

Systematics and Acoustic Behavior of United States and Caribbean Short-Tailed Crickets (Orthoptera: Gryllidae: *Anurogryllus*)¹

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ABSTRACT

Anurogryllus muticus (De Geer) occurs from northern South America, through the Lesser Antilles, to Puerto Rico and Jamaica. *A. celerinictus*, n. sp., is known from Jamaica, Grand Cayman, and Big Pine Key, Florida. *A. arboreus*, n. sp., occurs from New Jersey and Oklahoma southward to Big Pine Key and Texas. *A. antillarum* (Saussure) and *A. abortivus* (Saussure) are known only from the Cuban types. All nongeneral adults of *arboreus* and most of *celerinictus* and *muticus* are dealated; only *celerinictus* and *muticus* fly. Seasonal life history, subsocial behavior, and characteristics of the burrows of females and juveniles are known only for *arboreus* and Argentine *muticus*.

Calling behavior is known for males of three species. *A. arboreus* and *celerinictus* restrict their calling to the

first two hours after sunset; *muticus* calls as late as four hours after sunset. *A. celerinictus* and *muticus* call from the ground; *arboreus* usually calls from vegetation 0.3–2 meters above the ground. The calling songs are long-sustained, intense trills with wingstroke rates at 25°C of 77 per second for *arboreus*, 140 per second for *muticus*, and 180 per second for *celerinictus*. *A. celerinictus* has the highest long-sustained wingstroke rate yet reported for crickets. Acoustic behavior during courtship and mating has been observed only in *arboreus*. The male produces short trills during courtship, and after the spermatophore tube has been inserted and the still-coupled pair has turned end-to-end, the male produces a five- to 20-minute song. No other cricket is known to sing while coupled.

Members of the genus *Anurogryllus*, known as short-tailed crickets, are of special interest because of their subsocial behavior (Liebermann 1955; Alexander 1961; West and Alexander 1963) and economic importance (Weaver and Somers 1969; Campbell 1971). Like mole crickets, females lack well-developed ovipositors and lay their eggs in underground burrows.

Anurogryllus is generally placed in the subfamily Gryllinae (e.g., Chopard 1967), but Alexander and Otte (1967) suggested that it belongs with *Brachytrupes* and *Urogryllus* in the subfamily Brachytrupinae. The close relationship of *Anurogryllus* and *Urogryllus* seems certain (Randell 1964), but most of the features cited by Alexander and Otte as evidence of a close relationship between *Anurogryllus* and *Brachytrupes* are adaptations to a subterranean, subsocial life that may have been acquired independently. The characteristics of *Urogryllus* are noteworthy in this regard. Its way of life is unknown but morphologically it differs from *Anurogryllus* in ways suggesting a more typically grylline existence: (1) well-developed ovipositor (eggs inserted in ground?), (2) combined length of hind tibia and basitarsus greater than length of hind femur (knees high when walking?), (3) median ocellus beyond line drawn between lower margins of lateral ocelli (vertex not shaped for tunneling?). *Urogryllus* could have acquired grylline characteristics secondarily, but a simpler supposition is that *Urogryllus* descended with little change from an earlier stage in the evolution of *Anurogryllus*. If the latter be the case, *Anurogryllus* is more properly a grylline than a brachytrupine.

Of the 6 species of *Anurogryllus* in Chopard's (1967) catalogue, only *muticus* (De Geer), *antillarum* (Saussure), and *abortivus* (Saussure) occur in the United States or West Indies; the 2 last mentioned are known only from Cuba and are easily distinguished from *muticus* (see key following). The type-locality of *muticus* is Surinam, and it has been reported from Mexico, throughout the West Indies, N to New Jersey. However, this study shows that mainland United States populations of "*muticus*" (so-called) are specifically distinct from the West Indies populations and that at least 2 species occur in the West Indies. On the basis of morphology and geographic range, one of these is conspecific with the type of *muticus* and hence should be called *muticus*.

The following abbreviations are used here, detailing the specimens examined: ANSP, Philadelphia Academy of Natural Sciences; FSCA, Florida State Collection of Arthropods, Gainesville; PCD, P. C. Drummond; JJW, J. J. Whitesell; TJW, T. J. Walker; UFT, University of Florida, tape; USNM, United States National Museum of Natural History.

KEY TO UNITED STATES AND CARIBBEAN *Anurogryllus*

Anurogryllus is characterized by a rudimentary ovipositor, by a combined length of the hind tibia and basitarsus no greater than length of the hind femur, and by 3 ocelli in a nearly transverse row (a line drawn between the lower margins of the lateral ocelli cuts the median ocellus).

- 1 Abdomen of male wholly covered by tegmina; female tegmina longer than pronotum, not scalelike 2
- 1' Not more than ¾ of male abdomen covered by tegmina; female tegmina shorter than pronotum and scalelike 4
- 2 (1) Number of teeth in stridulatory file fewer than 60; pulse rate in calling song more than 100/sec at 25°C; caudal width of pronotum sometimes greater than 5.4 mm; from Big Pine Key, Fla., and southward 3.

