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The *uhleri* group of the genus *Amblycorypha* (Orthoptera: Tettigoniidae): extraordinarily complex songs and new species

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Abstract

The *uhleri* group of the genus *Amblycorypha* consists of *A. uhleri* Stål and 4 new species: *arenicola*, *cajuni*, *longinicta*, and *rivograndis*. The species are easily distinguished in the field by features of their songs, and most specimens can be identified by size and features of the ovipositor and male stridulatory apparatus. Males of the *uhleri* group produce the most complex calls known for ensiferan Orthoptera and thus earn the common name of "virtuoso katydids". Each species uses 4 types of wing-movement cycles to produce 4 types of syllable sequences. During these sequences there are gradual and sudden changes in intensity. The 4 types of sequences are produced in more or less predictable order, with a complete song requiring 4 to > 60 s depending on the species, the population, and the temperature. In response to these songs, sexually responsive females make nondescript answering "ticks" immediately before and during the place in the songs where the males produce "type IV" syllables. Available evidence suggests that sequences of type I and II syllables are of special significance in eliciting ticks from females, that type III sequences may function in causing females to approach the male from afar, and that type IV sequences may lessen the chances of cuckoldry by eavesdropping males.

Key words

Phaneropterinae, *Amblycorypha*, complex calling songs, female phonoresponse

Introduction

In their 1914 revision of North American *Amblycorypha*, Rehn and Hebard recognized 3 subdivisions of the genus. One of these, consisting of taxa closely related to *Amblycorypha rotundifolia* (Scudder), was recently revised by Walker *et al.* (2003). Another consisted of species of large size as exemplified by *Amblycorypha oblongifolia* (DeGeer). The 3rd subdivision consisted of a single species of small size, *Amblycorypha uhleri* Stål, which they noted was "very plastic, varying considerably in size, both individually and geographically, and appreciably in the proportionate width of the tegmina and in the length and relative depth of the ovipositor".

This paper describes 4 new species in the *A. uhleri* group and compares their geographical distributions, morphology, acoustic behavior and ecology.

Methods

Most fieldwork was at night. Most males were collected by homing on their calling songs. Females were collected in habitats where males were calling, by shining light on foliage or by sweeping vegetation with a net. Specimens were often held alive with access to water and fragments of dry dog food in screen cages or small jars with screen tops. Songs were recorded full track on 0.25 inch

tape at 15 ips with an Ampex 351, Nagra III, or Nagra IV analog tape recorder and an American D33 or ElectroVoice 655C dynamic microphone. Most recordings were made of caged individuals in the laboratory, but others were made of caged individuals outdoors and of free individuals in the field. A 61-cm diameter parabolic reflector aided the recording of free individuals. Many of the recordings of *A. longinicta* were part of a study of the effects of temperature on calling in which temperatures were measured within the cages with a copper-constantan thermocouple and a Leeds and Northrup potentiometer (Walker 1962). Otherwise, temperatures were read from a mercury laboratory thermometer at the cage or parabola. Initially recordings were analyzed with a Kay Elemetrics Model 7029A sound spectrograph. Recently some of the recordings were digitized at a sample rate of 44,100/s and analyzed with CoolEdit 2000 (Syntrillium Software) running on a Pentium II, 333 MHz PC.

Male katydids make their calling songs by moving a sharp, up-turned edge (*scraper*) at the base of the right tegmen along a series of downward projecting teeth (*file*) at the base of the left tegmen. The teeth are on a *stridulatory vein* that is visible from above as a prominent feature of the *stridulatory field* of the left tegmen. The set of sounds made by one cycle of tegmental movement is called a *syllable*. Determining what sounds are made during particular parts of a cycle requires that tegmental movement and sound be recorded simultaneously. The details of ensiferan stridulatory movements have been recorded with high-speed photography (Walker *et al.* 1970) and with an opto-electronic device developed by Helversen and Elsner (1977). Walker and Dew (1972) applied the former method to the song of *Amblycorypha longinicta* to learn its tegmental movements during calling and how these relate to the components of its 4 types of syllables, which they designated as type I, II, III, and IV. Their results are used here to infer the relation between tegmental movements and syllable components for the other species in the *uhleri* group.

Rates of type I syllables were based on the duration of the last 10 syllables in the type I sequence, prior to any change in syllable period presaging the transition to type II syllables. If fewer than 10 type I syllables were produced, all that were essentially even in period were measured. Rates of type II syllables were based on the duration of one fewer syllables than the total number in the type II sequence, as measured from the first to the last C2 sound in the sequence (see Fig. 7). In *A. longinicta*, *arenicola*, and *uhleri*, rates of type III syllables were based on the time from the start of the second to the start of the penultimate C sound (Fig. 7A, B, E). In *A. rivograndis* and *cajuni*, these rates were based on the time from the start of the first to the start of the last C sound (Fig. 7C, D).

Rates of type IV syllables were measured from the start of the first to the start of the last syllable in sequences in which the syllables were evenly spaced. Linear regression was used to establish trend lines for graphs showing syllable rate as a function of temperature. CoolEdit's Blackmann-Harris FFT analyses were used to examine the carrier frequencies of the recorded songs (FFT size = 2048, Range = 120dB).

A calibrated ocular micrometer of a Zeiss stereomicroscope was used to measure pronotal length, tegminal width, hind wing exposure, ovipositor length, and width of the stridulatory field. Pronotal length was measured medially. Tegminal width was measured at the widest point of a tegmen. Hind wing exposure was the minimum distance from the tip of the hind wing (at rest) to the corresponding tegmen. Ovipositor length was measured as the straight-line distance from the apex to where the ventral edge of the ovipositor normally met the subgenital plate. Stridulatory field width was measured as the maximum distance between the outer edges of the tegmina as viewed from above (and thus included the stridulatory fields of both tegmina). Tegminal and femoral lengths were measured with a dial micrometer. For measurements of paired structures, the left side was favored over the right.

Features of stridulatory files were assayed by cutting the stridulatory field from the left tegmen of males, inverting it, and microscopically examining the file. File teeth were counted by moving them, with the aid of a mechanical stage, across a line on an ocular micrometer of a compound microscope, or by counting the teeth on a digital image made with a Syncroscopy Auto-Montage system (<http://www.syncroscopy.com/syncroscopy/>). To be counted as file teeth, candidate structures had to be elongate with the long axis perpendicular to the axis of the file and evenly spaced or nearly so. File length was measured as the straight-line distance from the center of the first file tooth to the center of the last file tooth, using either the calibrated ocular micrometer of the compound scope or the calibrated scale of the auto-montage system.

Collections are abbreviated as follows: ANSP, Academy of Natural Sciences of Philadelphia; FSCA, Florida State Collection of Arthropods; UMMZ, University of Michigan Museum of Zoology; USNM, National Museum of Natural History; and WTL, Walker Tape Library.

The recordings in WTL will be archived and made available on the web by the Macaulay Library of Natural Sounds at Cornell University. Excerpts of representative recordings, including those of the *A. uhleri* group, are already accessible on the web (Walker 2004). At this same site are spreadsheets with the data used to develop Figs 5, 8, and 9 and other aspects of this paper and a database that substantiates the localities mapped in Fig. 4, along with detailed information about the collecting sites of many of the specimens reported in this study.

Results and Discussion

Amblycorypha Stål

Type species.— *Amblycorypha oblongifolia* (De Geer)

Recognition.— Distance between antennal sockets at least twice width of basal antennal segment; hind femur reaching to rear 1/4 of tegmen or beyond; ovipositor elongate and curving gradually upward.

North American species of *Amblycorypha* fall easily into 3 groups: the *rotundifolia* group, consisting of *rotundifolia* (Scudder), *alexanderi* Walker, *bartrami* Walker, and *parvipennis* (Stål) (Walker *et al.* 2003);

the *oblongifolia* group (species listed below); and the *uhleri* group.

Specimens can be assigned to group with the following key.

- 1 Humeral sinus of lateral lobe of pronotum deep (Fig. 1A); each metasternal lobe longer than wide (Fig. 1B) 2
- 1' Humeral sinus of lateral lobe of pronotum shallow; each metasternal lobe wider than long (Fig. 6 of Walker *et al.* 2003)
- *rotundifolia* group
- 2 Males with 4 dark marks on outside edges of pronotal disk (Fig. 2); ovipositors no longer than 10 mm, with acuminate teeth (Fig. 3); specimens usually small for genus (maximum length of tegmen, 31 mm; of pronotum, 6.6 mm) *uhleri* group
- 2' Males without 4 dark marks on outside edges of pronotal disk (though sometimes with a heavy dark line along each edge); ovipositors no shorter than 11 mm, with short teeth; specimens usually large for genus (minimum length of tegmen, 29 mm; of pronotum, 5.6 mm) *oblongifolia* group

Rehn and Hebard (1914) placed 5 taxa in the *Amblycorypha oblongifolia* group: *A. oblongifolia* (DeGeer), *A. floridana floridana* Rehn, *A. floridana carinata* Rehn and Hebard, *A. huasteca* Saussure, and *A. insolita* Rehn and Hebard. Subsequent studies have added no taxa, but *A. carinata* is here raised to species status because its song differs greatly from that of *A. floridana*, and the 2 species overlap in geographic distribution without apparent hybridization (Walker 2004).

The only species of *Amblycorypha* that do not occur in the United States are *A. tepaneca* and *A. guatemalae*. Both were described by Saussure and Pictet (1897) and are known only from holotypic males from Mexico and Guatemala. On the basis of the key above and photographs of the holotypes on the web (Naskrecki 2004), neither belongs to the *uhleri* group. *A. guatemalae* keys to the *oblongifolia* group. *A. tepaneca* would also, except for its small size. As recorded in the original description, its tegminal and pronotal lengths are respectively 27.5 and 3.5 mm.

