Hapithus melodius and H. brevipennis: Musical and Mute Sister Species in Florida (Orthoptera: Gryllidae)¹

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ABSTRACT

Hapithus melodius, n. sp., and H. brevipennis (Saussure) are morphologically similar, contiguously allopatric species. The former is restricted to south peninsular Florida and sings; the latter occurs northward to southern Georgia and westward to Louisiana and is mute. The calling song of melodius has a unique pulse rhythm. Pulse sequences last 10-20 sec with pulses delivered at an irregular, gradually increasing rate.

Like many other cricket genera, Hapithus is known largely from descriptions of pinned specimens. Fifteen species have been named, all from the warmer, moister parts of the New World. The tegmina of males have typical gryllid specializations for sound production. However, a calling song has been described for only one species, Hapithus agitator Uhler of eastern United States, and in that species the northern populations do not produce calling songs whereas the southern ones do (Alexander and Otte 1967). No other species of cricket is known to vary geographically in the occurrence of calling songs. For a while I believed that the only other species of *Hapithus* known from the United States, H. brevipennis (Saussure), was a 2nd example.3 South Florida males produced distinctive, melodious calling songs while north Florida males were mute. However, further study revealed that members of the south Florida populations differed morphologically from those of the more northern ones. The variation was not clinal, and no intermediate individuals or populations were discovered. The south Florida populations evidently represent an undescribed species that is contiguously allopatric with H. brevipennis.

Key to U.S. Hapithus

- 1 Tegmina covering less than two-thirds of abdomen
- Tegmina covering more than two-thirds (usually all) of abdomenagitator
- More than 70 teeth in stridulatory file; length of tegmina usually greater than 2.3 (3) or 2.2 (9) times medial length of pronotum; south peninsularmelodius Florida
- 2' Fewer than 70 teeth in stridulatory file; length of tegmina usually less than 2.3 (\Diamond) or 2.2 (\Diamond) times medial length of pronotum; Lee and Glades Counties, Florida, and northward.....brevipennis

Hapithus melodius, n.sp. Musical Bush Cricket (Fig. 1A)

The name melodius refers to the musical calling song. The species is similar to H. brevipennis but differs in length of tegmina and number of file teeth (see key above).

Holotype.—Male, FLORIDA, Dade Co., Everglades National Park between Mahogany Hammock and Pahayokee, 21 June 1964, Coll. No. 4, T. J. Walker and R. E. Love. Sawgress near roadside. Deposited in U.S. National Museum (Natural History). Light brown with pale pubescence. Each tegmen with pale yellow stripe at junction of dorsal and lateral field bordered by piceous stipe on lateral field. Dorsal field of tegmen with apical piceous splotch, 5 lateral piceous spots, and 3 piceous bars along lateral ends of major veins. Yellow spot, with piceous anterior edge, at mesad end of stridulatory vein. Length of body, 15.0 mm; pronotal length X width, 2.7×3.7 ; length of tegmen, 7.8; length of exposed abdomen, 3.5; length of hind femur 11.8.

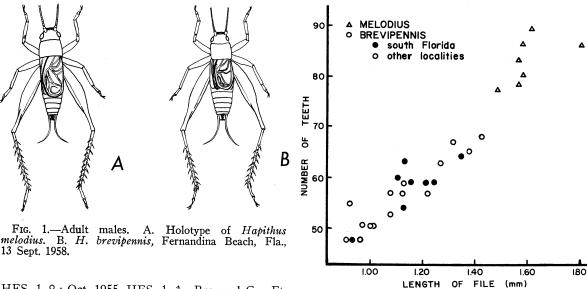
Allotype.—Female, FLORIDA, Dade Co., Everglades National Park, 1 mile w of entrance, 20 June 1964, Coll. No. 3, T. J. Walker, R. E. Love, K. J. Stone. Sawgrass and matted vegetation near roadside. Deposited in U.S. National Museum (Natural History). Similar to holotype. Piceous spots on tegmen small and inconspicuous. Length of body, 16 mm; pronotal length \times width, 2.8 \times 3.9; length of tegmen, 6.8; length of exposed abdomen, 4.0; length of hind femur, 13.7; length of ovipositor, 10.0.