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- 2' Number of teeth in stridulatory file more than 60; pulse rate in calling song less than 90/sec at 25°C; caudal width of pronotum no greater than 5.4 mm; from Big Pine Key and northward *arboreus*
- 3 (2) Pulse rate in calling song more than 160/sec at 25°C (Fig. 1); caudal width of male pronotum 5.5–6.5 mm (5.7–6.5 in Jamaica); file tooth density 16–19 teeth/mm (Fig. 2) *celerimictus*
- 3' Pulse rate in calling song less than 160/sec at 25°C (Fig. 1); caudal width of male pronotum 4.5–5.6 mm; file tooth density 18–26 teeth/mm (Fig. 2) *muticus*
- 4 (1') Tegmina of female touching medially; male tegmina covering only $\frac{2}{3}$ of abdomen *antillarum*
- 4' Tegmina of female not touching medially (male unknown) *abortivus*

Anurogryllus muticus (De Geer)

De Geer's Short-tailed Cricket

Synonymy.—*Gryllus muticus* De Geer, 1773: 520 (Type-locality: Surinam).

Acheta guadeloupensis F., 1793: 32 (Type-locality: Guadeloupe, W. I.).

Gryllus comptus F. Walker, 1869: 23 (Type-locality: Constanca, South America).

Gryllus angustulus F. Walker, 1869: 21 (Type-locality: St. Vincent; Jamaica, W. I.).

Gryllodes clarazianus Saussure, 1874: 412 (Type-locality: Argentina).

Gryllus caraibeus Saussure, 1874: 413 (Type-locality: St. Thomas, Guiana).

The initial evidence that the crickets previously known as "*A. muticus*" belong to 3 species was their 3 distinctive calling songs (Fig. 1). Two of these were heard in Jamaica (*muticus* and *celerimictus*) and 2 were heard on Big Pine Key, Fla. (*celerimictus* and *muticus*). Subsequent morphological study revealed that *arboreus* males have a distinctive stridulatory file (Fig. 2), but that the other 2 species cannot always be separated on this basis. However, all specimens of known song from Jamaica (the only locality where both *celerimictus* and *muticus* are known to occur) could be separated on the basis of caudal width of the pronotum, with range 5.2–5.6 mm for *muticus* ($n = 4$) and 5.7–6.1 for *celerimictus* ($n = 9$). One would expect overlap with a larger sample, but of 24 ♂ from Jamaica (song unknown), only 3 had pronotal widths of 5.6 or 5.7 mm. On the basis of stridulatory file, the 5.6-mm specimen was *muticus* and the two 5.7-mm specimens were *celerimictus*. (None of the 3 files fell in the area of overlap shown in Fig. 2.)

There are two reasons for assigning the name *muticus* to the slower-singing Jamaican population (rather than the faster). First, tape recordings from Puerto Rico, St. Croix, and Trinidad (Fig. 1) revealed only the slower song, and these islands, especially Trinidad, are zoogeographically closer to Surinam than are Jamaica and other localities of the faster-singing species. Second, the pronotal width of the lectotype of *muticus* is 5.2 mm. The stridula-

tory file of the lectotype is ambiguous but within the range of specimens of the slower-singing species from Jamaica (Fig. 2).

None of 10 ♀ from Jamaica was collected with a male. Consequently none can be identified with certainty. However, pronotal widths vary from 5.0 to 6.2 mm. In *arboreus*, the only species for which I have positively identified females, female pronotal widths are similar to those of the male. On this basis I have identified 1 ♀ (5.0 mm) as *muticus* and 5 (5.8–6.2 mm) as *celerimictus*.

The Argentine *Anurogryllus* "*muticus*" studied by Liebermann (1955) may or may not belong to the species termed *muticus* here.

Specimens Examined (46:42 ♂, 4 ♀).—All except types and 9 specimens from USNM are in FSCA. JAMAICA: Westmoreland Par., nr. Negril, 10 Dec. 1969, PCD, 1 ♂; Hanover Par., n. of Negril, 22 June 1970, TJW, JJW, PCD, 1 ♂; St. Ann Par., St. Ann's Bay, 21 Nov. 1968, TJW, 1 ♂ (song recorded, UFT 68–650); Clarendon Par., Portland Ridge, 18 June 1970, TJW, JJW, PCD, 1 ♂; St. Catherine Par., Worthy Park, 16 Nov. 1968, TJW, 4 ♂; 18 Nov. 1968, TJW, 1 ♂ (UFT 68–514); 3 mi E Worthy Park, 28 Nov. 1968, TJW, 2 ♂; Portland Par., 3 mi E Port Antonio, 17 Mar. 1969, PCD, 1 ♀. HIS-PANIOLA: San Domingo, Jan. 1921, G. N. Wolcott, 1 ♀ (USNM). PUERTO RICO: Mayagüez to Neguabo, sea level to 1000 m, 8–21 Jan. 1969, TJW, PCD, 12 ♂ (including UFT 69–95); Rio Piedras, 2 Nov. 1958, A. Boike, 1 ♂; 3 mi E San Juan, 26 June 1966, TJW, 1 ♂. ST. CROIX: nr. Little Fountain, 24 Jan. 1969, TJW, PCD, 3 ♂. DOMINICA: 7 Mar. 1964, 1 ♂; 13, 20, Apr. 1964, 2 ♂; 25–27 May 1964, 2 ♂; 11 June 1964, 1 ♂; 7 Jan. 1965, 1 ♂; 19–21 Oct. 1966, 1 ♂ (Bredin-Archbold-Smithsonian Biol. Surv., USNM). GRENADA: 16 May 1968, PCD, 2 ♂. TRINIDAD: Arima Valley, 28–29 June 1966, TJW, 2 ♂ (including UFT 66-1-E); Waller Field, nr. Arima, 30 June 1966, TJW, 1 ♂ (UFT 66-4-H). SURINAM: 1 ♂ (here designated lectotype), 2 ♀ from De Geer Collection, Riksmuseum, Stockholm.