Amblycorypha uhleri species group

The *uhleri* group has at least 5 species. All have distinctive songs, and, unlike species of the *rotundifolia* group, specimens are generally identifiable by morphological features.

Amblycorypha uhleri Stål 1876: 57

Uhler's virtuoso katydid

(Figs 4D, 5, 6E, 7E)

Stål's type of *A. uhleri* is in the Naturhistoriska Riksmuseum in Stockholm (Naskrecki 2004). Harold Grant, of ANSP, visited the Riksmuseum in the early 1960's and reported in notes made available to me, that there were 2 specimens identified as *A. uhleri* in addition to a male with these 3 labels: "Texas" [print], "Typus" [print], "uhleri/ Stål" [hand]. Grant concluded that one of the 2 specimens, another Texas male, was "absolutely conspecific" with the one labeled as type and borrowed it for further study. He later allowed me to examine this specimen, which on the basis of its overall size, coloration, and stridulatory field I judged to be conspecific with specimens I had collected in Kerr County, Texas.

The type and the specimen I examined were almost certainly collected by Gustaf W. Belfrage, a Swedish nobleman who lived in Bosque County, Texas, from 1868 to 1882. Belfrage was a prodigious

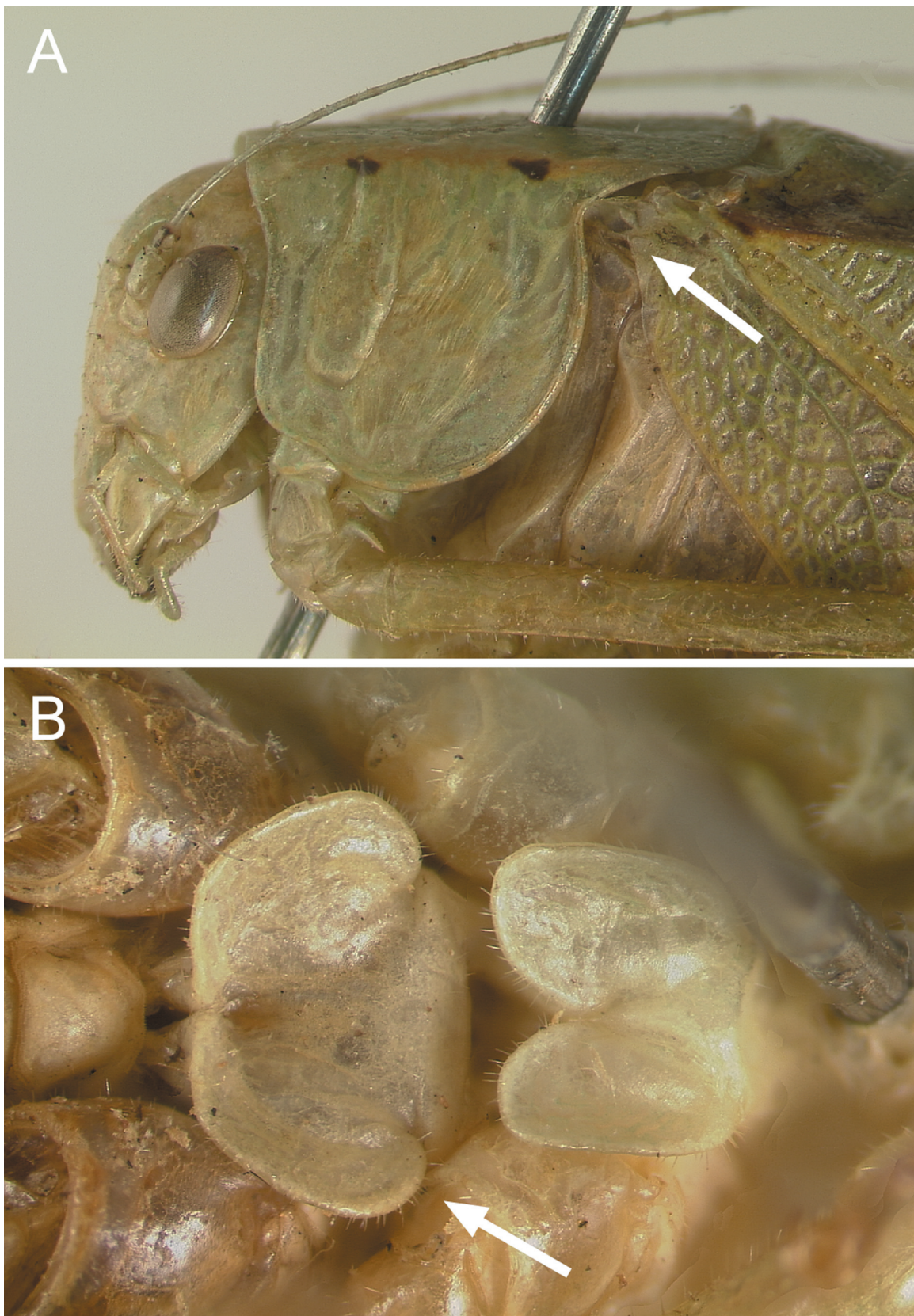


Fig. 1. Features that separate species of the *Amblycorypha uhleri* complex from those of the *A. rotundifolia* complex. A. Deep humeral sinus (white arrow) of lateral lobe of pronotum. B. Each metasternal lobe (white arrow) longer than wide (specimen is inverted with the head to the right; the lobes of the mesosternum are between the metasternal lobes and the pin shaft at extreme right). Photographs are of a male *A. arenicola* from Gainesville, Florida.

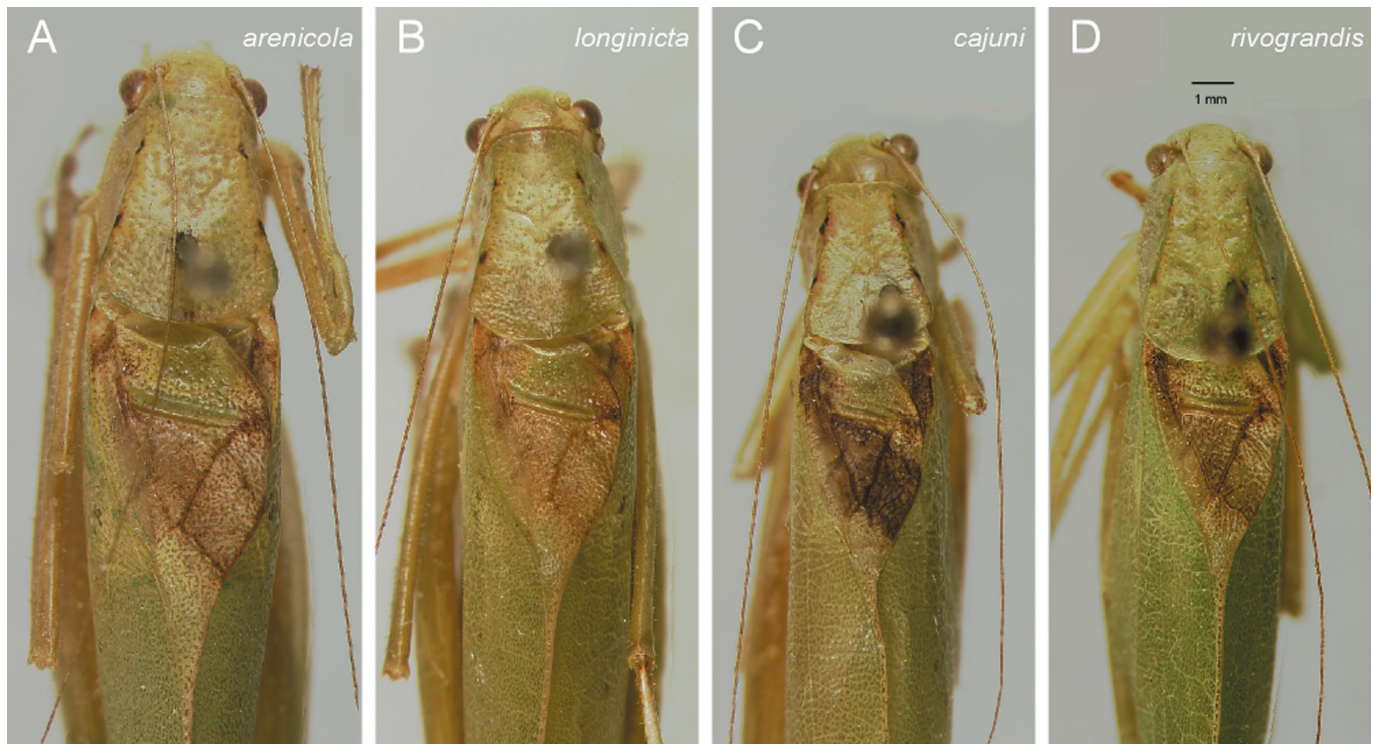


Fig. 2. Stridulatory fields and pronotal disks of males of 4 new species of the *Amblycorypha uhleri* group. A. *arenicola*, Gainesville, Florida. B. *longinicta*, Gainesville, Florida. C. *cajuni*, Holmes County, Mississippi. D. *rivograndis*, Hidalgo County, Texas. (All magnifications as in D.)

collector of insects, and from 1868 to 1871 sold large numbers to the Swedish Academy of Science of Stockholm (Geiser 1937). Most, though not all, of Belfrage's specimens came from Bosque County, making that county the presumptive type locality of *uhleri*.