Paratypes.—Florida State Collection of Arthropods (FSCA) (21 &, 11 \, 2 \, juv.): FLORIDA. Dade County, same data as holotype, 5 & (including Univ. Fla. Tape recording UFT 672-6), 2 9 (reared from juveniles), 1 juv.; same data as allotype, 2 & (incl. UFT 672-5), 2 9; Everglades National Park (ENP), Long Pine Key Campground, 1 July 1962, J. D. Spooner, 1 & (UFT 672-1); ENP, Pinelands Trail, 21 June 1964, T. J. Walker (TJW), R. E. Love (REL), 2 9 (reared from juveniles); ENP, Long Pine Key, 22 June 1964, TJW, REL, 1 &; ENP, nr. Taylor Slough, 22 June 1964, TJW, REL, 1 8, 1 juv.; Miami, July 1938, H. F. Strohecker (HFS), 2 &; Miami, 21 Aug. 1939, HFS, 1 &; Miami, 24 Aug. 1939, HFS, 1 &, 2 9; Coral Gables,

¹ Florida Agric. Exp. Stn. Journal Series No. 6184. This study was aided by NSF Grant DEB76-10019. I thank Drs. J. E. Lloyd and R. C. Paul for reviewing the manuscript. Received for publication July 19, 1976.

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³ The most recent catalog of crickets (Chopard 1968) lists Hapithus quadratus Scudder as a species occurring in Texas, Missouri, Florida, Mexico, and Cuba. I agree with Blatchley (1920) and Alexander and Otte (1967) that U. S. crickets called H. quadratus are not specifically distinct from H. agitator.



13 Sept. 1958.

HFS, 1 9; Oct. 1955, HFS, 1 8. Broward Co., Ft. Lauderdale, 31 July 1937, HFS, 2 &. Palm Beach Co., Jupiter, 9 Oct. 1970, TJW, 1 & (UFT 672-10). Martin Co., Jonathan Dickinson State Park, 25 Sept. 1964, TJW, 3 & (incl. UFT 672-8), 2 9. Collier Co., Marco Island, 6 July 1965, tape only (UFT 672-9).

Academy of Natural Science, Philadelphia (ANSP) (1 ô, 1 juv.). FLORIDA. Broward Co., Ft. Lauderdale, 31 July 1937, HFS, 1 &, 5 Sept. 1936, Rehn & Rehn, 1 juv.

> Hapithus brevipennis (Saussure) Short-Winged Bush Cricket (Fig. 1B)

Apithes brevipennis Saussure, 1897:268. Hapithus brevipennis, Rehn and Hebard 1905:802.

The specimens examined were from Academy of Natural Science, Philadelphia (n=195), and Florida State Collection of Arthropods (n=55).

Morphology.-Males of H. melodius and brevipennis can always be identified by the number of teeth and length of the stridulatory file. South Florida brevipennis are no more similar to melodius in file measurements than are north Florida brevipennis (Fig. 2). For both melodius and brevipennis the file-tooth density approximates 50/mm.

A more convenient identifying feature, and one that applies to both sexes, is the ratio of tegminal length to medial pronotal length. Unfortunately the 2 species overlap slightly in this ratio. The mean, standard deviation, and range for the ratio in 22 & of melodius are 2.7, 0.2, $2.\overline{3}$ -3.1; in 13 \circ , 2.4, 0.1, 2.2-2.6. The same statistics for the ratios in 23 & of brevipennis from central and south peninsular Florida (where brevipennis is geographically closest to melodius) are 2.1, 0.2, 1.8-2.5, in 17 9, 2.0, 0.2, 1.6-2.3. Use of the ratio as proposed in couplet 2 of the above key results in identifications that are 80-95% correct. Specimens of brevipennis from Fort Myers, within 50 mi of the northwesternmost locality for melodius, were not significantly different in teg-

Fig. 2.—Length and tooth number of stridulatory files of Hapithus melodius and H. brevipennis. South Florida localities for brevipennis were in Charlotte, Lee, Desoto, and Glades Counties.

minal-pronotal ratios from those from central peninsular Florida.

Geographical Distribution. — Fig. 3 shows the known and predicted distributions of the two species. All records for melodius are substantiated in the list of paratypes. Peripheral records of brevipennis are as follows: LOUISIANA, no specific locality (Saussure 1897); ALABAMA, Springhill, Mobile Co., (ANSP), Dothan, Houston Co. (ANSP); GEORGIA, Claxton, Evans Co. (ANSP), Sandfly, Chatham Co. (ANSP); FLORIDA, Glades Co. (FSCA), Ft. Myers, Lee Co. (ANSP, FSCA).