Anurogryllus celerimictus, n. sp.

Fast-calling Short-tailed Cricket

This species is similar to *A. muticus* but is distinguished from it by the characters above and listed in the key. The 2 species are known to occur together only in Jamaica. Since *celerimictus* is not known from the Lesser Antilles or South America, none of the synonyms listed for *muticus* is likely to be *celerimictus*. The name *celerimictus* (*celeri*-, fast; *nictus*, calling, refers to the rapid wingstroke rate during calling.

Measurements of Holotypic Male and Allotypic Female (mm).—Length of body 21 (♂), 25 (♀); length of pronotum 3.9, 3.9; caudal width of pronotum 6.0, 6.2; length of tegmina 13.0, 13.3; length of exposed wings 0, 11.8 (male without visible wings); length of hind femur 11.6, 12.9; length of hind tibia

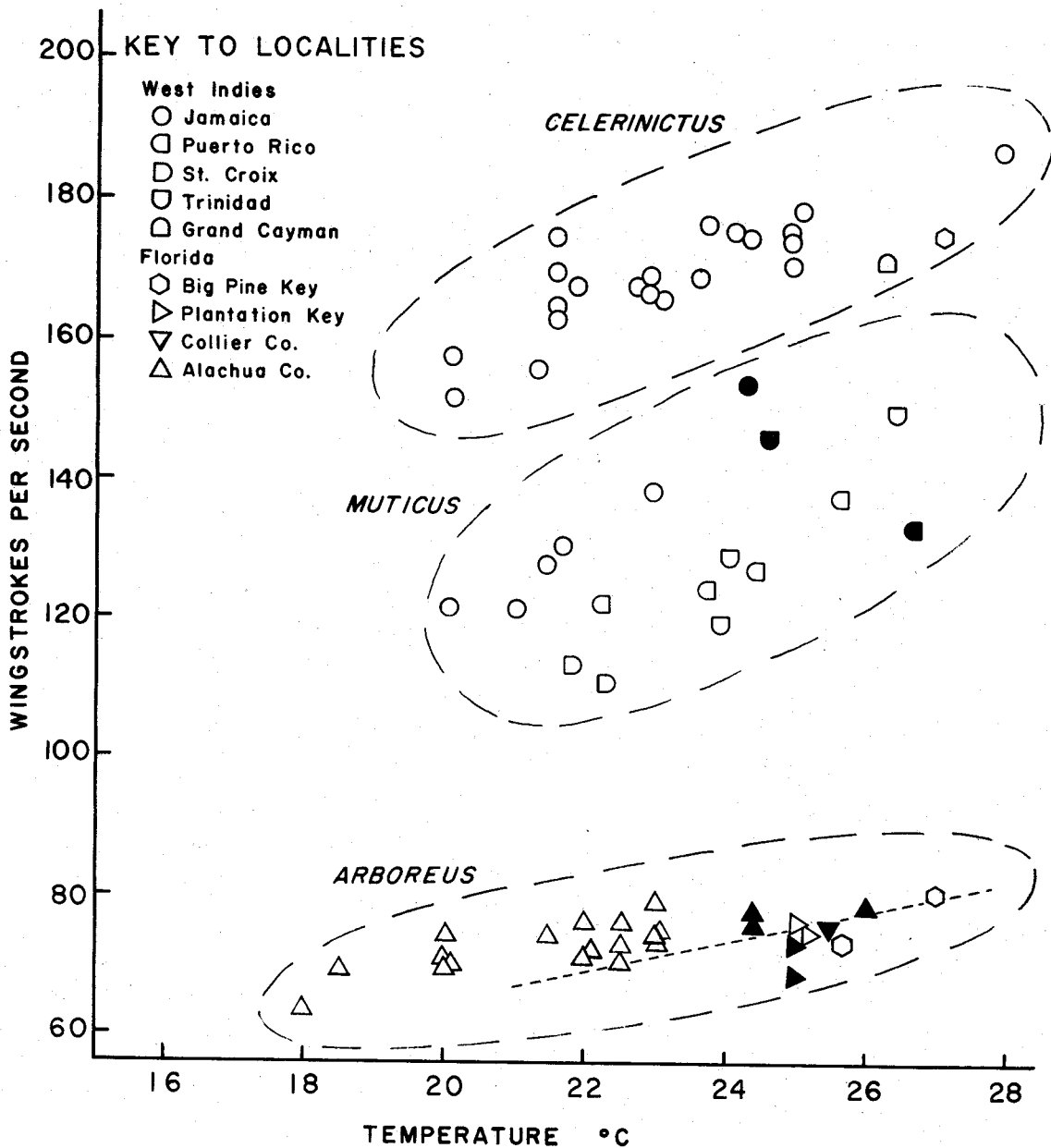


FIG. 1.—Wingstroke rates (deduced from pulse rates) during calling in Floridian and West Indian *Anurogryllus*. Solid symbols are for laboratory tape recordings; open symbols are for tapes made in field. Dotted line for *arboreus* is regression line for unpublished laboratory data.

8.1, 8.0; length of hind basitarsus 3.4, 3.6; length of stridulatory file 2.66; number of teeth in file 42; length of ovipositor 0.6.

