveniles survived to the middle stadia with low mortality, but then their numbers declined week after week. At the same time a few of the juveniles became much larger than their sibs as they reached the final juvenile stadia. This suggested cannibalism, as did finding partially eaten crickets. I therefore divided each laboratory cohort among two or three rearing containers and succeeded in rearing 30 adults. Most of the adults were used in experimental crosses with *G. fultoni* and *G. ovisopis*, the two wood crickets that occur in Florida north of the range of *G. cayensis*.

All *G. fultoni* and *G. ovisopis* used in experimental crosses were second laboratory generation crickets from stock collected in Alachua County, Florida. Five replicates of these four crosses were set up in the spring of 1973 as appropriate crickets matured: *cayensis* × *cayensis*, *cayensis* × *fultoni*, *fultoni* × *cayensis*, and *ovisopis* × *cayensis* (male parent listed first). Because of a shortage of crickets, only four replicates of *cayensis* × *ovisopis* and one replicate each of *fultoni* × *fultoni*, and *ovisopis* × *ovisopis* were established. Neither the C × O nor O × C crosses produced progeny. All other

types of crosses produced progeny: $C \times C$ (4 of 5 replicates), $C \times F$ (4 of 5), $F \times C$ (3 of 5), $F \times F$ (1 of 1), $O \times O$ (1 of 1).

Two F_1 males of the $C \times F$ cross were monitored for calling for one month in my bedroom. Neither was ever heard.

No further crosses were set up, but the progeny from one of the $C \times F$ crosses produced numerous F_2 hatchlings from which seven males and a female were reared. The males were monitored for calling and the songs of four were tape recorded (WTL 475 \times 484-1, 2, 4, 5; 20.0-22.2°C). The chirp rate was ca. 2.0/s and the principal frequency was ca. 5.0 kHz. The songs were reminiscent of G. fultoni though weaker.

Phylogeny and Species Status

Results of the laboratory crosses indicated that *G. cayensis* was more closely related to *G. fultoni* than to *G. ovisopis*. They did not prove that *G. cayensis* and *G. fultoni* were conspecific, because species of *Gryllus* that fail to hybridize where they occur together in the field often produce fertile hybrids in the laboratory. For example, in no-choice, laboratory crosses *G. rubens* will hybridize with *G. assimilis* and with *G. texensis* Cade and Otte, species with which *G. rubens* lives in south Florida and west Florida respectively (Bigelow 1960; Walker 2000).

North American Gryllus have been used for numerous comparative studies of physiology, behavior, and ecology. Such studies have been hampered by the lack of a consensus phylogeny of the species. Molecular techniques now promise to provide one. Harrison and Bogdanowicz (1995) studied the mitochondrial DNA restriction site maps for eight Gryllus species from eastern North America, including the six that occur in peninsular Florida. They concluded that G. cayensis and G. fultoni were sister species and that G. veletis (Alexander and Bigelow) and one or more unidentified Gryllus species from western U.S. were a sister group to the G. fultoni/G. cayensis group. Gryllus ovisopis (the other taciturn wood cricket), G. pennsylvanicus Burmeister, and G. firmus formed a distinct group, well separated from the G. cavensis/G. fultoni/G. veletis group. The sequence divergence between G. cayensis and G. fultoni was much greater than that between G. ovisopis and either G. firmus or G. pennsylvanicus (0.027 vs. 0.002-0.010), which adds to the evidence that G. cayensis merits species status. [Note: The two *G. cayensis* used by Harrison and Bogdanowicz were from Long Pine Key (19 Aug 1978) rather than from Key Largo.]

Huang et al. (2000) expanded the mt DNA database for North American *Gryllus* to include three more U.S. species and the complete cytochrome b gene and a portion of the 16S rRNA gene. They did not include *G. cayensis*, but other-

wise confirmed the relationships reported above, while adding *G. integer* (from California) to the *G. veletis/G.fultoni[/G. cayensis*] clade.

The origin of *G. cayensis* and *G. fultoni* from a common ancestral species seems likely to have occurred when Pleistocene fluctuations in sea levels isolated south Florida woods and wood crickets from north Florida ones. Some crickets that occur in tropical south Florida apparently got there by flying or rafting from Cuba; however, *G. cayensis* is flightless, and rafting seems unlikely since the eggs are laid in soil. Zayas (1974) makes no mention of a Cuban counterpart to *G. cayensis*.