Habitat.—Both H. brevipennis and H. melodius occur in a variety of habitats but always within a few feet of the ground and in fire-susceptible sites. Most records for *melodius* are from the edges of sawgrass (Mariscus jamaicensis) marshes and from the

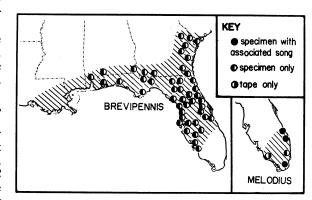


Fig. 3.—Distribution of Hapithus melodius and H. brevipennis. Circles indicate county records. The predicted general distribution for each species is shaded.

undergrowth of southern-slash-pine (*Pinus elliottii densa*) forests. One record is from a stand of cabbage palms (*Sabal palmetto*) and another is from a grassy coastal dune. Most records for *brevipennis* are from pine flatwoods, often on saw palmetto (*Serenoa repens*) or in grassy areas. The species has been taken in coastal scrub and in grassy flats protected by dunes. Two *brevipennis* adults received by the Florida Department of Agriculture were described as "feeding on leaves of young citrus."

Seasonal Life History.—Both H. brevipennis and H. melodius are probably univoltine. The evidence is compelling only for brevipennis. In Alachua Co., Fla., juveniles of brevipennis have been collected as early as 8 April but no adults are known prior to 16 August. Adults are commonly encountered in September and October and the latest record is 23 December. Elsewhere, collecting dates for brevipennis fit the same pattern. The earliest record for an adult is 2 Aug. (Sumter Co., Fla). Adults of melodius have been collected as early as 20 June, as late at 9 Oct., and during all intervening months. Large juveniles of melodius were collected 20 and 21 June and 5 September.

Acoustic Behavior and Mating. - Like solitary males of most species of crickets, those of melodius frequently call for minutes at a time whether outdoors at night or in cages in a darkened room. On the other hand, I have never heard a male of brevipennis make a sound. For solitary Alachua County males I have accumulated more than 100 crickethours of nocturnal listening both indoors and out. No calling song of normal loudness could have been missed outdoors, and even a nearly inaudible calling song should have been detected indoors. The occurrence of courtship sounds is more difficult to dismiss—I have never observed courtship. I have placed males with field-collected adult females but observed no mating or behavior resembling courtship. In melodius the courtship singing is loud enough to call attention to a pair in the field.

The evidence against sound production by brevipennis is strong only for Alachua Co. and southward. Although brevipennis might call to the north or to the west, substantial field-work suggests otherwise. Geographical uniformity in muteness in brevipennis would agree with its geographical uniformity in morphology.

The calling song of *melodius* is similar to that of *Hapithus agitator* (Alexander and Otte 1967) in frequency but not in its other physical characteristics. The frequency corresponds to the rate at which file teeth are struck (Walker 1962) and varies with temperature. It is 3.5–5.2 kHz for *melodius* and 3.8–5.6 for *agitator*. Each song pulse (produced by a tegminal closure) in *melodius* lasts 15–25 msec and in *agitator* about half that long. The shorter pulse in *agitator* is predictable from its shorter file—about half as long as in *melodius* and with only half as many teeth (0.78–0.82 mm and 36–38 teeth, n=3).

The pulse rhythm during the calling song of melodius (Fig. 4) is different from that known for

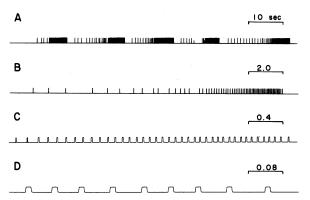


Fig. 4.—Timing of pulses in the calling song of *Hapithus melodius*. Holotype at 24.4 C in cage in laboratory (Univ. Fla. tape 672-4-a). Each vertical mark (A, B) or rectangle (C, D) represents one pulse. A. 75 sec of calling. B. The 2nd sequence in A. C. The terminal 40 pulses of the 2nd sequence in A. D. The terminal 9 pulses of the 2nd sequence in A.

any other species of cricket. The pulses are produced in sequences lasting 10-20 sec. Within each sequence pulses are delivered at an irregular, gradually increasing rate. A human listener hears the initial pulses of a sequence as individual musical tinks and the terminal pulses as a trill lasting longer than 1 sec. A few other crickets deliver pulses at an increasing rate, but the increase is smooth or stepwise rather than erratic. In most crickets the pattern of acoustically effective tegminal closures (i.e., the pulse rhythm) during calling conforms to the assumption that one temperature-influenced neural oscillator is switched on and off. In a few crickets 2 such oscillators, alternatively employed, must be postulated, and in a few a more complicated oscillator—one that smoothly changes rate at constant ambient temperature—may be required. A gross analysis of the pulse rhythm of melodius suggests a smoothly changing oscillator with a variance-increasing circuit, or imperfection. More detailed analysis reveals that the crickets favor 2 modes having a 1:2 ratio—suggesting the added complexity of a frequency doubler (or halver).