Other specimens.— 8 ♂♂, 2 ♀♀. TEXAS: Bosque Co., 28 Jun 1959, 2 ♂♂, UMMZ; Coryell Co., 5 Jul 1955, 2 ♂♂, UMMZ; Ellis Co., 1 Sep 1954, 1 ♂, UMMZ; Kerr Co., 17-18 Aug 1921, 1 ♀, ANSP, 20 Aug 1964, 1 ♂ (WTL-014-3), FSCA; Uvalde Co., 21-22 Aug 1912, 2 ♂♂, 1 ♀, ANSP.

***Amblycorypha arenicola*, new species**
sandhill virtuoso katydid
(Figs 1, 2A, 3A, 4B, 5, 6B, 7B, 8B, 9)

Holotype.— Male. Gainesville, Alachua Co., Florida, 27 Jun 1961, T.J. Walker, WTL002-18, FSCA. Green; possessing the characters that distinguish the species group (see key); hind femur reaching tip of tegmen. Pronotal length 5.6 mm, width 4.1; tegminal length 28, width 8.5; hind femur length 26; hindwing exposure 6.5.

Allotype.— Female. Gainesville, Alachua Co., Florida, 10 Jun 1963, Coll. #1, T.J. Walker & R.E. Love, WTL002-22, FSCA. Like the holotype but hind femora exceeding tips of tegmina by 2 mm. Pronotal length 5.6 mm, width 3.9; tegminal length 29, width 8.1; hind femur length 29; hindwing exposure >3.0; ovipositor length 9.4.

Other specimens.— 213 ♂♂, 83 ♀♀. ANSP, 10 ♂♂, 13 ♀♀; FSCA, 92 ♂♂, 15 ♀♀; UMMZ, 111 ♂♂, 55 females. Counties represented: ALABAMA: Mobile. FLORIDA: Alachua, Baker, Brevard, Clay, Columbia, Dade, Duval, Escambia, Gilchrist, Hillsborough, Jackson, Jefferson, Lake, Leon, Liberty, Marion, Martin, Orange, Polk, Putnam, Union,

Volusia, Walton. GEORGIA: Bryan, Decatur, Dougherty, Houston, Jeff Davis, Montgomery, Richmond, Tift. NORTH CAROLINA: Hoke, Moore. SOUTH CAROLINA: Colleton, Dillon, Jasper.

Etymology.— This species is named for its association with sandhill habitats (*areni*, sand; *cola*, dweller).

***Amblycorypha longinicta*, new species**
common virtuoso katydid
(Figs 2B, 3B, 4A, 5, 6A, 7A, 8A)

Holotype.— Male, Gainesville, Alachua Co., Florida, 1 Jul 1961, T. J. Walker, WTL004-10, FSCA. Green; possessing the characters that distinguish the species group (see key); hind femur reaching tip of tegmen. Pronotal length 5.0 mm, width 3.5; tegminal length 26, width 7.3; hind femur length 24; hindwing exposure 5.5.

Allotype.— Female, Gainesville, Alachua Co., Florida, 28 Jul 1963, T.J. Walker, WTL004-26, FSCA. Like the holotype but hind femora exceeding tips of tegmina by 6 mm. Pronotal length 5.1 mm, width 3.4; tegminal length 23, width 6.3; hind femur length 26; hindwing exposure 2.0; ovipositor length 7.7.

Other specimens.— 457 ♂♂, 171 ♀♀. ANSP, 94 ♂♂, 49 ♀♀; FSCA, 187 ♂♂, 43 ♀♀; UMMZ, 172 ♂♂, 78 ♀♀; USNM, 4 ♂♂, 1 ♀. Counties and parishes represented: ALABAMA: Baldwin, Butler, Calhoun, Cleburne, Conecuh, Dallas, Escambia, Houston, Lee, Madison, Mobile, Montgomery, Tuscaloosa. ARKANSAS: Benton, Carroll, Garland, Hempstead, Johnson, Lee, Madison, Mississippi, Pike, Washington. FLORIDA: Alachua, Charlotte, Dade, Duval, Escambia, Gadsden, Glades, Hamilton, Holmes, Jackson, Jefferson, Lake, Leon, Levy, Liberty, Manatee, Marion, Osceola, Putnam,

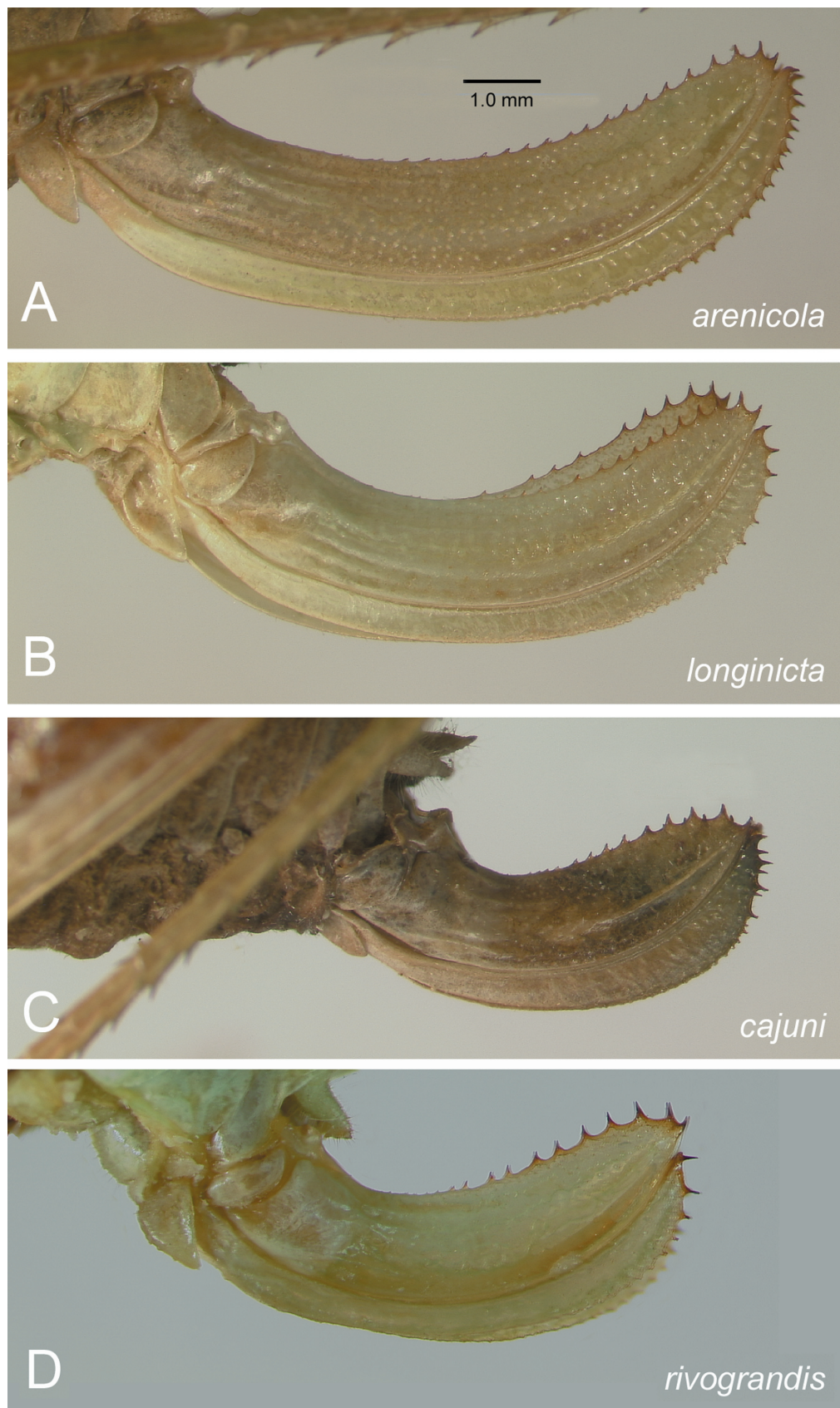


Fig. 3. Ovipositors of 4 new species of the *Amblycorypha uhleri* group. A. *arenicola*, Gainesville, Florida (allotype). B. *longinicta*, Gainesville, Florida. C. *cajuni*, St. Mary Parish, Louisiana. D. *rivograndis*, Bell County, Texas (allotype). Blurring along right lower margin of the ovipositor in D is caused by the right valves being splayed and out of focus. (All magnifications as in A.)

Sarasota, Suwannee, Wakulla. GEORGIA: Bibb, Bulloch, Butts, Camden, Chatham, Decatur, Dougherty, Emanuel, Evans, Fulton, Glynn, Gwinnett, Habersham, Hancock, Houston, Jackson, Morgan, Pickens, Rabun, Seminole, Stephens, Tattall, Thomas, Tift, Williams. ILLINOIS: Jackson, Massac, Morgan, Pope. INDIANA: Crawford, Harrison, Knox, Monroe, Vigo. KANSAS: Franklin. KENTUCKY: Harrison, Larue, Madison, McCracken. LOUISIANA: Evangeline, Lincoln, Livingston, Rapides, St. Mary, St. Tammany. MARYLAND: Cecil, Prince Georges. MISSOURI: Cape Girardeau, Carter, Greene, Jefferson, Maries, Perry, Saline, St. Francois, Worcester, Wright. MISSISSIPPI: Amite, Attala, Clarke, Hinds, Warren. NORTH CAROLINA: Avery, Brunswick, Clay, Columbus, Cumberland, Graham, Halifax, Moore, Wake, Wayne. NEW JERSEY: Atlantic, Burlington, Cape May, Ocean. OHIO: Athens, Clermont, Hamilton, Knox, Washington. OKLAHOMA: Choctaw, Craig, Delaware, Hughes, Le Flore, Osage, Pawnee, Payne, Rogers. SOUTH CAROLINA: Barnwell, Beaufort, Clarendon, Dillon, Hampton, Horry, Orangeburg, Pickens, Richland. TENNESSEE: Benton, Cumberland, Davidson, Decatur, Dyer, Fentress, Giles, Lake, Lauderdale, Lawrence, Madison, Marshall, Obion, Ramsay, Roane, Sevier, Shelby, Tipton, Washington. TEXAS: Anderson, Brazoria, Ellis, Fayette, Fort Bend, Goliad, Gregg, Grimes, Harris, Harrison, Liberty, McLennan, Tyler, Van Zandt, Victoria. VIRGINIA: Brunswick, Essex, Norfolk, Spotsylvania.