Probable Extirpation from the Florida Keys

My first experience with G. cayensis was at mid-morning, 23 August 1958, when I observed numerous individuals in the leaf litter of a tropical hammock on north Key Largo. I easily collected five adults and a large nymph. Since then, I've collected only three individuals in the Keys: one nymph from hammock leaf litter on Sugarloaf Key in June 1964 and two nymphs feeding at a trail of oatmeal laid in a hammock on north Key Largo, 9 Aug 1972. (Oatmeal was dribbled as a trail shortly after sunset and the trail was repeatedly searched with a light during the first half of the night.) On 1 and 2 June 1973, I got no specimens from oatmeal trails through the hammock that was successfully searched in 1972. On 5 Aug 1987, I found no specimens along oatmeal trails laid in two hammock areas near where I'd first found G. cayensis in 1958. On 6 Aug 1987 and 12 Jul 1988 I unsuccessfully searched three oatmeal trails laid on Big Pine Key. The 1987 trail was in hammock and pineland. The two 1988 trails were in Watson's and Cactus Hammocks.

The failure to collect *G. cayensis* along oatmeal trails in the Florida Keys from 1973 forward contrasts with the success of the same technique on the mainland. Each time oatmeal trails were laid in the pineland of Long Pine Key, three or more individuals were collected: 16 Aug 1978 (n = 3), 22 and 23 Sept 1980 (n = 8), 13 Jul 1988 (n = 5).

The most likely cause of the apparent disappearance of *G. cayensis* from the Florida Keys is aerial and ground application of insecticides by the Monroe County Mosquito Control District. Fogging with truck-mounted units began in 1951 and aerial spraying began in 1962. However, until 1967, all applications were in the well-populated parts of the Keys from mid Key Largo south. In that year the District began malathion fogging of north Key Largo from trucks. In 1972 they switched to ultra low volume application of 93% fenthion (Baytex) from trucks and aerial application of 4% naled (Dibrom) from DC-3 aircraft (Emmel 1995).

The switch to organophosphate insecticides and to aerial spraying thus coincided with the ap-

parent disappearance of G. cayensis from north Key Largo. Several lines of evidence suggest, but do not prove, that the spraying caused the disappearance. First, organophosphate insecticides are nonspecific and highly toxic (Matsumura 1985). Second, when I sought G. cayensis on Key Largo in 1973, I noted that there were no crickets calling in the hammocks. This was strange because on all previous visits to hammocks in the Keys the tinkling chirps of Cyrtoxipha gundlachi Saussure had been heard in abundance. Thirdly, the population history of *Papilio ponceanus* Schaus (Schaus' swallowtail) on north Key Largo supports the contention that mosquito control had lasting effects on nontarget insects. Papilio ponceanus once occurred throughout the Keys and adjacent mainland Florida but by 1976 was officially classed as "threatened" and by 1984 as "endangered" (Emmel 1995). Through 1972 it was commonly seen and collected on north Key Largo. From 1973 through the mid 1980s, it was rare or missing (Emmel 1995). Studies of the toxicity of fenthion and naled to Papilio cresphontes Cramer (a standin for P. ponceanus) showed that the concentrations sprayed on the hammocks of Key Largo were at least 400 times greater than the LC-50 for P. cresphontes (Eliazar 1992; Emmel 1994).

When spraying of north Key Largo hammocks ended, in the mid 1980s, *P. ponceanus* began to return, probably by immigration from Old Rhodes, Elliott and smaller keys in Biscayne National Park. On these keys, which were never sprayed, *P. ponceanus* populations were continuously present. The same keys may be home to permanent populations of *G. cayensis*, unless, perhaps, they were eliminated by the saltwater storm surge that temporarily covered them during Hurricane Andrew's assault in August 1992.

Unlike *P. ponceanus*, *G. cayensis* is flightless. If *G. cayensis* has been eliminated from Key Largo, it is unlikely to reestablish soon even if abundant populations exist on Old Rhodes and Elliott Keys.

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