Specimens Examined (37:31 ♂, 6 ♀).—Holotype and allotype are deposited in USNM. All others are in FSCA and are designated paratypes. JAMAICA: Westmoreland Par., nr. Negril, 10 Dec. 1969, E. G. Farnworth, 4 ♀ (at UV light) (including ALLOTYPE); 21 June 1970, TJW, JJW, PCD, 4 ♂ (including UFT 70-251, 253, 259); Shafston, 8 Dec. 1969, PCD, 1 ♂; Hanover Par., nr. Orange Bay, 20 Nov. 1968, TJW, 1 ♂;

Manchester Par., Grove Place, 12 May 1969, PCD, 1 ♂; Mandeville, 9 Dec. 1969, E. G. Farnworth, 1 ♀; St. Catherine Par., Worthy Park, 16 Nov. 1968, TJW, 7 ♂, 1 ♀; 18 Nov. 1968, TJW, 1 ♂; 12 June 1970, TJW, JJW, PCD, 1 ♂ (UFT 70-51) (HOLOTYPE); 13 June 1970, TJW, JJW, PCD, 3 ♂ (UFT 70-59, 62, 69); 3 mi E Worthy Park, 28 Nov. 1968, TJW, 1 ♂ (UFT 68-670); St. Andrew Par., Palisadoes, 29 Nov. 1968, TJW, 2 ♂; Kingston, 8 May 1969, PCD, 3 ♂; St. Thomas Par., nr. Norris, 25 Nov. 1968, TJW, 1 ♂; Bath Fountain, 14 June 1970, TJW, JJW, PCD, 2 ♂ (UFT 70-82, 83). GRAND

CAYMAN: nr. George Town, 27 June 1970, TJW, JJW, PCD, 1 ♂ (UFT 70-385). FLORIDA: Big Pine Key, 24 Jan. 1970, TJW, JJW, 1 ♂; 11 June 1970, TJW, JJW, PCD 1 ♂ (UFT 492-1).

Anurogryllus arboreus, n. sp.

Arboreal Short-tailed Cricket

All previous records of "*muticus*" from the United States refer to this species. It differs from the closely similar *muticus* and *celerinctus* by characters discussed above and summarized in the key. Furthermore, specimens of *arboreus* are conspicuously lighter in hue than those of *muticus* and *celerinctus*, having much less dark pigment infused with the brown. The name *arboreus* refers to the frequent use of trees as perches by calling males. The other 2 species call only from the ground.

Measurements of Holotypic Male and Allotypic Female (mm).—Length of body 18 (♂), 16 (♀); length of pronotum 3.5, 3.2; caudal width of pronotum 4.7, 4.7; length of tegmina 11.1, 8.4; length of hind femur 13.1, 12.7; length of hind tibia 7.5, 7.9; length of hind basitarsus 3.6, 3.4; length of ovipositor, 0.8.

Specimens Examined (102:62 ♂, 23 ♀, 17 juv.).—The following collections were studied: USNM (5 ♂, 7 ♀, 2 juv.), ANSP (8 ♂, 6 ♀, 5 juv.), FSCA (49 ♂, 10 ♀, 10 juv.). The HOLOTYPE (213 SW, 41st St., Gainesville, Fla., 12 Apr. 1962, T. J. Walker; UFT 491-15) and ALLOTYPE (ibid., 21 Apr. 1964, T. J. Walker) are deposited in the USNM. The 67 specimens remaining in the FSCA were labeled as paratypes. Peripheral records (Fig. 3) are as follows: Victoria, Tex. (ANSP); Stillwater, Okla. (ANSP); Illinois (Hebard 1934); Chatanooga, Tenn. (USNM); Vinton Station, Va. (USNM); Charlottesville, Va. (ANSP); Washington, D. C. (ANSP); Ocean View, N. J. (ANSP); Big Pine Key, Fla. (FSCA, UFT 71-7); Tucson, Ariz., 19 Sep. 1958, 1 dealated ♂, H. V. Weems, Jr. (FSCA).

Anurogryllus antillarum (Saussure)

Saussure (1874: 414; Fig. 10, 13) described this species from a male and female from Cuba. Caudell (1922) reported a female from Antigua, but 1 suspect he had *Urogryllus rufipes* (Redtenbacher) instead. Except for a longer ovipositor, *U. rufipes* fits the description of *A. antillarum*.

Anurogryllus arborivus (Saussure)

This species is known from a single female from Cuba (Saussure 1874: 415, Fig. 11); however, a juvenile (last-instar) male from Guanajay, Cuba, is perhaps of this species (USNM, 1 Sep. 1915, W. W. Vincint).

SEASONAL LIFE HISTORIES

Only *arboreus* is well-known; it is apparently univoltine throughout its range. In Gainesville, Fla., where I have observed it for 13 years, adult males are present only during April, May, and early June. Adult females generally live longer and tend their

eggs and young juveniles in burrows until late June. One ♀ lived in a laboratory burrow with its juveniles until late August. The juveniles reach next-to-last instar by early fall and mature by April or May.

