The *rotundifolia* Complex of the Genus *Amblycorypha* (Orthoptera: Tettigoniidae): Songs Reveal New Species

T. J. WALKER,[1] T. G. FORREST,[2] AND J. D. SPOONER[3]

ABSTRACT Since 1934, the *rotundifolia* complex of *Amblycorypha* has consisted of two named species: *Amblycorypha parvipennis* Stal, occurring from the Mississippi River westward into the eastern edges of the Great Plains, and *Amblycorypha rotundifolia*, occurring in most of the eastern United States. The latter entity is here shown to consist of at least three species with distinctive calling songs and different but overlapping geographical distributions. At 25°C, *A. rotundifolia* (Scudder) produces ≈26 calling song units (phonatomes) per s, whereas *Amblycorypha bartrami* n. sp. Walker, *A. parvipennis*, and *Amblycorypha alexanderi* n. sp. Walker produce ≈10, 5, and 2.8 ph/s respectively. *Amblycorypha rotundifolia* occurs from Illinois to New York and southward along the Appalachians to northern Georgia. *Amblycorypha bartrami* occurs in the southeastern states, and *A. alexanderi* broadly overlaps the distributions of the other two eastern species. Where *A. alexanderi* and *A. rotundifolia* are sympatric, the two occur in similar habitats; where *A. alexanderi* and *A. bartrami* are sympatric, *A. bartrami* occurs in more xeric habitats. No morphological characters were found that reliably identify the three eastern species, yet no fewer than three species must be recognized to provide names for populations that behave as distinct species where they co-occur.

KEY WORDS Phaneropterinae, katydids, calling songs, female phonoresponse, sibling species, species concepts

IN THEIR 1914 REVISION of North American *Amblycorypha*, Rehn and Hebard divided the genus into two groups. Group I contained species with the humeral sinus of the lateral lobes of the pronotum "well impressed, at least rectangulate" and having the "individual metasternal lobes not transverse." Group II had forms with the humeral sinus "less impressed (and not rectangulate) or subobsolete" and having "individual metasternal lobes transverse." In Group II, here called the *rotundifolia* complex, they placed three forms that they considered to be geographic races of a single species, *Amblycorypha rotundifolia* (Scudder). In 1934, Hebard elevated one of the forms, *A. r. parvipennis* (Stal) to species status. In 1960, R. D. Alexander concluded that the species known as *A. rotundifolia* consisted of two sibling species that were inseparable morphologically but had distinctive calling songs. He informally named the species by their song types and reported that "rattler" was a northern species extending southward to the southern border of the Appalachian mountains and that "clicker" was a southern species extending northward into southern Ohio. When T.J.W. began studying the songs of katydids >40 yr ago, he soon discovered that based on song, Florida was home to two species of the *rotundifolia* complex. One species seemed to be Alexander's "clicker"; the other was a previously unrecognized species that he dubbed "fast ticker." In the years following, he and J.D.S. accumulated specimens, tape recordings of songs, and field notes pertaining to populations of the three presumptive species of *A. rotundifolia* and, to a lesser extent, populations of *Amblycorypha parvipennis.* More recently T.G.F. began studying rattler and clicker populations near Asheville, NC. This paper summarizes what we know about four species in the *A. rotundifolia* complex and provides formal names for two that have none.

Nomenclature

The *rotundifolia* complex has at least four species, as will become evident after their songs, ecology, and geographical distributions are described. To facilitate those descriptions, we will first attend to the requirements of formal nomenclature.

Amblycorypha rotundifolia (Scudder) 1862: 445
rattler round-winged katydid
(Figs. 1 and 5, 7–10)

Scudder's types of *A. rotundifolia* are lost, but because they came from four New England states and Illinois, the name must be assigned to the species that Alexander termed "rattler."

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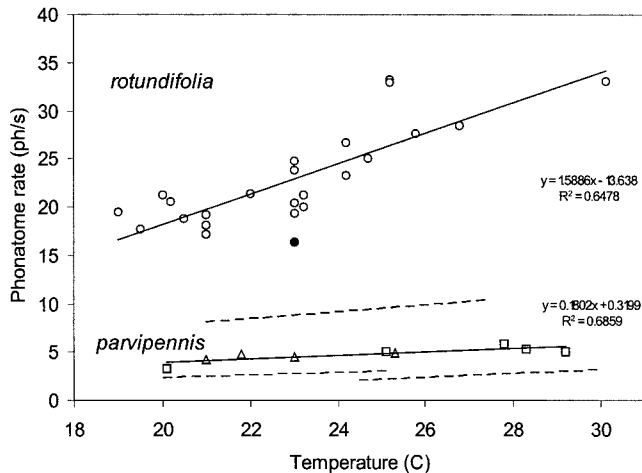[3] Department of Biology and Geology, University of South Carolina Aiken, Aiken, SC 29801.

Fig. 1. Phonatome rate as a function of temperature in *A. rotundifolia* (24 tapes of 19 males from 10 counties in Georgia, Illinois, Indiana, New Jersey, Ohio, Pennsylvania, Tennessee, and Virginia) and *A. parvipennis* (nine tapes of five males). The triangles are recordings by T.J.W. from Carter Co., MO, and the squares are recordings by J.D.S. from Bell Co., TX. The filled circle is an *A. rotundifolia* recording from Dyer Co., TN, with atypical phonatomes. The dashed lines are the trend lines for *A. bartrami* and *A. alexanderi* from Fig. 2.

Material Examined. 47 ♂, 16 ♀, Florida State Collection of Arthropods, Gainesville, FL (FSCA). Georgia: Murray Co.: 2 ♂, 2 ♀, 11-VI-67, T.J.W.; Rabun Co.: 1 ♂, 1-VIII-68, J.D.S. Illinois: Douglas Co.: 8 ♂, 4 ♀, 25-VII-65, T.J.W. Indiana: Parke Co.: 4 ♂, 1 ♀, 25-VII-65, T.J.W. New Jersey: Middlesex Co.: 1 ♂, 17-VIII-67, T.J.W. New York: Schuyler Co.: 2 ♂, 12-VIII-65, T.J.W. and G.K. Morris. North Carolina: Buncombe Co.: 3 ♂, 4 ♀, 16-VIII-01, 3 ♂, 2 ♀, 26-VII-01, 3 ♂, 2 ♀, 4-VIII-01, T.G.F. Ohio: Shelby Co.: 2 ♂, 12-VIII-67, 1 ♂, 24-VIII-67, T.J.W.; Washington Co.: 1 ♂, 21-VIII-68, 1 ♂, 21-VIII-70, T.J.W. Pennsylvania: Berks Co.: 6 ♂, 1 ♀, 24-VII-64, T.J.W.; Butler Co.: 1 ♂, 11-VIII-65, T.J.W. Tennessee: Dyer Co.: 1 ♂, 4-VIII-67, T.J.W. Virginia: Bland Co.: 1 ♂, 31-VIII-68, T.J.W.; Westmoreland Co.: 2 ♂, 25-VIII-64, T.J.W. West Virginia: Greenbrier Co.: 4 ♂, 1-IX-72, T.J.W.

Amblycorypha parvipennis Stal 1876: 58
western round-winged katydid
(Figs. 1, 5, and 10)

A. rotundifolia parvipennis Rehn and Hebard 1914: 339.

A. brachyptera Ball 1897: 237. [Ames & northwestern Iowa]

A. iselyi Caudell 1904:50 [Wichita, KS]

Stal's type material was from Texas and is in the Naturhistoriska Rijksmuseum, Stockholm, Sweden (Otte 1997). When Hebard (1934) recognized *A. parvipennis* as specifically distinct from *A. rotundifolia*, he indicated that *A. parvipennis brachyptera* was a northern race of *A. parvipennis* and that *A. iselyi* was a synonym of *A. brachyptera.*

Otte (1997) placed *A. iselyi* as a synonym of the southern race (*A. p. parvipennis*) rather than the northern race (*A. p. brachyptera*). We do not recognize subspecies in *A. parvipennis* because to do so would imply that its geographical variation has discontinuities or steep clines and we know of neither.

Material Examined. 1 ♂, MO: Carter Co.: 23-VII-65, T.J.W., FSCA. T.J.W. also examined specimens at the University of Michigan Museum of Zoology, Ann Arbor, MI (UMMZ) (29 localities), Academy of Natural Sciences of Philadelphia, Philadelphia, PA (ANSP; 19 localities), and the National Museum of Natural History, Washington, D.C. (USNM) (five localities). These localities plus records from the literature are documented at http://buzz.ifas.ufl.edu/h00dbase. htm and mapped in Fig. 10.