The bimodality became apparent in a pulse-by-pulse analysis (n=299) of the 5 sequences in Fig. 4A. All pulses and following intervals were measured to the nearest 0.01 sec. Fifty percent of such measurements clustered about a mode of 0.07 sec, corresponding to 14 pulses/sec, and 28% clustered about a mode of 0.14 sec, corresponding to 7/sec. The percent of measurements falling at each .01 sec interval, starting at 0.05 (0.045–0.055 sec) and ending at 0.20, was 0, 5, 17, 13, 9, 6, 2, 6, 5, 8, 4, 5, 0, 1, 1, 1. (The 2 modes are italicized.) Less extensive analysis of songs of 2 other individuals revealed corresponding bimodalities. What aspects of the pulse rhythm of *melodius* are important to communication are unknown—as are such aspects in all other crickets that produce complex pulse rhythms.

During a melodius calling song the pulses are

delivered at approximately equal intensity. Occasionally the initial pulses, or a few of them, are less intense. The generally uniform intensity of pulses and the irregular acceleration keep the song of *melodius* from conforming to category E_1 in Alexander's (1962, p. 449) classification of patterns in cricket acoustical signals.

I have observed courtship in melodius once in the field and once in the laboratory (Univ. Fla. tape 672-8-c). Unlike agitator, courtship singing in melodius does not differ noticeably from calling in tonal quality. The pulse rhythm is similar to that of calling but more irregular. Pulses are produced at slow rates for long periods with faster rates more frequent as courtship progresses. No terminal trills, as in calling, are produced. During the 1st mounting observed in the laboratory the female may not have received the spermatophore that was held by the male's terminalia even though their abdominal tips remained engaged for 10 minutes. Thirty-eight minutes later she mounted again and this time dismounted with a spermatophore attached. The same female received another spermatophore from the male 35 min later. Both melodius and brevipennis have a pair of shallow metanotal depressions each with a tuft of setae. These may be homologous or at least analogous to the metanotal glands of oecanthine crickets. The female was not seen to feed at the area, although her head was in the appropriate place during spermatophore transfer.

During both calling and courting the tegmina are held at an angle of approximately 35–45° with the thorax—compared to 50–70° for *agitator*.

Phylogeny.—H. melodius and brevipennis are apparently sister species—i.e., the only 2 species derived from the 1st precursor species they have in common. Their morphological similarity and their geographical relationships support this contention.

Reconstructing their history is complicated by the fact that no geographical barrier, present or past, coincides with the boundary between the 2 species. Perhaps they speciated farther north than their present zone of contact. During the successive glaciations of the Pleistocene, sea levels rose making an island or islands of the southern highlands of the Florida peninsula (see McCrone 1963 for a summary of earlier literature). H. brevipennis and melodius may have become species after populations of the stem species were isolated during whatever inter-glacial (Yarmouth?) left the 100 ft or Wicomico Shoreline (McCrone 1963). If so, the mainland, north Florida populations became brevipennis and the insular, Lake Wales Ridge populations became melodius. When the oceans receded (during the Illinoian glaciation?), both species expanded their ranges. When the 2 species came in contact, they kept their specific integrity. *H. brevipennis* continued moving southward competitively displacing *melodius* until *melodius* no longer occupied any of its place of origin.

If this scenario is generally correct, study of interactions of brevipennis and melodius at their places of contact might reveal how brevipennis was able to displace melodius from much of its former range. It might even reveal that the displacement is continuing.

The stem species of brevipennis and melodius was very likely musical. Most related crickets are. Furthermore if the stem species had lacked the complex genetic instructions required for singing, it is unlikely that melodius would have regained them—although its unique pulse rhythm could have originated in this manner. I have previously discussed circumstances that may lead to loss of calling song, as in brevipennis (Walker 1974). To these I would add the possible role of parasitoids that home in on their hosts' calling songs (Cade 1975, Soper et al. 1976). No one has studied pair formation in crickets lacking calling songs, but Paul (1976) has shown that chemicals may supplement acoustic cues in pair formation in ground crickets (Nemobiinae).

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