Etymology.— The specific name of this species refers to its long song and incorporates 2 Latin stems (*long-*, long; *nict-*, to beckon).

***Amblycorypha cajuni*, new species**

Cajun virtuoso katydid
(Figs 2C, 3C, 4C, 5, 6D, 7D)

Holotype.—Male. LA Rt 20, w of Chacahoula, Terrebonne Par., Louisiana, 18 Aug 1965, WTL 012-5, R.E. Love, FSCA. Green; possessing the characters that distinguish the species group (see key); hind femur slightly exceeding tip of tegmen. Pronotal length 4.1 mm, width 3.0; tegminal length 21, width 6.5; hind femur length 21; hindwing exposure 4.5.

Allotype.—Female. e of Belzoni on MS Rt 12, Humphreys Co., Mississippi, 30 Aug 1965, T. J. Walker, FSCA. Like the holotype but with hind femora exceeding tips of tegmina by 3 mm. Pronotal length 5.1 mm, width 3.1; tegminal length 24, width 6.0; hind femur length 24; hindwing exposure 3.5; ovipositor length 5.6.

Other specimens.—43 ♂♂, 20 ♀♀. ANSP, 19 ♂♂, 12 ♀♀; FSCA, 22 ♂♂, 8 ♀♀; UMMZ, 2 ♂♂. Parishes and counties represented: ARKANSAS, Prairie; LOUISIANA, Alexandria, Arcadia, Baton Rouge, Beauregard, Calcasieu, E. Baton Rouge, Lafayette, New Orleans, St. Mary, St Landry, Shreveport, Terrebonne, Tangipahoa, West Monroe; MISSISSIPPI, Adams, Hinds, Holmes, Montgomery, Rankin, Sharkey, Warren, Washington.

Etymology.— This species is named for its occurrence in the Cajun country of Louisiana.

***Amblycorypha rivograndis*, new species**

Rio Grande virtuoso katydid
(Figs 2D, 3D, 4E, 5, 6C, 7C)

Holotype.—Male, Bentsen Rio Grande Valley State Park, Hildago Co., Texas, 18 Aug 1964, WTL 010-10, T.J. Walker, FSCA. Green;

possessing the characters that distinguish the species group (see key); hind femur exceeding tip of tegmen by 2.5 mm. Pronotal length 5.1 mm, width 3.4; tegminal length 23, width 6.5; hind femur length 23; hindwing exposure 4.7.

Allotype.—Female, collected as 5th instar nr Belton Dam, Bell Co., Texas, 18 Jun 1966, J.D. Spooner, reared to maturity, FSCA. Like the holotype but hind femora exceeding tips of tegmina by 3 mm. Pronotal length 5.3 mm, width 3.3; tegminal length 23, width 6.1; hind femur length 23; hindwing exposure 4.0; ovipositor length 6.5.

Other specimens.—9 ♂♂, 6 ♀♀. TEXAS, Hildago Co., 18 Aug 1964, 3 ♂♂ (incl. WTL 010-8), 23 Jun 1966, 1 ♂♂, FSCA; Cameron Co., w of Brownsville, Rt 182, 7 Jun 1964, 2 ♂♂, UMMZ; Bell Co, nr Belton Dam, 18 Jun 1966, 1 ♂ 5th instar reared to maturity, FSCA; Jackson Co., 25 Aug 1967, 2 ♂♂, 4 ♀♀, FSCA; Uvalde Co., 21-22 Aug 1912, 1 ♀, ANSP; Austin Co., 15 Aug 1964, 1 ♀, FSCA.

Etymology.— This species is named for its type locality near the Rio Grande River (*rivo*, stream; *grandis*, great).

Geographical distribution

Fig. 4 shows the distribution of the 5 species as currently understood. The range of *longinicta* includes the ranges of *cajuni* and *arenicola*, but the ranges of the latter 2 species do not overlap. The distributions of *uhleri* and *rivograndis*, the 2 species known only from Texas, evidently overlap, at least narrowly. Uvalde County has both species (ANSP, identical label data), and Coryell and Bell Counties, which are contiguous, have *uhleri* and *rivograndis* respectively (UMMZ and FSCA). The ranges of *rivograndis* and *longinicta*

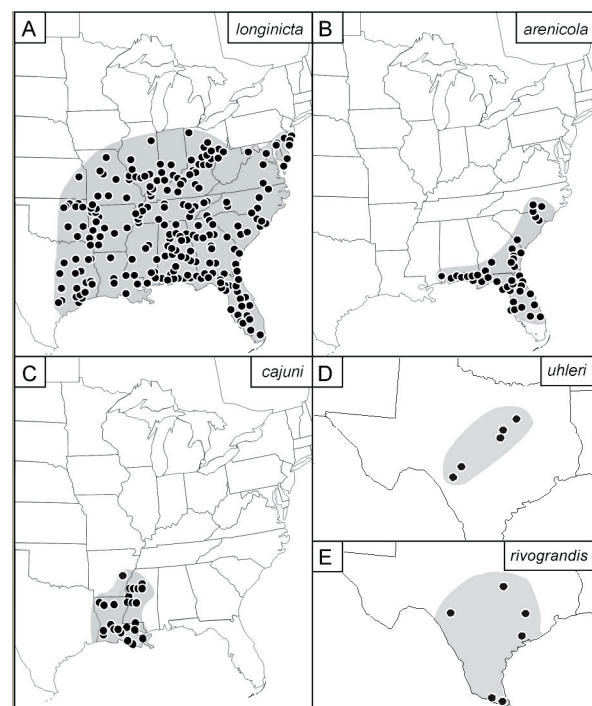


Fig. 4. Geographical distribution of the species in the *Amblycorypha uhleri* group. The dots represent county records for each species and the shaded areas indicate estimated geographical limits. A. *longinicta*. B. *arenicola*. C. *cajuni*. D. *uhleri*. E. *rivograndis*.

Table 1. Minimum and maximum dimensions, in mm, for species of the *uhleri* group of *Amblycorypha*. Values for *uhleri*, *cajuni*, and *rivograndis* are for all specimens; values for *arenicola* and *longinicta* are for FSCA specimens from Alachua County, Florida.

Measurement	<i>uhleri</i>	<i>arenicola</i>	<i>longinicta</i>	<i>cajuni</i>	<i>rivograndis</i>
Males (n=)	8	63	72	44	10
Pronotal length	5.0-6.0	5.3-5.9	4.7-5.3	4.1-5.0	4.6-5.5
Tegminal length	25-27	27-31	24-27	21-25	22-24
Tegminal ratio (L/W)	3.3-3.9	3.2-3.4	3.2-3.8	3.2-4.1	3.3-4.1
Hind femur length	24-27	25-29	24-27	21-24	21-25
Stridulatory field width	3.6-4.1	4.3-4.7	3.7-4.2	3.0-3.6	3.2-4.1
Females (n=)	2	13	12	18	7
Pronotal length	5.2-5.8	5.4-6.6	4.6-5.7	4.7-5.4	4.6-5.6
Tegminal length	22-25	26-31	22-27	20-24	20-23
Tegminal ratio (L/W)	3.4-3.9	3.2-3.9	3.3-3.9	3.4-4.1	3.8-4.3
Hind femur length	24-27	24-30	24-27	22-25	20-26
Ovipositor length	7.0-7.4	8.8-10.0	7.1-8.3	5.4-7.0	5.6-6.8

may overlap in eastern Texas. In the absence of song data, males from the area of possible overlap were tentatively identified on the basis of tegminal lengths as recorded in Table 1. This resulted in the southwest-most records of *longinicta* (Goliad and Victoria Counties) being west of the east-most records of *rivograndis* (Jackson and Austin Counties).

Additional species of the *uhleri* group may await discovery. I. J. Cantrall collected an *Amblycorypha* male with the pronotal markings typical of this group in Springerville, Apache County, Arizona, at 7500 ft, 16 August 1935 (UMMZ). Field notes at UMMZ describe the habitat as a low grassy ridge with some sage, rabbit brush, and juniper. The tegminal length of this specimen was 30 mm, which exceeds the known range for *uhleri*, the largest of the Texas species (Table 1).

Morphological characters

As explained in the methods section, the primary means of identifying specimens was by the distinctive songs of the males. In all but a few cases, populations at a single site produced a single type of calling song, allowing females to be identified by the song type of the males associated with them. With series of specimens identified by song type, it was relatively easy to find morphological characters that would separate species that broadly overlapped in their geographical distributions. *A. uhleri* was a special case. My only field work in Bosque County, Texas, the probable type locality of *uhleri*, was on 19 June 1995 and I neither heard nor saw any individuals of the *uhleri* group. However, in earlier fieldwork in Kerr County, Texas, I had collected a male that appeared conspecific with a male from the type series of *A. uhleri* and had recorded its song. I assigned this specimen and 9 other central Texas specimens of similar size to *A. uhleri* and used them in the morphological characterization of the species.