Amblycorypha alexanderi n. sp., T. J. Walker
clicker round-winged katydid
(Figs. 2, 4, and 6–10)

Holotype. Male, Torreya State Park, Liberty Co., FL, 16-VI-58, ravine forest, WTL-001-1, T.J.W., FSCA. Green; possessing the characters that distinguish the complex (Fig. 6A and B); ventral carina of hind femur with five teeth; hind femur reaching tip of tegmen. Pronotal length, 5.9 mm, width, 4.2; tegminal length, 32, width, 9.4; hind femur length, 28; hindwing exposure, 4.5.

Allotype. Female, FL Caverns State Park, Jackson Co., FL, 14-VI-62, moist broad-leaved forest, T.J.W. and J.D.S., FSCA. Like the male but with four and five teeth on carinae of left and right hind femora; hind femora exceeding tips of tegmina by 2 mm. Pronotal length, 5.8 mm, width, 3.9; tegminal length, 28, width, 8.3; hind femur length, 28; hindwing exposure, 3.5; ovipositor length, 10.4.

Paratypes. 31 ♂, 10 ♀, FSCA. Florida: Jackson Co.: 6 ♂, same data as allotype; Liberty Co.: 2 ♂, same data as holotype; 2 ♂, 17-VI-58, T.J.W., 1 ♂, 13-VI-62, T.J.W.
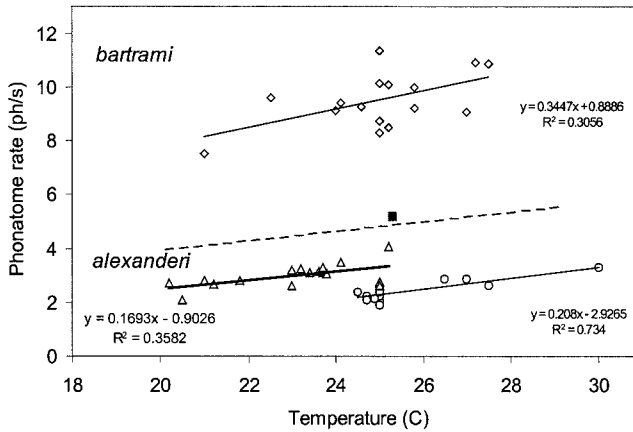
Fig. 2. Phonatome rate as a function of temperature in *A. bartrami* (16 tapes of 10 males, from four counties in Alabama, Florida, and North Carolina) and *A. alexanderi* from northern localities (triangles) (17 tapes of 13 males from counties in Georgia, North Carolina, and Ohio) and southern localities (circles) (13 tapes of seven males from Jackson and Liberty counties in Florida). The dashed line is the trend line for *A. parvipennis* from Fig. 1. The black square is a recording of *A. nr. bartrami* from near Aiken, SC. The cluster of seven points that are nearly on the line for northern *A. alexanderi* between 23 and 24°C are from Buncombe Co., NC. The two points at 25°C that nearly overlap those of southern *A. alexanderi* are from nearby McDowell Co., NC.

Georgia: Murray Co.: 1 ♂, 1 ♀, 11-VI-67, T.J.W.; Rabun Co.: 1 ♂, 20-VII-68, J.D.S. North Carolina: Buncombe Co.: 4 ♂, 24-VII-01, 3 ♂, 1 ♀, 30-VII-01, 1 ♀, 29-VI-02, 3 ♂, 1 ♀, 30-VI-02, 2 ♂, 4 ♀, 16-VII-02, 1 ♂, 2 ♀, 20-VII-02, 1 ♂, 27-VII-02, T.G.F.; Macon Co.: 1 ♂, 20-VII-68, J.D.S. Ohio: Ashland Co.: 3 ♂, 7-VIII-65, T.J.W.

Other specimens. 6 ♂, FSCA. Tennessee: Sevier Co.: 6 ♂, 13-VIII-66, T.J.W.

Etymology. This species is named for R.D. Alexander, who was first to recognize that it was distinct from *A. rotundifolia.*

Amblycorypha bartrami n. sp., T. J. Walker
Bartram's round-winged katydid
(Figs. 2, 3, and 7–10)

Holotype. Male, western Gainesville, Alachua Co., FL, 14-VI-63, interface of xeric hammock and dry old field, Walker Tape Library (WTL) 005–6a,b, T.J.W. and R. E. Love, FSCA. Green; possessing the characters that distinguish the complex; ventral carina of left hind femur with four teeth, of right, six teeth; hind femur slightly exceeding tip of tegmen. Pronotal length, 5.9 mm, width, 4.0; tegminal length, 30, width, 8.5; hind femur length, 28; hindwing exposure, 5.5.

Allotype. Female, 0.5 miles N of Alachua, Alachua Co., FL, 8-VI-24, F.W. Walker, low bushes, mostly dwarf chinquapin and oak, FSCA. Like the male but with three and five teeth on carinae of left and right hind femora; hind femora exceeding tips of tegmina by 2 mm. Pronotal length, 6.5 mm, width, 4.3; tegminal length, 29, width, 9.0; hind femur length, 28; hindwing exposure, 2.5; ovipositor length, 9.6.

Paratypes. 20 ♂, 4 ♀, FSCA. Alabama: Cleburne Co.: 1 ♂, 29-VIII-64, T.J.W.; Perry Co.: 3 ♂, 4 ♀, 9-VI-66, J.D.S., 6 ♂, 8-VI-67, T.J.W. Florida: Alachua Co.: 1 ♂,

29-VI-60, T.J.W., 1 ♂, 3-VIII-60, T.J.W., 1 ♂, 5-VI-62, T.J.W., 1 ♂, 3-VII-62, T.J.W., 1 ♂, 10-VI-63, T.J.W. and R.E. Love, 1 ♂, 2-VI-65, T.J.W. and R.E. Love; Leon Co.: 1 ♂, 11-VI-62, T.J.W. and J.D.S.; Liberty Co.: 1 ♂, 12-VI-62, T.J.W. and J.D.S. North Carolina: Hoke Co.: 1 ♂, 26-VII-64, T.J.W.; Stanly Co.: 1 ♂, 21-VI-62, T.J.W.

Other specimens. 4 ♂, 4 ♀, FSCA. South Carolina: Aiken Co.: 2 ♂, 17-VI-68, 1 ♀, 10-VII-87, 1 ♂, 7-VI-88, 1 ♂, 21-VI-88, 1 ♀, 14-VI-93, 1 ♀, 21-VI-93, JDS; Edgefield Co.: 1 ♀, 7-VI-88, J.D.S.

Etymology. This species is named for William Bartram, the earliest naturalist to explore the habitats in Florida where T.J.W. first encountered *A. bartrami.*

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 using a sweep 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. T.J.W. recorded songs 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. T.G.F. recorded songs using a Sennheiser ME66 shotgun microphone and a Tascam DAP-1 DAT recorder at a sampling frequency of 48kHz. J.D.S. recorded songs half-track on 0.25-inch tape at 7.5 ips with a Uher Report S or Uher Report L analog tape recorder and an Electrovoice 655C microphone. Most recordings were of caged specimens, although a few were made in the field with the aid of a 61-cm diameter parabolic reflector. T.J.W. and J.D.S. measured temperatures with a mercury laboratory thermometer at the cage or parabola; T.G.F. used a Tektronix ATP01 temperature
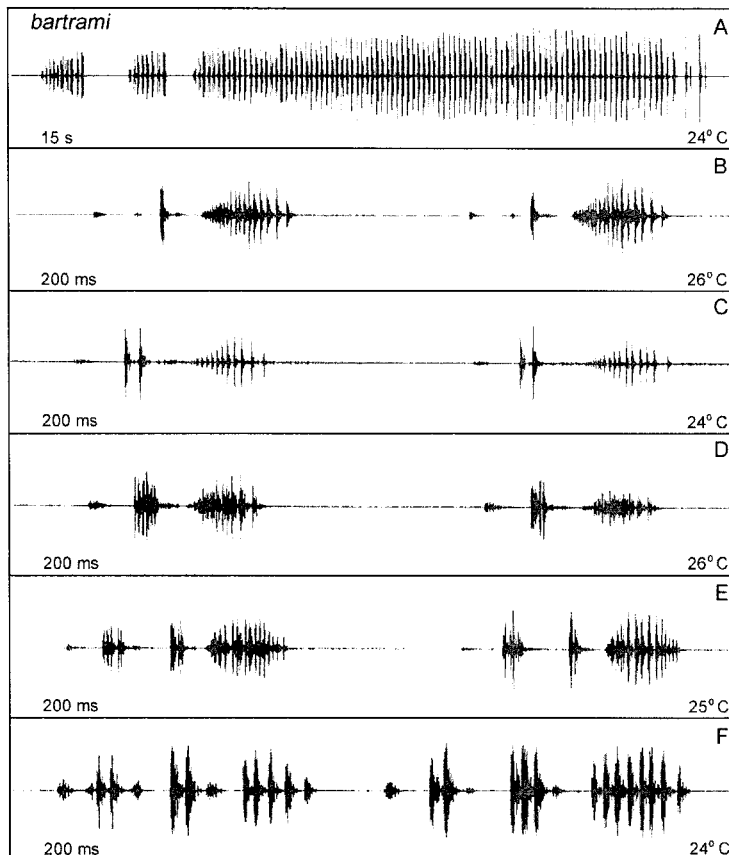
Fig. 3. Waveforms of the songs of *A. bartrami*. (A) 15 s of calling; mean phonatome rate during the long train is 9.1 ph/s (WTL 005–4a, Leon Co., FL). (B–E) Two consecutive phonatomes from prolonged trains of similar phonatomes. (B) Initial component a single pulse (WTL 005–4d, Leon Co., FL). (C) Initial components two single pulses (WTL 005–4a, Leon Co., FL). (D) Initial component a brief pulse train (WTL 005–6b, Alachua Co., FL). (E) Initial components two brief pulse trains (WTL 005–5c, Stanly Co., NC). (F) Pair of phonatomes in a sequence of pairs (WTL 005–14, Moore Co., NC).