North of Gainesville, *arboreus* matures slightly later. Records of adult males in New Jersey, Virginia, and central Mississippi are for mid-June. On Big Pine Key, Fla., the southernmost locality for *arboreus*, J. J. Whitesell and I made monthly observations of calling males from March 1970 through May 1971. The earliest *arboreus* songs were heard 26 Mar. and the latest 28 May. The only observations that conflict with this conclusion concerning spring-adult, univoltine *arboreus* are (1) 1 teneral ♂ dug from a burrow by me, 30 Jan. 1959, at Homestead, Fla., and (2) 1 ♂ collected in a residential area "at light" by H. V. Weems, Jr., 19 Sept. 1958, Tucson, Ariz.

Adults of *muticus* and *celerinctus* apparently occur at all times of year in West Indies (see dates under foregoing *Specimens Examined*). However, I heard only 1 ♂ *muticus* at Worthy Park, Jamaica, 12-24 June 1970, where they had been abundant 16-28 Nov. 1968. Liebermann (1955) studied the life cycle of *Anurogryllus muticus* in Buenos Aires, Argentina. It was univoltine with summer adults (December and January) and with late-stage juveniles during the winter.

Even though Mr. Whitesell and I visited Big Pine Key monthly for 15 months and have done occasional field work there before and since, we heard only 2 specimens of *celerinctus* (24 Jan. 1970; 11 June 1970). Consequently, I am not only unsure of its seasonal life cycle there but also of its occurrence there on a continuing basis. Perhaps Big Pine Key specimens migrated from Cuba.

MIGRATION AND MACROPTEROUSNESS

Many species of crickets are dimorphic in wing length. Micropterous individuals are flightless and have metathoracic wings so short they are completely covered by tegmina. The metathoracic wings of macropterous individuals extend beyond the tegmina, and such individuals generally fly at some time during their adult lives. (See Alexander 1968 for the most recent review of this phenomenon.)

Casual examination of pinned specimens of *Anurogryllus* indicates dimorphism in wing length, with only a few individuals macropterous: 7 of 36 *celerinctus* were macropterous; 9 of 51 *muticus*; and 4 (all teneral) of 85 *arboreus*. However, examination of presumed micropterous specimens revealed wing stumps rather than short wings. The dimorphism is not of wing length but of wing shedding, "micropterous" specimens being dealated (Walker 1972). Teneral adults of *arboreus* are macropterous, but soon shed their wings (Weaver and Sommers 1969), and they never fly.

None of the 16 macropterous *celerinctus* and *muticus* specimens are teneral, and at least 5 were collected at light. It is possible that all or most individuals fly before shedding their wings (Walker 1972). If so,

island and small-island demes (e.g. Puerto Rico and St. Croix) and a study of flight orientation in the vicinity of open sea might prove of value in understanding dispersive flights in *celerinictus* and *muticus*.

HABITAT AND BURROWS

In central Florida, *arboreus* occurs in greatest abundance in well-drained but moist soils. The associated vegetation varies: lawns and pastures; early stages of secondary succession; open stands of loblolly pine, southern red oak, or live oak; and closed-canopy mesic hammock. In spite of its broad spectrum of habitats and locally dense populations, *arboreus* is often absent in apparently suitable, accessible sites. In the pinelands of central Louisiana, Weaver and Sommers (1969) found the largest populations in soils with good internal drainage, and lesser numbers in wet, heavy soils with poor internal drainage. In the Florida Keys, I found singing males mostly in dense gumbo limbo hammocks and occasionally on sites from which such a hammock had been removed.

I know the habitats of *celerinictus* and *muticus* only from tracking down singing males. Habitats are similar. Unlike *arboreus*, neither species occurs in closed-canopy forest. The greatest abundance is along roads, in pastures, and in partially shaded, disturbed areas (e.g., new plantings of bananas, or citrus groves).

All short-tailed crickets burrow, but only for *arboreus* and Argentine *muticus* have significant numbers of burrows been studied in the field. In both Louisiana (Weaver and Sommers 1969, Fig. 4) and Florida, overwintering *arboreus* juveniles live in individual, self-constructed burrows. These burrows usually have 2 surface openings, 1 or 2 chambers a few centimeters in diameter, and 1 or more shafts filled or partially filled with wastes. The deepest part

of the burrow is usually about 20 cm below the surface. When an *arboreus* male matures, it first calls at the burrow entrance. After a few evenings of calling, it leaves its burrow and does not return (T. J. Walker, unpublished data). On 2 of 5 occasions when I excavated such male-abandoned burrows, I found adult females. These females would presumably have used these abandoned (or seized? or donated?) male burrows for egg laying and brood care. On the other hand, when given moist soil in the laboratory or in outdoor roofed pens, mated females excavated new burrows of the type just described and proceeded with egg laying and brood care. When *arboreus* males have left their home burrows, they generally spend the daylight hours in burrows abandoned by other individuals, in natural crevices, or in simple, short, self-excavated tunnels (T. J. Walker, unpublished data).

Liebermann (1955, Fig. 3) excavated hundreds of burrows of *muticus* near Buenos Aires. All burrows consisted of a single inclined tunnel ending in a chamber. In winter and spring the burrows contained a single mid- to late-stadium juvenile, and during summer he often found 1 ♀ with eggs or early-stadium juveniles.