As indicated by tegminal and hind femur lengths, *uhleri* and *longinicta* are of similar, intermediate size for species in the *uhleri* group (Table 1). Likewise *cajuni* and *rivograndis* are similar and small, and *arenicola* is large. The pronotum of *rivograndis* is longer than that of *cajuni*, relative to the length of the tegmina and hind femora (Table 1). The width of the stridulatory field is sufficient to separate the males of the 3 eastern species: *longinicta*, *arenicola*, and

cajuni (Table 1). Males of *uhleri* and *rivograndis*, known only from Texas, can be separated by the length of the tegmina. The number of teeth and stridulatory file length will separate males of the trio of eastern species and may be of some value in separating those of the 2 Texas-only species (Fig. 5).

Females within these same 2 geographically defined groups can be separated by the lengths of the ovipositors (Table 1). Differences in the shape of ovipositors (Fig. 3) seem to relate to differences in length. For example, although the *cajuni* ovipositor of Fig. 3C looks more spatulate than the 2 ovipositors pictured above, the longest *cajuni* ovipositors appear no more spatulate than the shortest *longinicta* ovipositors.

Male songs

The most remarkable feature of these otherwise small, plain phaneropterines is the complexity of the sounds broadcast by the males. Only the song of *longinicta* has been described previously. Allard (1910) and Fulton (1932) rendered it verbally. Alexander (1960) was first to analyze the song electronically. He depicted a 42-s song by means of a diagram and spectrograms, and noted that a complete song has 4 types of repeated sounds [syllables] and at least 3 different syllable repetition rates. Walker and Dew (1972) used high-speed photography to record the tegminal movements as *longinicta* made its 4 types of syllables and described the different cyclic wing movements responsible for the 4 types. Based on when each type first appears in a complete song, they assigned roman numerals to the 4 syllable types. Among the details of their findings were that (1) sounds may be made on both opening and closing movements, (2) a short pause occurs during the closing stroke of type I syllables, (3) a short, nearly silent close/open sequence usually precedes the main closing stroke of type II syllables, (4) a long pause occurs between the first and second portions of this main type II closing stroke, and (5) no mid-stroke pauses are evident in syllables of types III and IV. Fig. 7A illustrates these conclusions as to the stridulatory movements of *longinicta* during syllables of types I, II, and III.

Homologues of the 4 types of syllables documented in *longinicta* are evident in the songs of the other species of the *uhleri* group (Figs 6 and 7). All 5 species usually start with a sequence of type I

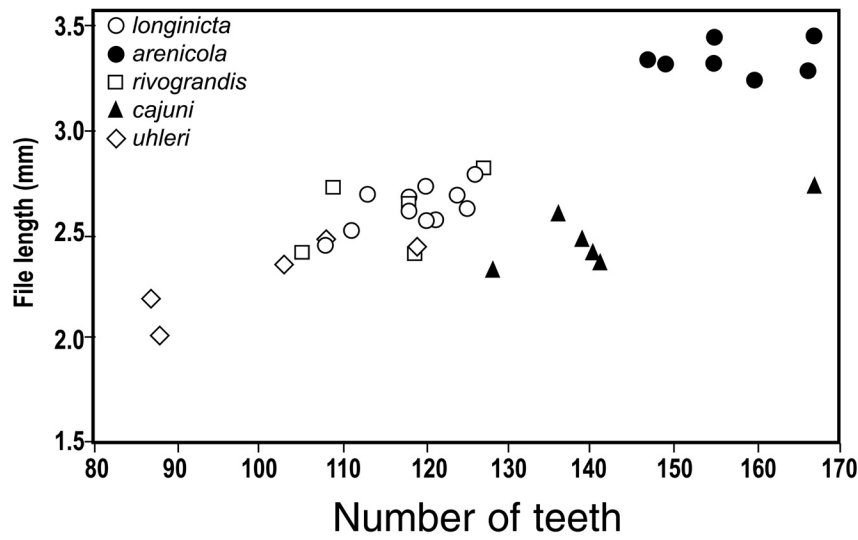


Fig. 5. Number of file teeth and length of stridulatory file for males of the *Amblycorypha uhleri* complex: *longinicta* (Florida, n=8; Tennessee, 2; Louisiana, 1), *arenicola* (Florida, n = 6; North Carolina, 1), *rivograndis* (Texas, n = 5), *cajuni* (Mississippi, n = 3; Louisiana, 3), *uhleri* (Texas, n = 5).

syllables that gradually increase in intensity until there is an abrupt transition to type II syllables; type II are more intense, produced at a slower rate, and have noteworthy silences between the first and second sounds of the two-stage main tegminal closure and between the weak opening sound (when present) and the first of the 2 strong closing sounds. Type II syllables are immediately followed by type III syllables, which are produced at a much higher rate than either of the previous types and begin at a high intensity that diminishes quickly. Next produced are type IV syllables, except by *longinicta* males, which make one or more additional type III sequences prior to producing type IV syllables. Type IV syllables are produced at the slowest rate and are the most variable in number and occurrence. When there is a single type III sequence in a song, there is always a silence of 0.4 s or more between the last type III syllable and the first type IV.

With songs as complex as those of the *uhleri* group, it is not surprising that the songs differ among the species in an abundance of features. Already mentioned is the fact that only in *longinicta* do the songs usually include multiple sequences of type III syllables. Counts of syllables in type I, II, and III sequences are, in combina-

tion, sufficient to distinguish the songs of all 5 species (Table 2).

The 5 species differ notably in the predictability of the pattern of presentation of the sequences of the 4 syllable types. In the next 2 paragraphs patterns will be specified by using the corresponding Arabic numbers for sequences of types I, II, III, and IV syllables. No spaces will separate the numbers except when there is a noteworthy pause between sequences.

In *uhleri* and *arenicola*, the songs are nearly always of pattern 1234, but a few songs of pattern 12 are produced. In *arenicola* the pattern 12 songs occur when a male resumes calling after flying to a new perch. Upon landing, the male usually makes 1 to 3 of the shortened songs before commencing a series of pattern 1234 songs usually lasting 1.5 to 3 min. In *cajuni* long series of 23 songs are sometimes heard, occasionally intermingled with 234 songs. Other variants include 123 and 2 4. In *rivograndis* patterns of 12343, 123434, and 1234343 are occasionally produced as well as repetitions of truncated patterns such as 12 or 2. One individual was heard to produce series of 1243 and 12434 patterns.

A. longinicta is highly variable in its song patterns, and the variability differs geographically. In Florida, where the variability

Table 2. Characteristics of broadcast male songs of the species of the *uhleri* group of *Amblycorypha*. Syllable rates at 25 °C for *longinicta* and *arenicola* are from trend lines in Fig. 8; those for *cajuni* and *uhleri* are from trend lines based on all analyzable songs; for *rivograndis* only songs from Hidalgo County, Texas, were used.

	<i>longinicta</i>	<i>arenicola</i>	<i>cajuni</i>	<i>rivograndis</i>	<i>uhleri</i>
Most frequent pattern of syllable sequences	I II III III IV III	I II III IV	I II III IV	I II III IV	I II III IV
Stereotypy of pattern	low	high	medium	low	high
Syllable counts in sequences (range)					
Type I	20-80	30-60	2-13	10-24	8-38
Type II	8-14	3	6-7	1-3	2
Type III	5-6	8-10	1-3	2-3	7-8
Syllable rate at 25 °C (s ⁻¹)					
Type I	14.5	16.9	9.9	11.5	15.2
Type II	9.0	7.0	6.9	4.0	7.0
Type III	23.6	31.5	19.2	21.7	33.9