probe. Initially recordings were analyzed with a Kay Elemetrics model 7029A sound spectrograph. Recently, most of the analog 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, upturned edge (scraper) of the base of the right tegmen along a series of downward projecting teeth (file) at the base of the left tegmen. The set of sounds made by one cycle of tegminal movement is called a "phonatome." The surest way to learn what sounds are made during a cycle is to capture the movement with high-speed photography or video and relate the movements to the sounds produced. This has been done with *Amblycorypha parvipennis* (Shaw et al. 1990). For the other three species of the complex, we inferred what sounds constituted a phonatome by looking for repeating patterns in the waveform of the calling song and comparing the results with what Shaw et al. had reported.

Phonatome rates were calculated by T.J.W. from times measured with a scale on sound spectrograms or with a mouse on CoolEdit 2000 displays. For *A. rotundifolia*, the rate was based on a 2-s sound spectrograph of the central portion of a prolonged train (i.e., sequence) of phonatomes. For the remaining species, rates were based on a set of almost uniformly spaced phonatomes in a prolonged train. For *A. alexanderi* and *A. parvipennis* songs, measurements were made from the beginning or end of the first phonatome in the train to the corresponding point on the last phonatome. For *A. bartrami*, in which phonatomes at the end of long trains are suddenly more widely spaced, the last phonatome measured was the one before the first phonatome interval that was longer than the previous one by >50%. In all cases, equal numbers of phonatomes and phonatome intervals were included in the measurement. Linear regression was used to establish trend lines for the graphs showing phonatome rate as a function of temperature.

The phonatome rates calculated as described above were the average rates in prolonged trains. In all species, phonatome rates usually decline gradually during prolonged trains. To quantify the decline, T.J.W. used CoolEdit measurements to calculate the average pho-

natome rates for the first 10 and the last 10 phonatomes in prolonged trains. The suddenly slowed phonatomes at the end of *A. bartrami* trains were again omitted. We used the difference in the two average rates, expressed as a percentage of the initial (faster) rate, to quantify the degree that the rates declined.

Modal carrier frequencies of songs were determined with CoolEdit's FFT analysis. The sampling rate was 44,100/s, and time-sample sizes were adjusted to minimize variation from reading to reading.

Specimens from all available localities for the three eastern species were measured in a search for dimensional differences. T.J.W. used a calibrated ocular micrometer of a Zeiss stereomicroscope to measure pronotal length, tegminal width, hindwing exposure, and ovipositor length. Pronotal length was measured medially. Tegminal width was measured at the widest point. Hindwing exposure was measured along the longitudinal axis of the tegmen. Ovipositor length was the straight-line distance from the apex to where the ventral edge of the ovipositor disappeared at the subgenital plate. Tegminal and femoral lengths were measured with a dial micrometer.

Stridulatory files were studied after cutting the stridulatory field from the left tegmen of males. The inverted field was then magnified to 50× with a Leica stereomicroscope and digitally photographed with a Syncroscopy Auto-Montage system (http://www.syncroscopy.com/syncroscopy). The number of file teeth and length of the files were determined by T.J.W. from hardcopy of 96× images. To be counted as file teeth, 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 the straight-line distance from the center of the first file tooth to the center of the last file tooth.

The recordings in WTL will be archived and made available on the Internet by the Macauly Library of Natural Sounds at Cornell University. Excerpts of representative recordings, including those of the *A. rotundifolia* complex, are already accessible through Singing Insects of North America (http://buzz.ifas.ufl.edu/). Also at this site are spreadsheets with the data used to develop Figs. 1, 2, 7, and 8 and other aspects of this paper (http://buzz.ifas.ufl.edu/g001a.htm) and a database that substantiates the localities mapped in Fig. 10 along with detailed information about the collecting sites of most specimens examined for this study (http://buzz.ifas.ufl.edu/h00dbase.htm).

Results and Discussion

Male Songs. The calling song feature most useful in identifying species in the *A. rotundifolia* complex is the phonatome rate during near-uniform trains of phonatomes. Phonatome rates are temperature dependent in all katydids (Walker 1975), although the differences among the three eastern species of the *A. rotundifolia* complex are so great that different field temperatures do little to impede identifications by song (Figs. 1 and 2).

A. rotundifolia has the fastest phonatome rate, averaging ≈26 ph/s at 25°C (Fig. 1). Calling males produce trains of phonatomes that last from <1 s to as long as 7 s. Because the constituent phonatomes come too rapidly to be heard individually, the human ear renders *A. rotundifolia* trains as "rattles." The song often begins with several brief trains that lead into a prolonged one. The prolonged train is often immediately followed by a few trains of <10 phonatomes each (Fig. 5A). During trains lasting >1 s, the phonatome rate decreases slightly. In laboratory recordings of seven individuals, the phonatome rate near the end of long trains was 4–14% slower (av. 10%) than the phonatome rate near the beginning of the train. During phonatome trains the intensity of the phonatomes often increases initially (e.g., first four trains in Fig. 5A).

A. alexanderi has the slowest phonatome rate, averaging <4 ph/s at 25°C. Phonatomes can be heard individually and are rendered as "clicks" by the human ear. Phonatomes are generally produced at nearly uniform rates for 5–30 s. During such trains the phonatome rate usually declines (16 of 19 recordings), with the average decline being 7% (range, 1–17%; 16 recordings of 12 individuals). These nearly regular trains are generally preceded by several more widely spaced clicks (Fig. 4A). During the prolonged trains the intensity of successive clicks usually increases initially and then remains fairly constant or, near the end of the sequence, decreases somewhat. The click rates for *A. alexanderi* from Jackson and Liberty counties in northern Florida are slower than the click rates for *A. alexanderi* from northern Georgia, North Carolina, and Ohio. The trend lines for phonatome rate as functions of temperature predict a rate of 2.27 for songs from two counties in Florida and 3.33 for songs from Murray County, GA, and northward (Fig. 2). Near Asheville, NC, T.G.F. recently discovered a population of the *A. rotundifolia* complex that produced phonatomes at the rate of *A. alexanderi* but in trains of 8–14 phonatomes with intervals between trains similar to the duration of the trains. Furthermore, calling males often inserted ticks between phonatomes within the trains. This caused TJW to reconsider his identification, as *A. alexanderi*, of a 1966 recording and six males from Greenbrier Cove, Sevier County, TN. Until these populations are studied further they should be excluded from what is here described as *A. alexanderi*.