The burrows of *muticus* and *celerinictus* I have examined were associated with calling males and were not necessarily excavated by the same individuals, or even by crickets. Only one of 27 calling *muticus* ♂ retreated into a burrow, whereas 12 of 31 calling *celerinictus* ♂ did so. A single male was found in each burrow examined. The only *muticus* burrow (St. Ann's Bay, Jamaica) was about 20 cm long, with the first 10 cm near the surface and the last 10 cm angling downward at about 70°. There was no chamber. The 12 *celerinictus* burrows were mostly simple tunnels 2-8 cm long and inclined at various angles. Two were tunnels with pronounced elbows (one went down and then leveled out, the other was at first slightly inclined and then bent sharply downward). Two had a distinct chamber at the end of an 8-cm tunnel. In one such chamber the cricket was singing facing the entrance (perhaps after retreating from its singing station at the entrance); in the other, the silent cricket was among bits of green leaves and 2 tiny conical snail shells.

I discovered no brood or juvenile burrows of *celerinictus* or *muticus*, but I did not make intensive searches.

ACOUSTIC BEHAVIOR

Males of *arboreus*, *celerinictus*, and *muticus* usually begin calling at sunset or shortly after and continue for at least 30 min. Calling of *arboreus*, at Gainesville, ceases by 2 h after sunset. I know no other cricket species that is as restricted in its daily singing period nor that calls in greatest numbers at twilight. The calling period of *muticus* in Puerto Rico in Jan. 1969 lasted as late as 4 h after sunset and it was much less concentrated in the crepuscle than in the case of *arboreus*. The calling period of *celerinictus* in Jamaica is probably as brief as that of *arboreus* at Gainesville. Presumably, my few records of later

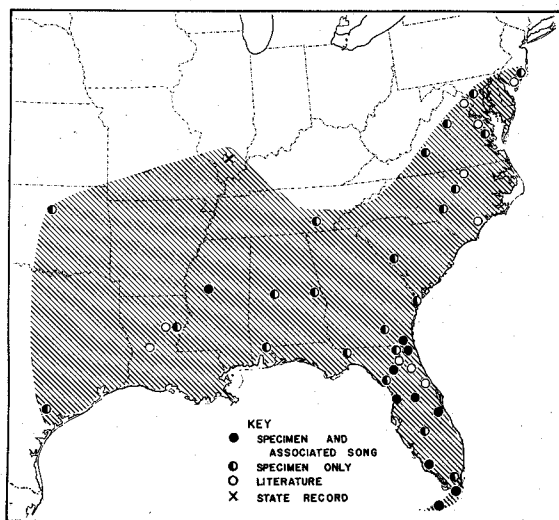
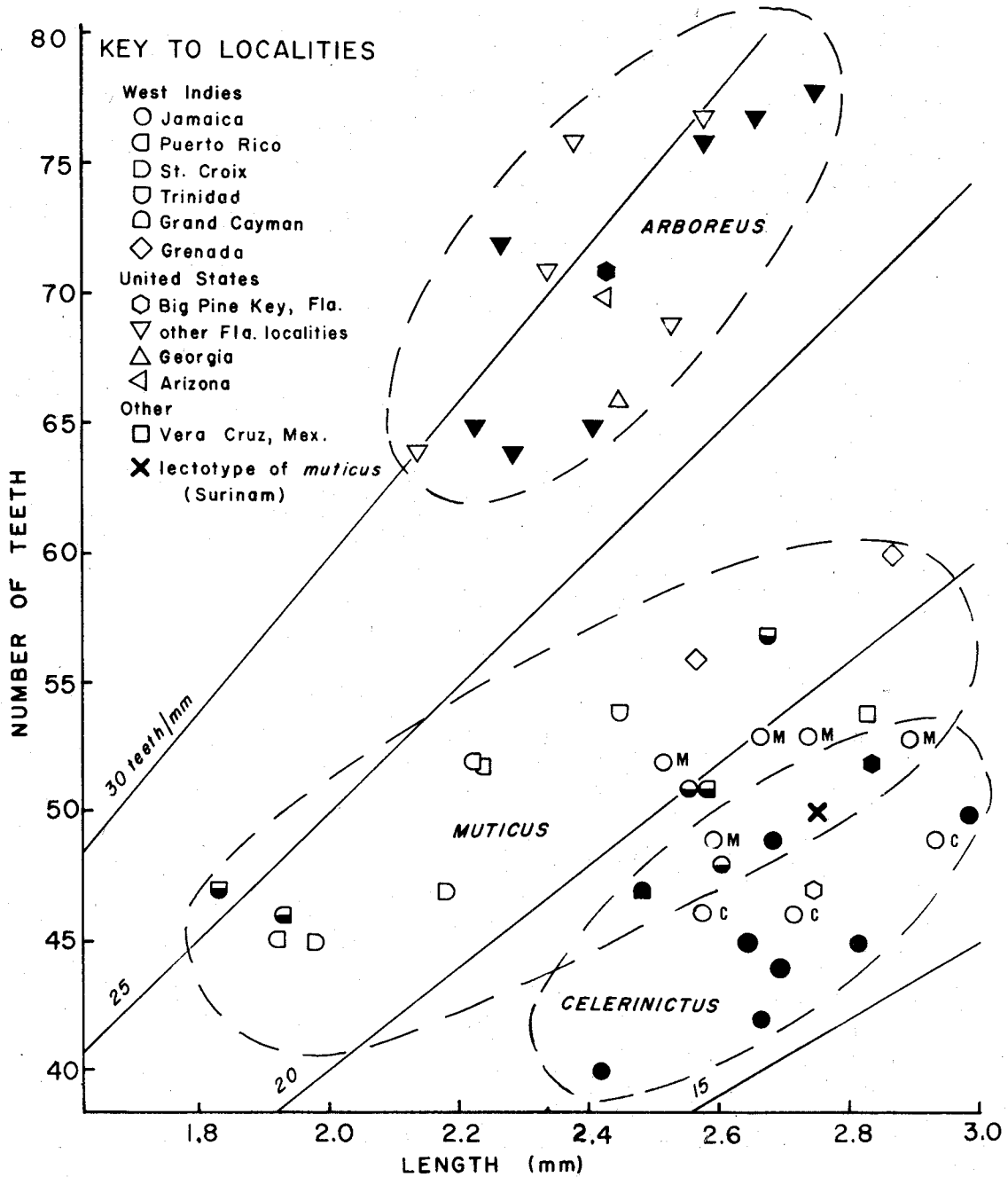