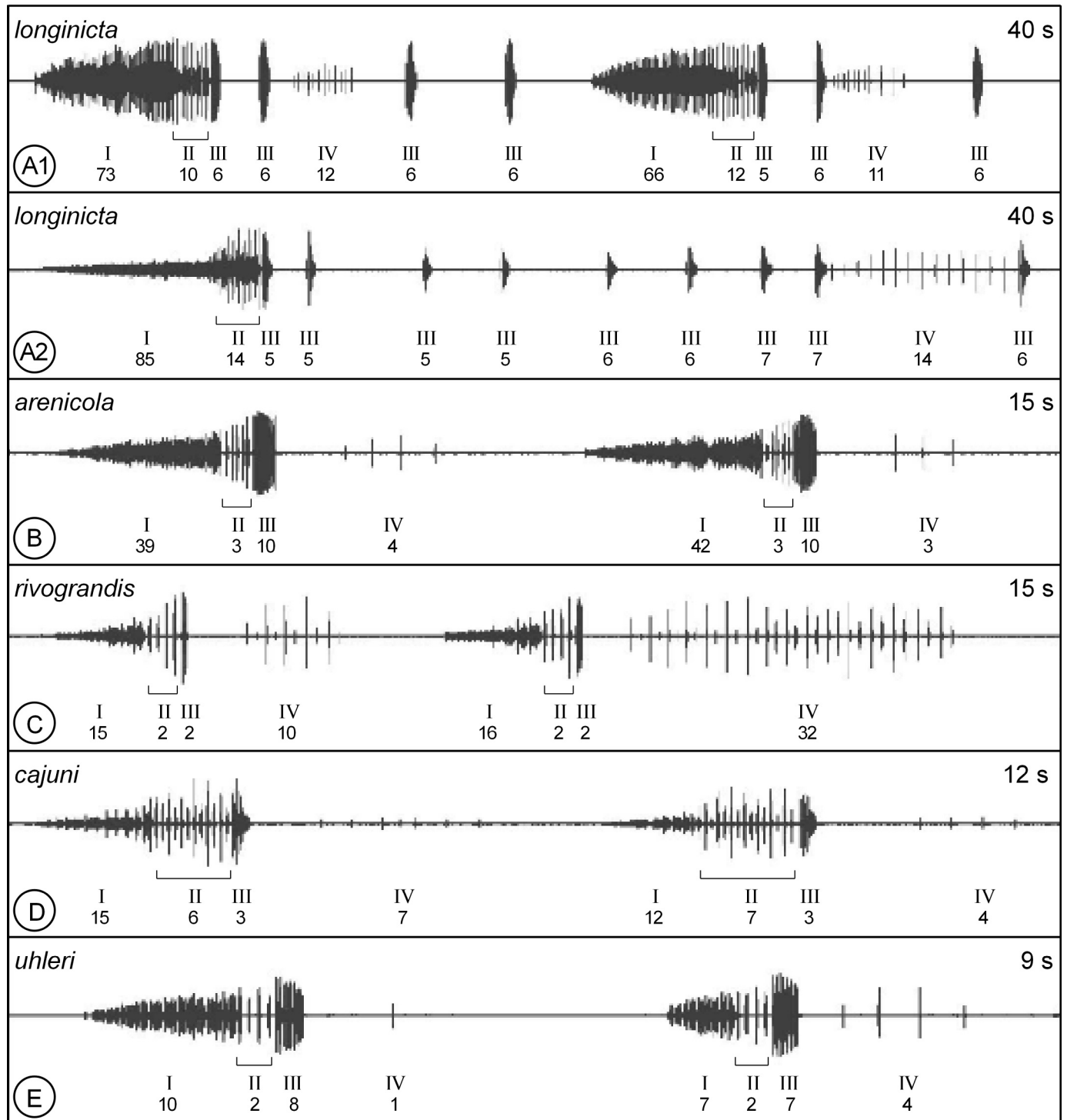
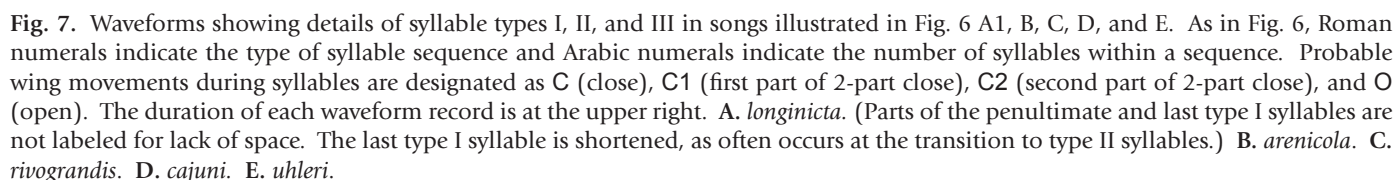


Fig. 6. Waveforms of songs of species of the *Amblycorypha uhleri* complex. Roman numerals indicate the type of syllable sequence and Arabic numerals indicate the number of syllables within a sequence. The duration of each waveform record is at the upper right. A1. *longinicta*, two songs, Charlotte County, Florida, WTL004-44, 24.7°C. A2. *longinicta*, Brunswick County, Virginia, WTL004-36b, 25.5°C. B. *arenicola*, two songs, Tift County, Georgia, WTL002-20b, 25.0°C. C. *rivograndis*, two songs, Hidalgo County, Texas, WTL010-10, 25.0°C. D. *cajuni*, two songs, Terrebonne Parish, Louisiana, WTL012-5, 24.6°C (holotype). E. *uhleri*, two songs, Kerr County, Texas, WTL014-3c, 24.8°C.



seconds of silence in the midst of a single song. Perhaps the most unusual pattern recorded was made by a male in Orangeburg County, South Carolina: 1233333 3 333343434343.

As in other ensiferan songs, the syllable rates of songs of the *uhleri* group of katydids are temperature dependent, with the rates approximating a linear function of temperature and tending to converge at the temperature where the extrapolated trend lines are 0 syllables s⁻¹ (Walker 1962, 1975). Fig. 8 shows the effects of temperature on the syllable rates of *longinicta* and *arenicola*. The trend line for type IV syllables in Fig. 8B is based on the slower of 2 rates that were measured in songs of *arenicola* (Fig. 9). The mean temperature for the expected syllable rate of 0 in the 4 syllable types of *longinicta* is 6.8°C (range = 5.8 to 7.9); in *arenicola* it is 8.8°C

(range = 8.1 to 9.9).

Obviously both temperature and syllable type must be taken into account when comparing syllable rates among the 5 species in the *uhleri* group. Because of the variability in type IV rates and the small numbers of recorded songs, I abandoned the attempt to establish trend lines for the rates of type IV syllables in the songs of *cajuni*, *rivograndis*, and *uhleri*. Table 2 shows how the 5 species compare, at 25 °C, in their other 3 rates. In each species the rate for syllables of type II is the lowest and the rate for syllables of type III is the highest. For each syllable type there are differences among species that are great enough to be diagnostic. For type II syllables, *rivograndis* has a much lower rate than the other species. For type I syllables, *cajuni* and *rivograndis* have rates much below the other 3 species. For type III syllables, *uhleri* and *arenicola* have much higher rates than the other species. When rates of syllable types I, II, and III are considered in combination, only *uhleri* and *arenicola* cannot be separated on the basis of the syllable rates of their songs.

The strongest frequencies of the songs generally fell between 9 and 17 kHz. *A. cajuni* and *rivograndis*, which have the smallest males, occupied the high side of this range (13 to 17 kHz), whereas *arenicola*, the species with the largest males, was on the low side (9 to 12 kHz). The other 2 species were intermediate (11 to 15 kHz).

Female answers

Unlike most other katydids, females of the subfamily Phaneropterinae may answer the song of a conspecific male with one or more brief, nondescript "ticks" that are similar to the type IV syllables of *uhleri* group males. Males use these answers to travel toward or to the female. The details of phaneropterine pair forming systems vary (Spooner 1968, 1995; Robinson 1990; Bailey 2003), and even within a genus some species may employ female answers and others not (Heller & Helversen 1993).

In *arenicola* and *longinicta*, the 2 species of the *uhleri* group whose pair-forming acoustical interchanges I have observed, sexually receptive females make nearly all of their ticks during periods when the male produces, or might be expected to produce, type IV syllables.

When I took 2 caged Gainesville females of *arenicola* outdoors to an area where their males were calling, the females answered songs of males calling as far away as 10 m, and each female succeeded in attracting a male to her cage (one cage was on the ground and the other was in a tree 1.2 m up). Almost without exception, neither female would tick in response to a male's song until after the male started producing type IV syllables (*i.e.*, male-produced "ticks"). However, laboratory tests with 4 virgin females made clear that male ticks were not essential for female answers. When pattern 123 was played 40 × in succession, the females answered, on average, 68% as frequently as when played pattern 1234 (Walker unpub.). Furthermore, when the entire song was played in laboratory tests, the females often made their first answering tick to a song prior to the first type IV syllable. For example, in the analysis of a tape-recorded test in which the same male song was played 40 × in succession to a receptive *arenicola* female, she began answering with the 6th repetition and answered 22 of the remaining songs. To 3 songs she responded with a single tick; to 11 songs, with 2 ticks; to 6, with 3 ticks; and to 2, with 4 ticks. The 1st tick of a response always fell in the silence after the male's last type III syllable. Her 2nd tick (if any) fell immediately before or soon after the male's first type IV syllable, and the remainder fell within the type IV sequence.

No field observations were made of answering *longinicta* females

but several females from Gainesville were observed in the laboratory, as was a single female from Brunswick County, Virginia. In response to the usual Gainesville pattern (123 343), the Gainesville females nearly always made their answering ticks between the 2nd and 3rd type III sequence. For example, in response to 7 consecutive playbacks of a recorded song of this pattern, a Gainesville female answered each song with 2 to 5 ticks during the period between the 2nd and 3rd type III sequence. For 5 songs, she made one or more ticks before the first type IV syllable of the male. Of the total of 24 ticks made during the playing of the 7 songs, 8 were made prior to the first type IV syllable, 14 were made during the type IV sequence of the male and 2 were made immediately following the final type III sequence of a song.

The Brunswick County, Virginia, *longinicta* female was from a population in which solitary males produced songs with 6 to 8 III sequences prior to any IV sequence. This female was recorded responding to a captive Dillon County, South Carolina, male that during solitary calling made songs with 3 or 4 III sequences prior to any IV sequence. In 10 of her 13 response sequences, the female's first tick came after the male had made 1 to 9 IV syllables (mean=4.7) of a longer IV sequence. This suggests that the female may wait to hear a male's type IV syllables before responding; however, in the other 3 response sequences, the female made 1 to 3 ticks prior to the male's first syllable in a IV sequence.

In 1966, in Bell County, Texas, J. D. Spooner collected a male and female fifth instar nymph of the *uhleri* group. He subsequently reared the 2 to maturity and tape recorded 4 min of the pair interacting acoustically at 25 °C in cages 5 cm apart. Recently he sent me the tape recording to be digitized and analyzed and donated the specimens to FSCA. Aided by the characters of the male's song, I identified the pair as *rivograndis*. The female answered 20 of the first 43 of the male's songs with 1 or 2 ticks, with the first tick coming 153 to 693 ms after the start of the male's last syllable-II closing sound (307±166; mean±s_x). The male seldom produced type III syllables, but when it did there were never more than 2 and they came prior to any female ticks. In most cases the male produced several type IV syllables after the female's 1 or 2 ticks. In a single case the male's first IV came between the female's 2 ticks.