A. bartrami produces ≈10 ph/s at 25°C (Fig. 2)—less than half the rate of *A. rotundifolia* and more than three times the rate of *A. alexanderi*. The usual phrasing of *A. bartrami* songs (Fig. 3A) resembles that of *A. rotundifolia* (Fig. 5A), but the phonatomes come slowly enough to be heard as discrete units making the calling males "fast tickers" rather than "rattlers." The several more widely spaced sounds that may terminate a prolonged phonatome train are single phonatomes rather than trains. During prolonged trains, the phonatome rate decreases by 5–32% (average = 13%, based on 16 recordings of 10 individuals). In his studies of populations of the *rotundifolia* complex near Aiken, SC, JDS originally considered them to be *A. bartrami*
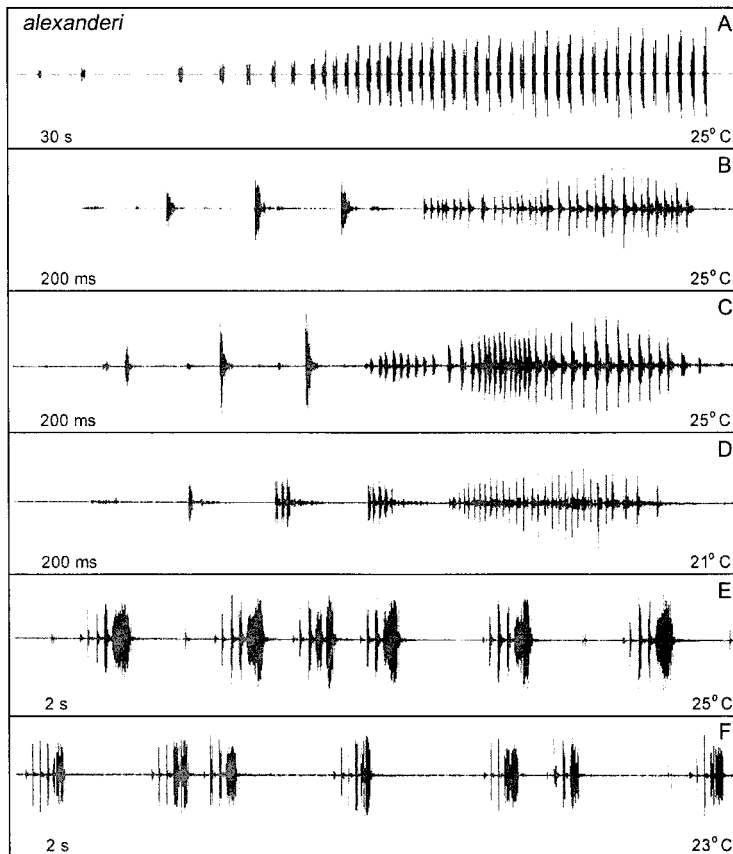
Fig. 4. Waveforms of the songs of *A. alexanderi*. (A) 30 s of calling; mean phonatome rate after initial seven phonatomes is 2.1 ph/s (WTL 001–8c, Jackson Co., FL). (B–D) Single phonatomes from trains of similar phonatomes. (B and C) Terminal pulse trains of these two phonatomes differ in length and complexity (WTL 001–8c, Jackson Co., FL). (D) Initial components are a single pulse and two brief pulse trains (WTL 001–16, Murray Co., GA). (E) Sequence of phonatomes with an interpolated phonatome (WTL 001–5b, Liberty Co., FL). (F) Sequence of phonatomes with two doubled phonatomes (WTL 001–12, Ashland Co., OH).

because their phonatome rates were intermediate between *A. rotundifolia* and *A. alexanderi* and they occurred in sandhill habitats. However, a recent analysis of a recording of the calling song of a male from near Aiken revealed a much slower phonatome rate than is typical for *bartrami* (Fig. 2, filled square). Therefore, we do not list specimens of Aiken "*A. nr. bartrami*" as paratypes of *A. bartrami* even though *A. bartrami* is the most appropriate available name for the Aiken populations. T.J.W. recorded the songs of two *A. bartrami* from Moore County, NC, but these are excluded from Fig. 2 because neither recording contained trains of more than four phonatomes and 66% of the phonatomes were in pairs (Fig. 3F). The phonatome rates based on these pairs were 11.2 at 24.8°C and 8.7 at 19.5°C, which conform fairly well to other rates for *A. bartrami* and even better when they are adjusted upward for being based on short (fewer than 20 phonatomes) rather than long phonatome trains. (When rates based on short and long trains were compared for 12 of the 16 *A. bartrami* recordings plotted in Fig. 2, the average adjustment factor was 1.18.)

A. parvipennis produces ≈5 ph/s at 25°C, which is approximately one-half the rate of *A. bartrami* and approaching twice the rate of *A. alexanderi* (Fig. 1). Phrasing usually consists of trains of 20–40 phonatomes with inter-train intervals shorter than the trains (Fig. 5D). As in other species, phonatome rate usually declines toward the end of a train. For eight recordings of five individuals the rates decreased 0–29% (average = 12%).

The frequency spectra of the calls of the four species were broad, varied, and of no use in separating species. There were usually several well-separated frequency peaks, and the most intense frequency was generally between 9 and 14 KHz. The mean most-intense frequency for songs of each of the four species fell between 9.8 and 11.1 kHz.

The phonatomes produced by males of the *A. rotundifolia* complex are noteworthy for their complexity and for their variation within and between species. A typical phonatome of *A. bartrami*, *A. alexanderi*, and *A. parvipennis* consists of one to four brief initial components followed by a longer terminal component
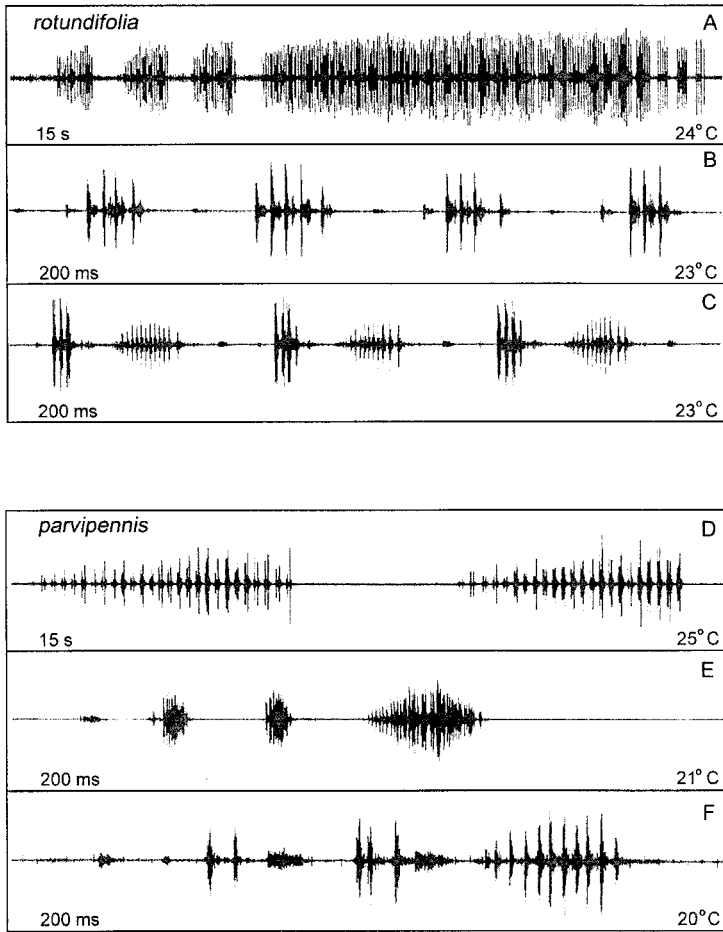
Fig. 5. Waveforms of the songs of *A. rotundifolia* (A–C) and *A. parvipennis* (D–E). (A) 15 s of *A. rotundifolia* calling; mean phonatome rate during long train is 23 ph/s. (WTL 008–1a, Berks Co., PA). (B) Four typical phonatomes (WTL 008–13, Parke Co., IN). (C) Three atypical phonatomes (WTL 008-18, Dyer Co., TN). (D) 15 s of *A. parvipennis* calling; phonatome rate during trains is 4.9 ph/s (WTL 013–2c, Carter Co., MO). (E and F) Single phonatomes. (E) WTL 013–2b, Carter Co., MO. (F) J.D.S. recording PAm2–1a, Bell Co., TX.

(Figs. 3B–E, 4B-D, and 5E and F). Each initial component has one to several pulses, whereas the terminal component has 10 or more pulses. Phonatomes of *A. rotundifolia* typically lack a longer, terminal component (Fig. 5B). In all species, the phonatomes of a given train usually have a common pattern, as illustrated by four and three consecutive phonatomes from *A. rotundifolia* trains in Fig. 5B and C and two consecutive phonatomes from each of four *A. bartrami* trains in Fig. 3B–E.

In most of the *A. bartrami* songs, phonatomes began with one or two intense exponentially decaying pulses (initial components) followed by the terminal pulse train, in which the intensity of the pulses first increased and then declined (Fig. 3B and C). As seen in Fig. 3D, the initial pulse or pulses were sometimes replaced with a brief pulse train. Males in the northern half of the range of *A. bartrami* (Stanly and Moore counties, NC, and Perry and Cleburne counties, AL) often made phonatomes with two brief pulse trains

before the longer terminal train (Fig. 3E and F). Such phonatomes were longer and were often associated with lower average phonatome rates. In fact, five of the six points that are well below the *A. bartrami* trend line in Fig. 2 represent northern localities. It should be noted that the characteristic slowing of phonatome rates within prolonged trains, in this and other species, resulted from longer phonatome intervals rather than longer phonatomes.