FIG. 3.—Distribution of *A. arboreus*. Peripheral records are listed in the text. Predicted general distribution is shaded. Points are county records except that upper and lower Florida Keys are plotted independent of continental Monroe County, Fla. A specimen-only record from Tucson, Ariz., is not shown.



the 2 dealated *celerinictus* ♂ captured on Big Pine Key may have flown there before losing their wings. The occurrence of macropterousness and dispersive flights in island-living *celerinictus* and *muticus*, but not in mainland *arboreus*, is counter to the generalization that island populations become more sedentary than mainland ones. However, *celerinictus* and *muticus* live in habitats (see following) that would be temporary except for man's activities. The macropterous individuals are able to quit sites that are no longer suitable and to colonize new suitable sites. A comparison of macropterousness in large-

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Anurogryllus singing in Jamaica refer to *muticus*, but I did not distinguish the 2 species at the time.

Males of *celerinictus* and *muticus* call from the ground. Those of *muticus* occasionally sing from the tops of large stones and from paved roads ($n = 5$). Two were observed in Puerto Rico singing from vertical surfaces—one up 3 cm on the side of a tree root, the other up 0.7 m on a clay bank. On the other hand, more than 90% of calling *arboreus* ♂ ($n = 500 +$) are 5 cm or more above the ground. Tree trunks are the most usual singing perches, but the crickets also utilize grass stems, forbs, shrubs, and sides of buildings. In a sample of 78 ♂ in a wooded area, the modal height was 0.8–1 m, and the maximum height was 3.5 m.

Males of all 3 species sometimes call just outside the entrance to a burrow and dart inside when approached. However, only in *celerinictus* (12 of 31) were a significant proportion of calling males so situated. In *arboreus* (see foregoing), males call at the burrow entrance only during the 1st few evenings of their reproductive life. An *arboreus* male that has retreated into its burrow from its station at the burrow entrance will sometimes resume singing in the burrow. The only evidence that *arboreus* ever initiates its singing within a burrow is one instance, shortly after sunset, of *arboreus* song issuing from a burrow with a plugged entrance. (Burrows are usually loosely plugged with dirt or pieces of vegetation during the day, and the cricket removes the plug before sunset.)

The calling songs of *arboreus*, *celerinictus*, and *muticus* are continuous, intense trills. They differ most notably in pulse-repetition rate (Fig. 1), which in cricket calling songs corresponds to the wingstroke rate (Walker 1962). *A. celerinictus* has the fastest long-sustained wingstroke rate known for crickets—180/sec. at 25°C. Some species of *Orocharis* (Walker 1969) exceed this rate, but their songs consist of chirps lasting less than 1 sec.

The frequency of the calling song averages lowest in *arboreus* and highest in *celerinictus*; *muticus* is intermediate but closer to *celerinictus* (Table 1). The intensity of the calling songs seems greatest in *celerinictus* and least in *arboreus*, but males of all 3 species can generally be heard at a distance of 30 m. The only sound-level measurements were made of *arboreus* with a General Radio Type 1551-B m. For 3 monitored ♂ the greatest distance for obtaining a 50 db reading (a weighting scale) was 3–4 m.

Courtship and mating, with accompanying acoustic behavior, has been observed only for *arboreus*. During field studies at Gainesville, I have observed all or portions of more than 40 matings. All but 1 occurred on vegetation (mostly tree trunks) 5 cm–3 m above the ground; 1 was on the ground at the entrance to a burrow. How frequently matings occur within burrows cannot be deduced from available field data. Alexander and Otte (1967) and I observed such matings in glass-sided laboratory cages.

The evidence is ambiguous as to how many times a single *arboreus* female normally copulates. In no case did a pair seen mating in the field remain to-

gether for a 2nd copulation. Furthermore, the maximum number of offspring for an *Anurogryllus* female is apparently less than 100 (cf. 700 + for *Gryllus*), so a single spermatophore might easily provide all the sperm a female could use. On the other hand, Alexander and Otte (1967) observed in the laboratory 2 ♀ copulating several times in succession with single males. When these 2 ♀ and 1 that had copulated only once were separated from males for a while, they would no longer copulate with introduced males, but behaved aggressively toward them. Alexander and Otte (1967, p. 26) concluded: "The female evidently copulates several times with a male, but only if the 'bout' of copulations is uninterrupted." I have observed multiple matings once, and these were not restricted to a single bout: a female was collected after it had mated with a male 2 m above the ground on a tree trunk. The female was caged with another male, and 2 days later they were observed mating within a burrow. Two days after that, the same pair mated twice on the surface within 2 h.