The above observations on 3 species suggest that females of *cajuni* and *uhleri* also produce answering ticks immediately before and sometimes during the IV sequences of the males.

Ecology

Both *cajuni* and *longinicta* are usually found no higher than 1 m up in herbaceous vegetation along roadsides, in old fields, and along woodland edges. *A. cajuni* is characteristic of moist, lowland situations, whereas *longinicta* is most often in better drained, more mesic habitats. In the area where the 2 species are sympatric, only rarely are they heard calling at the same site.

A. arenicola occurs in xeric to mesic areas, especially on sites that once supported the longleaf pine-dominated, fire-maintained community termed sandhill or high pine (Myers 1990). The original high pine sometimes had a substantial understory of scrub oaks, especially turkey oak (*Quercus laevis*). With the cutting of the pines and changes in fire frequency, turkey oaks flourished and now dominate many sites. Although *arenicola* is most often encountered in sandhill communities, it also occurs with *longinicta* in xeric to mesic old fields. Unlike *cajuni* and *longinicta*, which occur in sedentary colonies near the ground, *arenicola* intersperses flying with calling and often calls from perches in scrub oaks, usually no higher than

2 m from the ground.

Alexander and Hull collected *rivograndis* west of Brownsville, Texas, in a "lush area". During a drought I collected it in Bensen Rio Grande Valley State Park as it called from 0.6 to 1.2 m up and occasionally higher in dry thickets and their edges. Two years later, J.D. Spooner visited the same park at a time of abundant rain and described the thickets as lush and jungle-like (pers. com.). Farther north it has been collected on weeds in a park-like stand of trees (Austin County) and by sweeping weeds in open oak woods (Bell County).

Data on the habitat of *uhleri* are sparse. I found it in weeds and in a thicket on a hillside above the Guadalupe River in Kerr County, Texas, and T. J. Cohn (UMMZ field notes) collected it on roadside weeds by a pasture in Coryell County, Texas.

Females of all species of the *uhleri* group probably lay their eggs in soil. Supporting this conclusion is the fact that J. D. Spooner (pers. com.) watched a captive *longinicta* female oviposit in damp soil and, so far as known, females belonging to other species groups of *Amblycorypha* lay in soil (Walker *et al.* 2003). Eggs are undoubtedly the overwintering stage, but whether more than one winter may pass before they hatch is unknown. Data on the duration of embryonic development in *Amblycorypha* spp. are available only for 3 species of the *oblongifolia* group. Hancock (1916) reported that for eggs laid by a single *oblongifolia* female and kept in a screened insectary at Lakeside, Michigan, none hatched after the first winter, 10 hatched after the second winter, and 3 hatched after the third. J. D. Spooner (pers. com.) observed that *huasteca* and *carinata* eggs laid in damp sand in the laboratory hatched after a single period of chilling.

However long the eggs take to hatch, there seems to be a single annual peak of adult activity each year. In Alachua County, Florida, *arenicola* begins to call about the first of June and continues to do so until the end of August, whereas *longinicta* begins about the first of July and is no longer heard by the end of November (Walker 2004). Fulton (1951) reported that *longinicta* was heard as early as mid July and as late as early November in Raleigh, North Carolina. Inclusive seasonal dates for specimens examined are 3 August to 14 September for *cajuni*, 7 June to 25 August for *rivograndis*, and 28 Jun to 1 Sep for *uhleri*.

In regards to the egg stage, Hebard evidently realized that *arenicola* and *longinicta* were different species because he had separated specimens of the 2 and dissected eggs from several females of each (ANSP collection). On the basis of the eggs he preserved with the females, the 2 species are disjunct in egg size with the eggs of *arenicola* being larger than those of *longinicta*. This may relate to the former species laying its eggs in soils more subject to drought or to the hatchlings facing drier microclimates.

General Discussion

Species in Texas

The 2 species of the *uhleri* group that occur only in Texas are poorly characterized. Specimens come from few localities and the solitary songs of males are known for *uhleri* only from Kerr County in central Texas and for *rivograndis* from Hildago County in south-most Texas. Small specimens of the *uhleri* group from central Texas were identified as *rivograndis* on the basis of J. D. Spooner's recording of an acoustically interacting male and female from Bell County,

in central Texas. In most features, the interactive songs of the Bell County male resembled those of the solitary songs of Hildago County *rivograndis*, as summarized in Table 2. Specifically, counts for type I sequences ranged from 2 to 19 (9.6 ± 3.8 ; mean $\pm s_x$); type II sequences had 2 syllables, but in 21% of the sequences there were only 3 instead of 4 strong closing sounds. Type III sequences were rare and variable but never had more than 2 syllables. At 25 °C the type II syllable rate was 4.8 to 5.1 (5.0 ± 0.2). The type I syllable rate was 13.6 to 14.7 (14.2 ± 0.3), which was more like the songs of Kerr County *uhleri* than those of Hildago County *rivograndis*. Most of the patterns were 12 4, not a pattern heard in solitary singing of Hildago County males, although repetitions of patterns 12 and 12 43 were noted.

Populations of *uhleri* group species in Texas merit more study, especially in areas where *uhleri* and *rivograndis* overlap in their distributions and where *rivograndis* and *longinicta* apparently do so (Fig. 4).

Most complex insect sound?

Alexander (1960) opined that the song of *longinicta* is "probably the most complicated insect sound known in the world". As he pointed out, the male's song has 4 types of syllables, with both gradual and sudden changes in intensity during syllable sequences. Because he studied northern populations of *longinicta*, in which males produce many III sequences before starting the next song, he correctly noted that 40 s or more was routinely required to produce a complete song. In attempting to determine whether Alexander's choice of the song of *longinicta* as the most complex known insect sound was still defensible after more than 40 y, I found 2 orthopteran groups that must be considered as having contenders or runners up for the title—gomphocerine grasshoppers and barbitistine katydids.

Elsner (1974) reported that in courting males of many gomphocerines the left and right hind leg differ in the sound patterns produced and that the hind legs change their role from time to time. These complexities are difficult to rank relative to producing a long-lasting complicated calling song by using 4 types of syllables, but the description by Ragge and Reynolds (1998) of the courtship song of *Myrmeleotettix maculatus* makes it a contender for "most complicated".

Heller (1990) devised a phylogeny of the song patterns of the Barbitistini, a tribe of Phaneropterinae with more than 250 species that is remarkable for its complex stridulatory movements and song patterns. Of the 87 species whose songs are known, *Polysarcus denticaudus* (Charpentier) may give *longinicta* the strongest competition. Its songs last from about 30 to 90s. During the first and longest phase of the song ("phase I"), the male walks about on the ground or vegetation producing syllables at a rate of about 13 s⁻¹. After a minute or less, he stops walking and increases the syllable rate to about 26 s⁻¹ (phase II); after 8 to 14 s he begins to interrupt the syllable sequence about every 2 s with one of a new type of syllable, which is much louder and is followed by a pause of about 150 ms, during which a female may answer (phase III). After 6 to 9 of these regular interruptions, phase III ends with a few seconds of quicker, softer interruptions. Soon the male resumes walking and producing phase I syllables (Heller 1988, 1990). Although complete songs of *P. denticaudus* last longer than those of *longinicta*, the sound sequence is less complex in number of syllable types and in changes in intensity.