Phonatomes in *A. alexanderi* began with 2–4 (usually 3) brief initial components. They ended with a terminal pulse train that lasted more than twice as long as the corresponding train in *A. bartrami* and included complex variations in pulse rate and intensity (Figs. 4B–D). *A. alexanderi* phonatomes lasted approximately three times as long as *A. bartrami* phonatomes at the same temperature. This accounted for most, but not all, of the difference in phonatome rates between the two species; the rest of the difference was a result of longer intervals between phonatomes. Two atypical

songs, illustrated in Fig. 4E and F, demonstrate that the interval between phonatomes can be as brief as 40 msec, whereas the typical interval at 25°C is more than three times as great.

Phonatomes in *A. parvipennis* always ended with a train of 10 or more pulses (Fig. 5E and F). Preceding this were two or more isolated pulses or brief pulse trains or a combination of the two.

In *A. rotundifolia*, the species with the highest phonatome rate and the briefest phonatomes, each phonatome was typically a brief series of 2–5 (usually 3 or 4) intense pulses. There was no terminal train—except for the song of a male from western-most Tennessee (Fig. 5C). In this song, each phonatome consisted of a rapid group of 3–4 intense pulses followed by a train of 10 or more less-intense pulses that had the same graded changes in pulse intensity seen in the terminal pulse trains in other species within the complex. The extra train increased phonatome duration, and lowered the phonatome rate of this recording relative to the trend line for all recordings of this species (Fig. 1, filled circle).

Detection of different songs within "*A. rotundifolia*" long predates this paper. Allard (1912, p. 462) noted that "The stridulations of *Amblycorypha rotundifolia* may consist of brief soft, shuffling phrases, sh-sh-sh-sh, repeated at intervals. At other times the notes become more lisping and continuous, tsip-i-tsip-i-tsip-i-tsip." The songs that Allard rendered onomatopoeically are probably those of *A. rotundifolia* and *A. alexanderi*, respectively. Fulton (1932) described two songs for North Carolina *A. rotundifolia*. One is clearly rattler, "on bushes in mountains"; the other is evidently either *A. bartrami* or *A. alexanderi*, probably the former, because it was "on oaks in sand hills." Alexander (1960) described and illustrated the songs of "clicker" and "rattler" (his Fig. 16 and selection 5 on an accompanying 12-inch LP record.) As mentioned earlier, he concluded that they were distinct species with overlapping geographical ranges. In the overlap area he sometimes found them in mixed colonies, but he showed that each was unaffected by the singing of the other. When caged males of either species called, only males of the same species were stimulated to join the chorus.

The song of *A. parvipennis* was first described by Fulton (1928), who was also first to note that neighboring males calling at the same time almost perfectly synchronize the phonatomes of their overlapping trains. Galliart and Shaw (1991, 1992, 1996) showed that males that avoid such overlap at the beginnings of their phrases have an advantage in the competition for females.

Exactly what movements of the file and scraper produce the fine structure of the phonatomes are not known. High-speed recordings of tegminal movements during calling in *Amblycorypha* nr. *uheri* (Walker and Dew 1972) and in >20 species of barbitistine phaneropterines (Heller 1990) show that the possibilities are enormous. When Shaw et al. (1990) reported that sounds of *A. parvipennis* equivalent to those in Fig. 5E were made during a single cycle of

wing movement, they did not parse the sounds between the opening and closing portions of the cycle. However, in other studies of phaneropterine tegminal movements during calling, most or all of the sounds have been made on closure. In any case, each pulse in the phonatome probably represents the engagement and release of a single file tooth, with the amount of energy stored before release determining the intensity of the pulse.

Female Answers. Unlike most other katydids, females of most species in the subfamily Phaneropterinae make brief, nondescript answers (ticks) to songs, or to certain songs, of conspecific males (Spooner 1968). The details of phaneropterine pair forming systems vary (Spooner 1995), and even within a genus some species may employ female answers and others not (Heller and von Helversen 1993).

Shaw et al. (1990) were first to report on female acoustic responses for a species in the *A. rotundifolia* complex. Using specimens of *A. parvipennis* from Ames, IA, they found that females made ticks that fell between the phonatomes of the male's phonatome train. Responding females produced an average of 3.2 ticks per phonatome train with the last tick coming after the last phonatome in the train 36% of the time. At 24–25°C, the delay between the beginning of a phonatome and the tick produced in the following interval averaged 120 ms. Galliart and Shaw (1991) found that when a female phonoresponded, the calling male walked to the female if both were unrestrained. Galliart and Shaw (1992) reported that if the male was restrained and the female was free, the responding female moved to the calling male. Galliart and Shaw (1996) used computer-generated calls to further study female phonoresponse and phonotaxis in *A. parvipennis*.

In 1966, J.D.S. recorded acoustic exchanges between caged males and females of *A. bartrami* from Perry County, AL. In these recordings the males usually made successive trains of five or six phonatomes and the females ticked one or more times after each train. At 23°C, the time between the end of the phonatome train and the first female tick varied from 138 to 688 ms ($n = 10$, mean = 416). When a male produced a longer train, the answering female would sometimes start ticking before the train ended. In these cases, the females showed no tendency to time their ticks relative to the phase of the phonatome cycle.

Years later, J.D.S. studied acoustic pair formation in *A.* nr. *bartrami* collected near Aiken, SC. In a 1988 recording of a caged male and female (J.D.S.-Pam1–8,-9; 25.3°C), the female at first ticked only in phase with the phonatome intervals of prolonged trains. To trains of 21, 24, and 21 phonatomes, she did not begin answering until the seventh phonatome in the train or later. The timing of the answers (always a single tick) varied little relative to the beginning or end of the preceding phonatome. In a sample of 10, the delay from the beginning was 103–140 ms (mean = 134) and from the end, 21–43 (mean = 35). No more than 6 phonatomes in a train were answered with the earliest

answer coming after the seventh phonatome and the last phonatome being answered in two of the three trains analyzed. When the male began to produce trains of 4–7 phonatomes, the female would answer one or two phonatomes keeping the timing as before. When the male started to produce long trains again, the female would sometimes produce multiple ticks with little or no regard to the phase of the phonatome period and at other times would deliver single ticks in the intervals as earlier. Overall, in this recording, *A. nr. bartrami* resembled *A. parvipennis* more than *A. bartrami* in both phonatome rate (5.20/s) and in the timing and placement of female ticks.

In a report summarizing his studies of *A. nr. bartrami*, J.D.S. (Spooner 1995) noted that responsive females, after hearing the first few short trains in a song, made one to three ticks at the end of each additional short train. When a long train was produced, they would begin to vigorously tick before it ended and, following the end, make several more ticks. (These phonoresponses resemble those of the Perry Co., AL *bartrami*.) If either sex was restrained, the unrestrained sex moved to the restrained. If both male and female were freed as they called and ticked 4 m apart, they moved toward each other and met about midway between their release points.

The phonatome rates and intervals of the remaining two species fall on either side of those treated above. The phonatome rate of *A. rotundifolia* is more than double that of *A. bartrami*, suggesting that female ticks would not be restricted to a specific part of the phonatome period and would more likely come at the end of pulse trains. In keeping with these expectations, when a caged female from Berks County, PA, answered the rattle of a male from the same locality, in 12 of 17 cases the ticks began after the rattle ended. In the other five cases, the ticks began during the rattle, usually near the end. When the ticks began after the rattle, the delays averaged ≈130 ms (range, = 91–366; 24.7°C; WTL-8–1b). T.G.F. recorded >220 tick answers from four *A. rotundifolia* females duetting with three different *A. rotundifolia* males (Buncombe County, NC; at 22.3–23.7°C). Twenty-six percent of the answers occurred during the rattle; the rest occurred during the intervals between phrases, usually between the short phrases following the prolonged portion of the song. On average the delays were ≈200ms but were highly variable and ranged from 140 to >600ms.

The phonatome rate of *A. alexanderi* is little more than half that of *A. parvipennis*, suggesting that females should tick in the intervals between phonatomes. In two recordings of a pair of *A. alexanderi* from Buncombe County, NC, T.G.F. found that the female's answers ($N = 69$) usually occurred between the phonatomes in the last half of the male's series of clicks and never during the first four clicks in the series. At 22.7 and 23.3°C, the delays in the female's answers averaged ≈270ms (range, 29–335ms). The variation in the delay was in part because of the variability in the period of the males' clicks. When the female's delays are expressed as a percent of the cycle period of the clicks, 42 of the 69 answers were produced during the last 15% of the phonatome cycle. For six of the nine trains answered, the female responded to the final phonatome in a train.