Except where noted, the following description of mating behavior refers to field observations of matings on tree trunks or other vegetation: The female is attracted to the calling male from at least as far as 3 m. The female runs toward the male with periodic brief pauses. In 3 of 4 cases observed, it reached the male quickly. In the other, the female climbed up and down several oak sprouts before climbing the one the male was on. When the female contacts the male, the latter ceases continuous calling, and the female either immediately mounts or the male begins to make short trills (ca. 1 sec) at nearly regular intervals (ca. 3 sec). The male soon turns its rear toward the female and lowers its wings as the female mounts. Their genitalia engage, the spermatophore tube is inserted, and within 10 sec of mounting the female rotates off with the genitalia still engaged. The pair assumes a 180° end-to-end position immediately or following a short time at a lesser angle. The male holds the spermatophore and may be dragged if the female moves. The male resumes continuous trilling a few seconds after the end-to-end position is assumed. The male's copulatory song is identical to its calling song and continues during the 5–20 min the pair remains attached. When the female detaches, it does not have the spermatophore, which either falls free or remains with the male. In 1 instance, the male removed the spermatophore from its terminalia with its hind tibia. The just-mated female usually quickly leaves the male, but on 2 occasions 1 ♀ stayed within 0.5

Table 1.—Frequencies of calling songs of three species of *Anurogryllus*.

	Species		
	<i>arboreus</i>	<i>muticus</i>	<i>celerinictus</i>
Number of tapes	108	17	23
Temperatures (°C)	18.0–34.0	20.0–26.3	20.0–27.8
Range (kHz)	4.7–6.0	5.8–7.2	6.0–7.4
Mean ± SD	5.3±0.3	6.5±0.4	6.8±0.4

m of the male for several minutes. The now solitary male does not alter its behavior, but remains stationary and continues to trill continuously. Its song, though unchanged, should now be termed "calling" again, and it continues until the calling period is over. The longest period noted for a male to continue calling after mating was 91 min.

No cricket except *arboreus* is known to produce a copulatory song (i.e., "sing" while still coupled); however, Alexander and Otte (1967) reported that *Miogryllus verticalis* Audinet-Serville produces a postcopulatory song indistinguishable from calling, with the pair end-to-end and the cerci apparently in contact. They did not state whether the spermatophore is still attached to the female. If it is, the circumstances in *M. verticalis* and *A. arboreus* are nearly identical. Indeed, the "copulatory" song in *arboreus* could be termed postcopulatory if spermatophore-tube insertion rather than genital attachment is equated with copulation (Mays 1971, p. 124). Furthermore, the male *arboreus* may not be directly coupled with the female, since it may only be holding the spermatophore, which in turn attaches to the female.

The copulatory song occurred in all matings I observed in the field. However, in the 3 laboratory matings of 1 pair described above (1 mating in burrow, 2 on surface), it was not produced. Alexander and Otte (1967, p. 25) made no mention of a copulatory song during the in-burrow mating they described. In the only mating I observed on the surface in the field, the copulatory singing ended after 2 min, but the pair remained coupled 18 min longer. In 1 mating on a tree trunk, the male ceased singing when I made a strobe-lighted photograph. The pair did not separate for another 16 min. Since I discovered most mating pairs in the field by locating singing males, it is possible that a significant proportion of pairs on perches remain silent after coupling. On the other hand, the data suggest that coupling males on perches are more likely to sing than those mating on the ground or in burrows. The copulatory song must increase the risk of disturbance both by acoustically oriented predators (Walker 1964) and by other ready-to-mate females. The frequent omission of the copulatory song by males mating in burrows or on surface suggests that the balance between the song's increasing the chance that the female will remain until inseminated, and its increasing the chance that the pair will be disturbed or destroyed, differs depending on the site of the mating.

There is support for the contention that females mating on surface or in burrows are less likely to depart before the spermatophore empties than are females mating on perches. The burrow-mating described by Alexander and Otte (1967, p. 25; exact geographic origin of specimens not stated) differed from any I observed in that the female did not rotate off the male for 10 min. In addition the pair remained with ends together (coupled?) for 36 min after the female dismounted. The longest end-to-end coupling I observed was 30 min, and it was during a mating on the surface, in a laboratory cage.

A. arboreus males sometimes produce aggressive songs. When they are wandering about on the surface, after descending from their singing perches, they may encounter males either on the surface or at burrow entrances. In such instances 1 or both males sometimes emit several brief trills (0.4–1.0 sec) at short intervals (ca. 2 sec). Then the 2 ♂ separate. These trills are produced at a wingstroke rate ca. 25% greater than during calling at the same temperature ($n = 3$ tapes).

An interesting feature of behavior of males singing on perches is that there is no aggression toward nearby conspecific singers. Two or more ♂ often sing from the same tree trunk, and occasionally males sing within 7–15 cm of one another. Such pairs show no interaction and usually remain in the same position for the duration of the singing period.

Leroy (1966) described calling, aggressive, and courtship songs of Tahitian *A. australis* Saussure, the only Old World species of *Anurogryllus*. Her description of the calling song and of the stridulatory file does not distinguish *australis* from *muticus*. (Aggressive and courtship songs have not been described for *muticus*. The courtship song, but not the aggressive song, of *australis* is qualitatively different from that of *arboreus*.) Although Leroy's "*australis*" might be *muticus* introduced to Tahiti, the type of *australis* from Australia has shorter tegmina than *muticus* (Chopard 1951, Fig. 2).

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