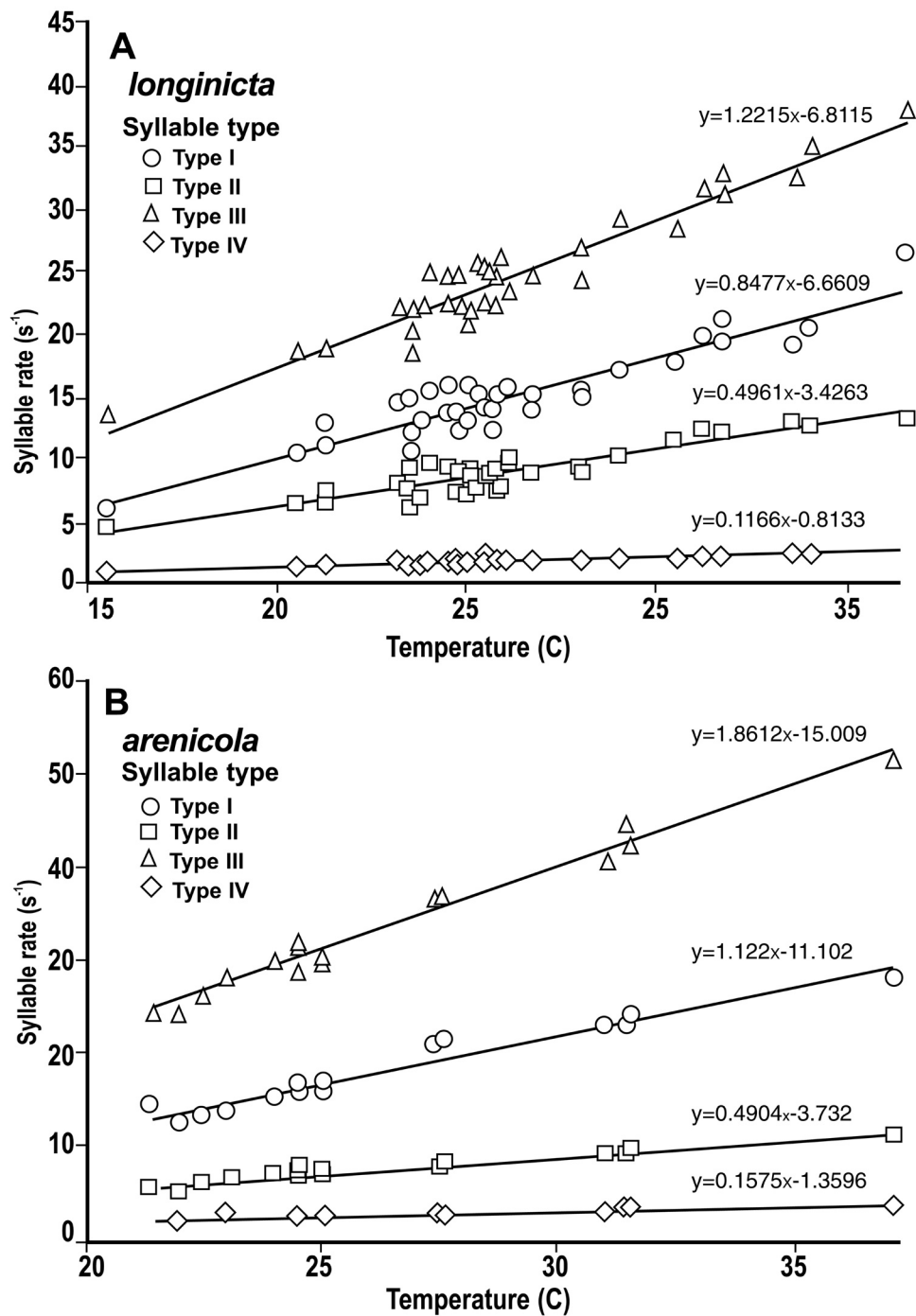


Fig. 8. Syllable rate as a function of temperature and type of syllable in two species in the *Amblycorypha uhleri* complex. A. *longinicta* (32 tapes of 16 males from Alachua County, Florida, plus 1 tape of a male, at 15.5°C, from Gwinnett County, Georgia.) B. *arenicola* (16 tapes of 15 males from Alachua County, Florida, plus 3 tapes of a male, at 25.0 to 27.4°C, from Tift County, Georgia).

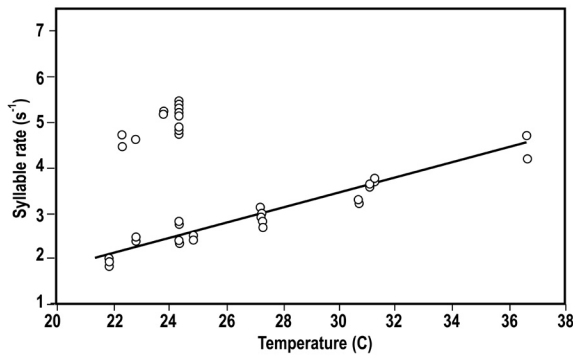


Fig. 9. Rate as a function of temperature for type IV syllables of *Amblycorypha arenicola*. In 16 of the 18 recordings used in Fig. 8B, Type IV rate could be measured in 3 songs. Of the 48 rates determined (and shown here), 14 were nearly twice as high as the remaining 34. The trend line in this figure (repeated in Fig. 8B) is calculated from the means of the slow rates for the 12 recordings that had either 2 or 3 slow rates measured.

Why such complex songs?

The calling songs of most katydids consist of one, sometimes 2, types of syllables and become repetitious after no more than a few seconds. Why then do species of the *uhleri* group produce songs that require 6 to 60 s to become repetitious and that include sequences of syllables of four types made in more or less stereotypic order?

To begin with, songs of phaneropterine katydids are especially likely to be complex because they are made in more complex contexts than the songs of most other katydids. Rather than merely advertising the species, position, and prowess of the male, the song usually functions to induce a female to reveal her location and sexual readiness by answering with nondescript "ticks" after a species-specific delay. The male-female duet that ensues provides listening males of the same species the opportunity to get to the answering female first or even to insert a special "satellite call" to take over the phonotaxis of a female that is making her way to the male with which she is duetting (Spooner 1968, Bailey & Field 2000).

Studies of the acoustic behavior of other phaneropterines offer clues to the origins of different syllable types in the *uhleri* group. For instance, male phaneropterines, in response to female answers, often produce sounds that have the probable or proven effect of thwarting eavesdropping males (Spooner 1968, Hammond & Bailey 2003). Thus the type IV syllable sequence may have evolved in this context. If eavesdropping is shown to occur in *uhleri* group katydids, experiments could show whether type IV sequences lessen its payoffs.

Spooner's (1964, 1968) studies of the acoustic behaviors of 10 species of Florida phaneropterines revealed that males of 2 species had separate calls that cause females to approach and that elicit answering ticks from females. In *Scudderia texensis* the approach-inducing [AI] call is a series of 3- or 4-syllable phrases produced every few seconds for long periods, whereas the tick-eliciting [TE] call consists of a 5- to 7-syllable phrase, followed immediately by a longer phrase of up to 22 pulses. The syllable rate in the AI call is *ca* 17 s⁻¹, whereas the syllable rate in the TE call is *ca* 11 s⁻¹. Spooner (1964) demonstrated that the AI call is only effective when received at low intensity, indicating that it attracts females to the vicinity of the male where the TE call may establish a duet leading to final

pair formation. In *Microcentrum rhombifolium* the AI call is a long series of 22- to 30-ms lisps, each made by a quick closure of the tegmina and produced at intervals of 2 to 3 s. Its TE call is a series of ticks delivered at a rate of *ca* 8 s⁻¹, lasting 3 to 4 s, and made by a single slow closure of the tegmina. As in *S. texensis*, Spooner (1968) showed that the AI call was only effective when it was received at low intensity, indicating that it attracted females to the vicinity of the male where the TE call could enable a duet. In both species, the AI call is produced more frequently than the TE call and the TE call is usually made after a series of AI calls.

A comparison of the songs of *uhleri* group katydids to the calls of *M. rhombifolium* and *S. texensis* suggests that type III syllable sequences, which are loud, carry far, and are sometimes produced many more times than the other types of syllable sequences, may have evolved in an AI context. They may still function that way, with the most likely case of continuing AI function being in songs of *longinicta*, which include multiple type III sequences made by males in sedentary colonies. In contrast, *arenicola* changes calling locations every few minutes, making it unlikely that its type III sequences, made no more than once per song, retain their former (hypothetical) AI function.

Should type IV and type III sequences have evolved in the contexts suggested above, that would leave types I and II sequences to have evolved in the TE context. Evidence from 3 species suggests that this may be the case.

In the recently analyzed recording of Spooner's Bell County, Texas, pair of *rivograndis*, most answered songs were of pattern 12 4 with the female making her ticks after the last syllable II sound and before the first IV syllable. The few songs of pattern 1234 did not elicit answers at a significantly higher rate than the 12 4 songs. Furthermore, omission of type III sequences in the presence of a nearby answering female would accord with the hypothesized AI function of those sequences.

More than 40 years ago, I played to a Gainesville *longinicta* female recorded songs in which all syllable sequences except types I and II had been replaced with silence—that is, a song with 123 343 pattern was truncated to a 12 pattern and the usual time between songs maintained (Walker unpub.). The female answered 17 of 27 repetitions and, what was most revealing, did so at times appropriate to the full song—*i.e.*, 7 to 8 s after the pattern ended, which was ± 0.5 s from the first IV syllable of the entire song.

In more extensive experiments I played entire and partially silenced *arenicola* songs to 4 *arenicola* females (Walker unpub.). None of the 4 single-part patterns (1, 2, 3, 4) solicited a response nor did any of the 6 two-part patterns (12, 1 3, 1 4, 23, 2 4, 34) solicit female answers more than 4% as often as the entire song. The 3 three-part patterns that contained the syllable II sequence (123, 12 4, and 234) each solicited female answers, on average, 68 to 72% as often as the entire song. Pattern 1 34 came in at 33%. These results suggest that in the song of *arenicola* all syllable sequences contribute to the TE function but that the type II sequence, which consists of only 3 syllables (Fig. 7B, Table 2), is of special importance.

Whatever may be the origins of the 4 syllable types made by species in the *uhleri* group, why should they be produced in more or less stereotyped order? Varying degrees of stereotypy are evident within the group; therefore, thorough field studies of the acoustic behaviors of the 5 species could give clues to the evolution of stereotypy. No such studies have been done, but it is perhaps relevant that *arenicola*, which may have the most stereotyped song pattern of the 5 species, has a sing-and-fly behavior that could favor short stereotyped songs, whereas, *longinicta*, which has one of the least

stereotyped patterns, calls in sedentary colonies where more extended and complex acoustical interactions could favor more flexible patterning. Spooner's (1964) field observations and interpretation of the acoustic behaviors of *Scudderella texensis* may be relevant to the origins of stereotypy. At night, males produce series of AI songs followed by a TE song. After a pause, the sequence begins again. Thus, in the absence of female answers, males have a standard sequence. However, successive iterations are not identical because as the evening progresses, males lengthen the AI sequences that precede the TE song.

Another feature of the songs of the *uhleri* species group is the complexity of the amplitude modulation patterns that occur within type I and II syllables (Fig. 7). Such complexity is not limited to the *uhleri* group. Although songs of the *rotundifolia* species group seem to contain a single syllable type, the putative syllables often have more complex patterns than any of those of the *uhleri* group (Walker *et al.* 2003). Heller's studies of Barbitistini (1988, 1990) provide the only extensive comparative information on how file-stroking movements in phaneropterines relate to the waveforms produced. The astonishing variety of movements he documents suggests that similar studies in the genus *Amblycorypha* and related groups might provide insight into the evolution of complex intrasyllabic patterns and allow for testing as to their importance in the functions of the songs.

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