Ecology. Throughout their ranges, *A. rotundifolia* and *A. alexanderi* occur in the understory of broadleaved woods and in weedy roadsides and fencerows (Alexander 1956, 1960; current study). No differences in habitat preferences have been identified, and the two species sometimes occur in mixed colonies (Alexander 1960). In 4 yr, near Asheville, NC, where T.G.F. studied five sites with *A. rotundifolia* populations and five with *A. alexanderi* populations, he neither found a site with both species nor developed a means of predicting which species would occur at an occupied site. On the access road to Black Rock Mountain in Rabon County, GA, J.D.S. found *A. alexanderi* and *A. rotundifolia* in similar habitats but ≈0.4 km apart.

In west Florida, where *A. alexanderi* and *A. bartrami* co-occur, the former species was found exclusively in mesic, broadleaved woods (beech-maple in Jackson County and ravine forest in Liberty County), whereas the latter was found exclusively in more xeric, sandhill habitats. Sandhills habitats are characterized by frequent fires and, now that most of the longleaf pines have been lumbered, generally are dominated by turkey oaks. Most other collections of *A. bartrami* were also in sandhills, but in Perry and Cleburne counties, AL, and Stanly County, NC, the species was found in the hardwood understory of loblolly pine woods.

The original habitat of *A. parvipennis* was apparently prairie and its interface with deciduous woodland. It is now numerous in weedy pastures and old fields as well as prairie remnants (Isely 1941; Shaw et al. 1981, 1990). It feeds avidly on flowers and on buds and young leaves of a variety of plants (Isely 1941).

The seasonal life cycles of the four species are so similar that in localities where two of the species occur, no differences have been noted. Overwintering is in the egg stage. Adults first occur in June in the southern states and in July to early August farther north. Adults soon reach a maximum abundance and then decline. No second peak of adult abundance occurs, which suggests a univoltine life cycle. However, because many katydids, including *Amblycorypha oblongifolia* (De Geer), have eggs that require >1 yr to hatch, a longer life cycle cannot be ruled out (Hancock 1916, Ingrisch 1986).

All females of the *A. rotundifolia* complex probably lay their eggs in soil. Isely (1941) described oviposition of *A. parvipennis* in north-central Texas, in which the female uses her mouthparts to help guide the ovipositor into the soil. With her ovipositor fully inserted, she continues to hold it with her jaws while as many as 14 eggs are deposited in the soil in a loose cluster. J.D.S. found that captive females of *A. rotundifolia* and *A. nr. bartrami* would lay in soil, although in this case no alternative oviposition substrates were offered. The role of the arrays of acuminate teeth on the distal margins of ovipositors in the *rotundifolia* complex is unknown (Fig. 9). No similar teeth occur on the ovi-
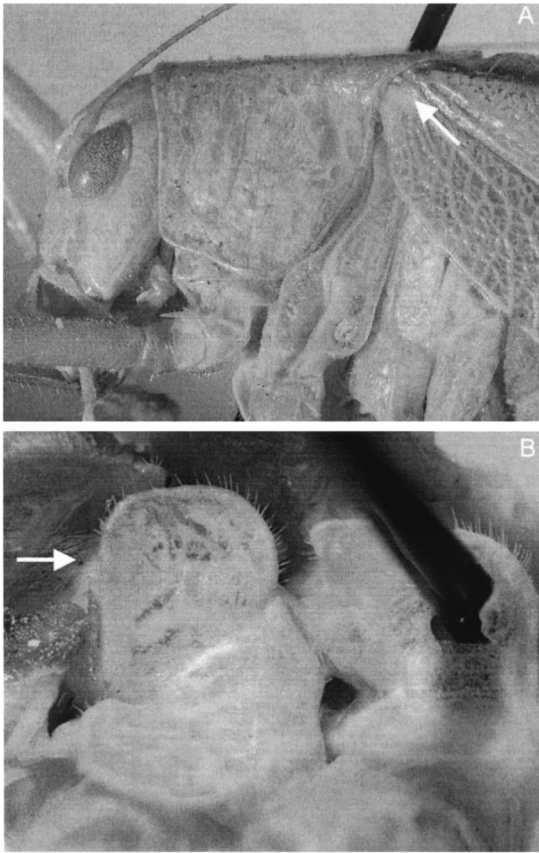
Fig. 6. Identifying characters of the *Amblycorypha rotundifolia* complex, as illustrated by the holotype of *A. alexanderi*. (A) Left lateral lobe of the pronotum. Arrow points to shallow humeral sinus. (B) Right metasternal lobe (specimen is inverted with the head to the right; pin pierces right mesosternal lobe). Arrow points to the lobe's caudal margin, which is truncated or nearly so. The width of the lobe, measured from the ventral midline and perpendicular to it, exceeds the length of the lobe as measured perpendicular to the caudal margin.

Table 1. Measurements in millimeters of the three eastern species of the *Amblycorypha rotundifolia* complex. Specimens of *A. alexanderi* from Florida and from more northern localities are listed separately because the means of their measurements differ significantly

Measurement	A. rotundifolia	A. alexanderi Northern	A. alexanderi Florida	A. bartrami
Males				
Pronotal length				
mean (n)	5.4 (31)	5.4 (11)	5.6 (12)	5.7 (21)
range	4.8–5.9	4.5–5.5	5.0–6.0	5.2–6.2
Tegminal length				
mean (n)	26 (30)	26 (11)	30 (11)	29 (19)
range	23–29	24–28	27–32	24–32
Tegminal ratio (L/W)				
mean (n)	3.0 (28)	3.0 (10)	3.3 (11)	3.3 (19)
range	2.7–3.4	2.8–3.2	3.1–3.7	2.9–3.5
Hindwing exposure				
mean (n)	4.3 (27)	4.1 (11)	5.2 (9)	4.9 (14)
range	3.1–5.2	3.3–4.7	4.6–5.8	3.1–6.0
Females				
Pronotal length				
mean (n)	6.1 (12)	6.1 (7)	5.9 (1)	5.8 (5)
range	5.8–6.4	5.8–6.4		5.4–6.5
Tegminal length				
mean (n)	26 (12)	25 (7)	28 (1)	26 (4)
range	23–28	23–27		23–29
Tegminal ratio (L/W)				
mean (n)	3.0 (12)	3.1 (7)	3.3 (1)	3.2 (4)
range	2.8–3.3	2.9–3.2		3.0–3.4
Hindwing exposure				
mean (n)	2.4 (12)	2.4 (7)	>3.4 (1)	2.5 (1)
range	1.6–3.2	1.9–3.0		
Ovipositor length				
mean (n)	9.9 (11)	10.1 (7)	10.2 (1)	9.7 (5)
range	9.3–11.0	9.7–10.9		9.3–10.0

positors of members of the *A. oblongifolia* complex, which also lay in soil.

Morphological Characters. Each of the species possesses the morphological characters that distinguish members of the *A. rotundifolia* complex from other species of *Amblycorypha*—namely, a shallow humeral sinus and transverse metasternal lobes. Because the state of neither of these characters is easy to judge without specimens to compare, we have illustrated them in Fig. 6A and B.

Only one of the four species in the complex can be reliably identified on the basis of morphological characters. In *A. parvipennis* the tegmina conceal the hindwings at rest, whereas in the other three species the tips of the hindwings, when normally developed, protrude 2–6 mm beyond the tips of the tegmina. A series of seven specimens of *A. bartrami* from Perry County, AL, 9 June 1966, prompted the caveat about normal

development: five had shriveled hindwings about half the length of the tegmina. In *A. parvipennis* the hindwings are normally developed and their tips nearly reach, but do not exceed, the tips of the tegmina.

Routine measurements of the remaining three species provided no identifying (nonoverlapping) features (Table 1). The measurements of *A. alexanderi* are noteworthy in that those from northern populations resemble those of *A. rotundifolia*, the northern species of the trio (first two columns of data in Table 1), and those from Florida populations resemble those of *A. bartrami*, the southern species of the trio (last two columns in Table 1). Indeed, the only populations that differed enough to be identifiable by their measurements were the northern and Florida populations of *A. alexanderi*. However, for univoltine species of tettigoniids with extensive distributions in eastern United States, clinal increase in size from north to south is commonplace. Therefore, if we had had specimens of *A. alexanderi* from intermediate localities, they would presumably have been intermediate in their measurements.

Because the songs of the eastern trio are so different, we looked for differences in characters of the stridulatory files. We found none that were of use in separating the species. Both in file length and number of file teeth the species broadly overlap (Fig. 7).
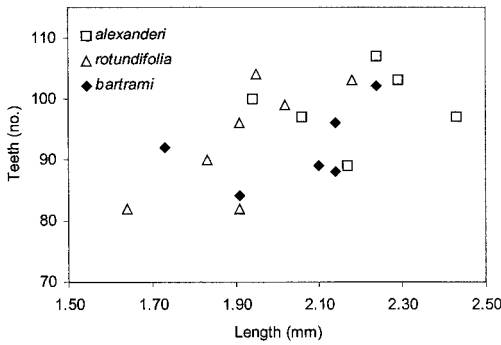
Fig. 7. Length of stridulatory file and number of file teeth for males of the three eastern species of the *A. rotundifolia* complex. *A. alexanderi* (*n* = 6; four counties in Florida, Georgia, and Ohio), *A. rotundifolia* (*n* = 7; six counties in Georgia Illinois, Ohio, Pennsylvania, and Tennessee), and *A. bartrami* (*n* = 6; five counties in Alabama, Florida, and North Carolina).

Characters of the ovipositor sometimes are useful in differentiating phaneropterine species, but our study of the ovipositors of *A. rotundifolia*, *A. alexanderi*, and *A. bartrami* revealed no species-identifying features. Neither the absolute length of the ovipositor nor the length relative to the pronotal length was species specific (Fig. 8). However, the ovipositors of Aiken *A. nr. bartrami* were longer than those of any other specimens examined. In the southern portion of its range, ovipositors of *A. rotundifolia* (*n* = 10, North Carolina, Georgia) had the marginal teeth produced into fine points, similar to those of *A. alexanderi* and *A. bartrami* (Fig. 9C). Farther north the teeth on *A. rotundifolia* ovipositors (*n* = 5, Illinois, Pennsylvania) lacked the fine, sharp points (Fig. 9D). Thus the apparent geographic variation in ovipositor teeth of *A. rotundifolia*, as in the geographic variation in the overall size of *A. alexanderi*, is in the direction that makes separating sympatric *A. rotundifolia* and *A. alexanderi* more difficult rather than less so.
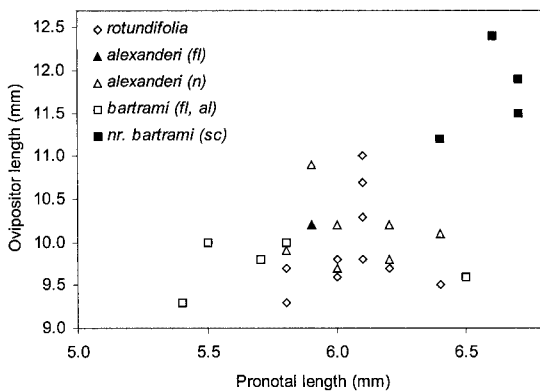

Fig. 8. Ovipositor length as a function of pronotal length. The black triangle is for the allotype and sole southern female specimen of *A. alexanderi*. The black squares are for females from populations near Aiken, SC.

Geographical Distribution. Figure 10 shows the distribution of the four species as currently understood. *A. rotundifolia* occurs farther to the north and west than the two new species with which it was confused. Records for Indiana and Illinois are abundant because of extensive published records that were deemed valid without confirming song data, as required in areas of sympatry. Most Ohio records are from the field notes of E. S. Thomas and R. D. Alexander, as made available to T.J.W. by Alexander (personal communication). The paucity of records in Kentucky and Tennessee may reflect scanty fieldwork in those states.

All records of *A. parvipennis* are from west of the Mississippi River. A study of calling songs of "*rotundifolia*" in Illinois and of "*parvipennis*" in eastern Iowa might reveal a geographical overlap not suspected from studies of museum specimens. For example, *A. parvipennis* could vary geographically in wing length but keep its reproductive integrity by virtue of its calling song.

A. alexanderi is broadly sympatric with *A. rotundifolia* in the north but extends much farther south. Its southern-most records are from a region of Florida known for its endemic plants and animals and for being the southern limit of many northern species (Hubbell et al. 1956). The Florida populations may be disjunct from those farther north, or, more likely, populations in habitats suited to *A. alexanderi* along the Chattahoochee River, may connect the Florida populations with those in the southern Appalachians.

A. bartrami probably occurs wherever there are sand-hill habitats in southeastern United States. However, the three records that mark its northwestern limits (Stanly County, NC, and Cleburne and Perry Counties, AL) are from more mesic habitats. This suggests that *A. bartrami* may occur farther to the north and west than the limits indicated in Fig. 10.

General Discussion

Studies of calling songs of North American crickets and katydids have revealed many previously unrecognized species and resolved several taxonomically difficult groups (e.g., Thomas and Alexander 1962, Walker et al. 1974). The usefulness of calling songs stems from the direct evidence they give of reproductive isolation among populations. Populations with different calling songs are using different signals to mediate sexual pair formation and hence are likely to be reproductively isolated. When laboratory crosses produce hybrids between populations with different songs, the hybrids have intermediate songs (Alexander 1968). Thus, a failure to maintain reproductive isolation between sympatric populations of song-defined species would be apparent from the occurrence of intermediate calling songs.

Once putative species have been defined on the basis of calling songs, morphological differences that correlate with the song differences are usually found. This makes possible identification of specimens that lack song data, thereby aiding further study and fa-
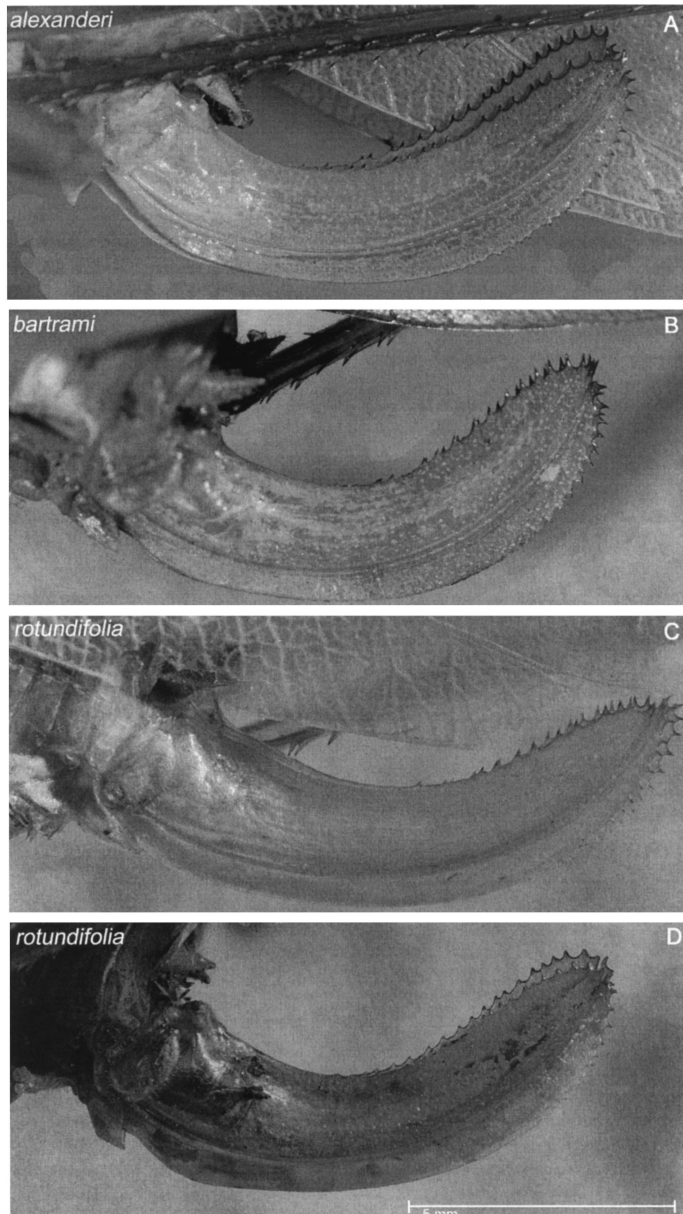
Fig. 9. Ovipositors. (A) *A. alexanderi*, allotype. (B) *A. bartrami*, allotype. (C) *A. rotundifolia* Murray Co., GA. (D) *A. rotundifolia*, Douglas Co., IL.

cilitating the description of the species that were first recognized by their songs.

On the basis of their calling songs, nearly all males of the *A. rotundifolia* complex can be unambiguously assigned to one of the four species we recognize here, but our studies of these males and associated females have uncovered no morphological characters that permit definite identification of the three eastern species. Our naming two new species before being able to separate them other than by song is driven by the sympatry of *A. rotundifolia* and *A. alexanderi* in most of the range of *A. alexanderi* and the sympatry of *A.*

alexanderi and *A. bartrami* in the southern portion of the range of *A. alexanderi*. When populations that differ in calling songs are in local contact and do not hybridize (no intermediate calling songs), they validate their status as species. To deny them formal names would make it unlikely that field biologists would know that two species of "*rotundifolia*" might exist in their study areas, and those who did so realize would be hindered in reporting their findings.

Female answers are apparently essential to pair formation for species in the *A. rotundifolia* complex. This means that males must make songs that have features
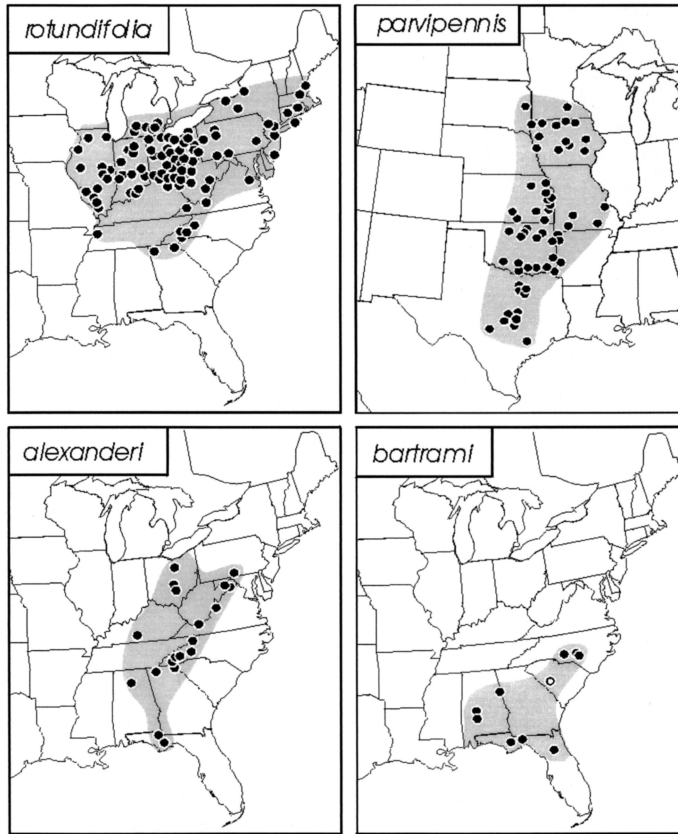
Fig. 10. Geographical distributions of the species in the *Amblycorypha rotundifolia* complex. In the map for each species, dots represent county records and shading indicates probable geographical limits. The open circle in the *A. bartrami* map is for a population near Aiken, SC, that has lower phonatome rates and longer ovipositors than populations elsewhere.

that stimulate their females to tick. Among the species here recognized, phonatome rate and phonatome structure are probably important. However, the ticks of females have no distinguishing physical features but must be delivered at times during the song that render them meaningful to their males. This suggests that studies to determine what features of calling songs make females tick and what timings of ticks stimulate males to approach will shed light on which of the variations in these two features noted here are likely to have roles in maintaining reproductive isolation among sympatric populations.

When considering species concepts, it is important to realize that *all species are local* (Lloyd 2002). This means, for example, that we cannot be certain that *A. alexanderi* in the southern Appalachians and *A. alexanderi* in northwestern Florida are the same species. We know that we can distinguish most specimens from the two areas by their sizes (and judge that to be of no consequence), yet we do not know whether individuals from the two areas would mate and produce fertile offspring were they given the chance. However, we have strong evidence that individuals we identified as *A. alexanderi* from Torreya State Park in Liberty County, FL, belong to a different species from those

individuals we identified as *A. bartrami* from the same place. Similarly, we know that *A. alexanderi* is a species distinct from *A. rotundifolia* at numerous sites in the southern Appalachians. In contrast, we can not be sure whether the sole species of the *A. rotundifolia* complex known from near Aiken, SC, is the same as or different from the species named *A. bartrami* with its holotype coming from Alachua County, FL. In this paper we have recognized a minimum number of species and described variations that we have found among the populations assigned to each of the four names.

It is important to understand that when sympatric populations have different songs they are almost certainly different species, but that when allopatric populations have the same song they are not necessarily conspecific. The case of the cricket genus *Pictonemobius* (Gross et al. 1990) exemplifies the difficulty of extending locally defined species to distant areas. Production of four types of calling songs among *Pictonemobius* populations in the vicinity of Gainesville, FL, indicated four species, and the reproductive isolation of the four was confirmed by laboratory crosses and electrophoretic analysis. Two of the species were morphologically distinct. However, when *Pictonemobius* populations to the north and west of Gainesville

were studied, their identities relative to the Gainesville species were different depending on whether appearance, songs, or allozymes were used to make the assignments. Local species in Gainesville did not necessarily correspond to any of the local species at places a few hundred kilometers away. Because all *Pictonemobius* are flightless and some species live in habitats that are spottily distributed, it is easy to understand how microgeographic variants might develop and remain distinct. So far as we know, all members of the *A. rotundifolia* complex are likewise flightless and the sandhill habitats occupied by *A. bartrami* are often discontinuous.

An intriguing aspect of differences among the songs of the four species in the *A. rotundifolia* complex is that their phonatome rates approximate a doubling series. This is surprising because closely related species of ensiferan Orthoptera usually have calling songs more modestly divergent in phonatome rates, making the differences easily attributable to gradual increases or declines (Otte 1992). Expected phonatome rates at 25°C, as calculated from the regressions depicted in Figs. 1 and 2, are 2.8 ph/s (mean for *A. alexanderi*), 4.8 (*parvipennis*), 9.5 (*bartrami*), and 26 (*rotundifolia*). The rates thus increase by factors of 1.7, 2.0, and 2.7. [In theory, the temperature selected for the comparison should not affect these factors because with repeated measurements under controlled conditions the phonatome versus temperature regressions for closely related ensiferan species tend to converge at some temperature for an expected rate of 0 — e.g., 11°C for *Orchelimum* species (Conocephalinae) (Walker 1975).] Doubling of phonatome rates among closely related species is rare but not unprecedented among ensiferans: The rates for two closely related species of *Cyrtoxipha* (Trigonidiinae) are 19 and 39 ph/s (Walker 1969), and Otte (1992) reported two examples among Hawaiian Trigonidiinae. Alexander and Thomas (1959) noted that the courtship phonatome rate for *Nemobius tinnulus* Fulton is about half that of the calling song rate. [In cricket songs, pulses and phonatomes are equivalent.]

If most of the differences among the phonatome rates in the *A. rotundifolia* complex resulted from doubling or halving the rates during speciation, variations in those directions should occur in the songs that are currently produced. A potential for doubling can be seen in the excerpts from *A. alexanderi* songs in Figs. 4E and F. *A. alexanderi* not only has the longest phonatome ($\approx$140 ms at 25°C), it also has the longest phonatome interval ($\approx$300 ms at 25°C) and the greatest proportion of the phonatome period (phonatome + phonatome interval) occupied by the interval ($\approx$68%). In other terms, the slow phonatome rate is attributable both to long phonatomes and long delays between phonatomes. The long delays could be a result of dropping alternate phonatomes. The minimum interval between successive phonatomes in *A. alexanderi* (Fig. 4) is brief enough to support this hypothesis.

In some species of phaneropterines, males produce different songs to induce females to approach (pho-notaxis) and to make answering ticks (phonore-sponse). Spooner (1968) designated the two as *calling songs* and *female tick elicitors*. Males of the *A. rotundifolia* complex make no such separate songs. What we have termed the calling song in our study of the *A. rotundifolia* complex probably has both functions in all four species, although the calling function has only been demonstrated in *A. parvipennis* and Aiken *A. nr. bartrami* (Galliart and Shaw 1991, Spooner 1995).

We believe that the four species treated here are monophyletic. In keeping with this, we used "round-winged katydid" (from Blatchley 1920) in each of the four vernacular names we proposed. However, those wishing to assign *Amblycorypha* specimens to the round-winged katydid group of species should be warned that most have tegmina that are little if any more rounded than specimens in other species groups of *Amblycorypha*. Rehn and Hebard (1914) recognized three morphological modes among North American *Amblycorypha*. Their Group I, included two modes, a group of four robust species typified by *A. oblongifolia* and a single species of small size, *A. uhleri*. As mentioned earlier, their Group II was the *A. rotundifolia* complex, which they distinguished from Group I by the states of the humeral sinus and the metasternal lobes. They also used differences in the caudal margin of the pronotal disk and the proportions of the tegmina as key characters. However, we have found these to be of little use. In regards to tegminal proportions, Rehn and Hebard (1914, p. 319) stated that the tegmina in Group II are "rarely over two and four-fifths times as long as greatest width," whereas our Table 1 shows that few of the specimens we examined had wings that round. All our mean values of tegminal ratio equaled or exceeded the 3.0 that Rehn and Hebard set as the minimum value for their Group I.

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