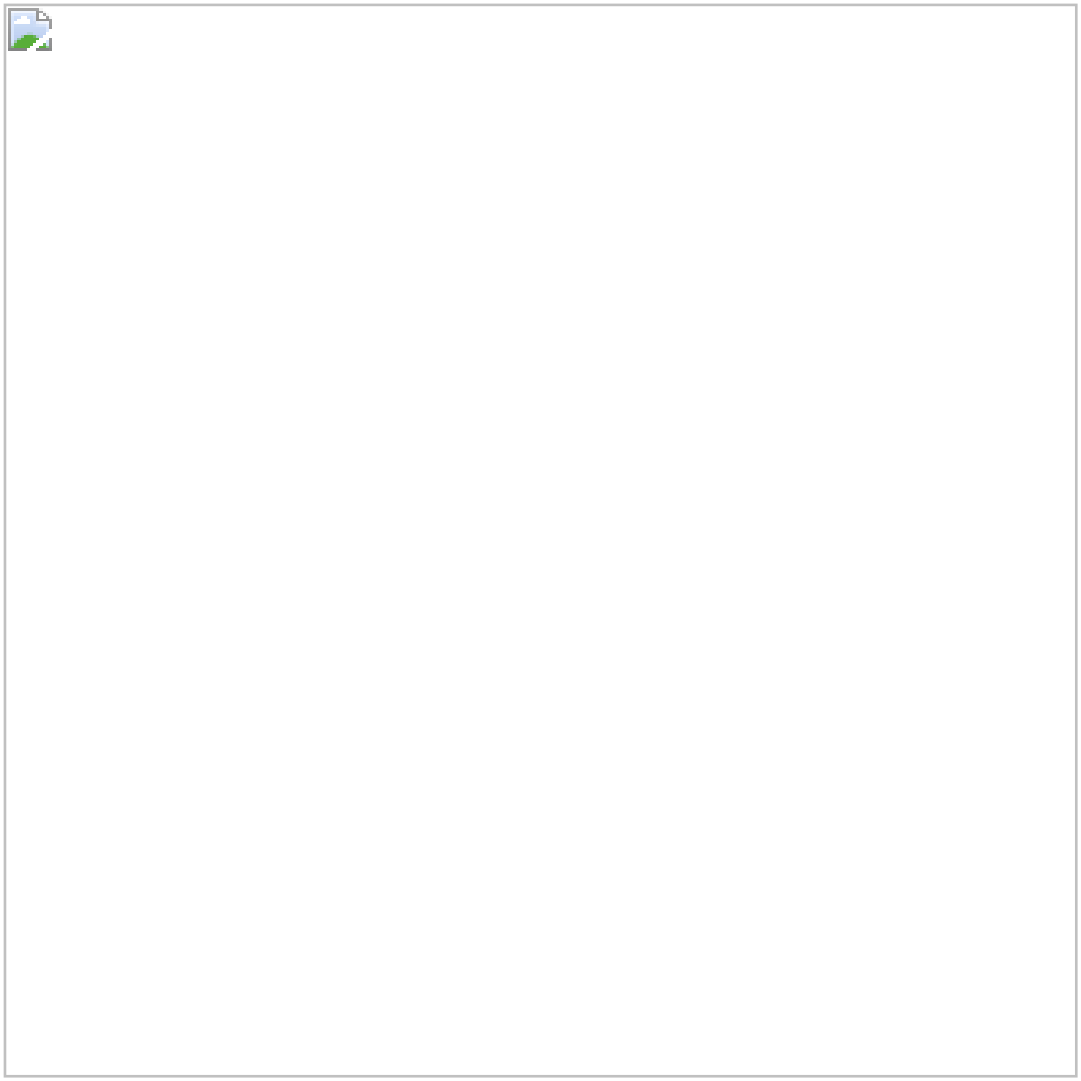

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Systematics and acoustics of North American *Anaxipha* (Gryllidae: Trigonidiinae)

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Abstract

The genus *Anaxipha* has at least 13 North American species, eight of which are described here. Ten species fall into these three species groups: *exigua* group (*exigua* Say, *scia* Hebard and n. spp. *thomasi*, *tinnulacita*, *tinnulenta*, and *tinnula*); *delicatula* group (*delicatula* Scudder and *vernalis* n. sp.); *litarena* group (*litarena* Fulton and *rosamacula* n.sp.). The remaining three (*imitator* Saussure, *fultoni* n.sp., and *calusa* n.sp.) have no close relatives among the other species. Most new species were initially distinguished by their calling songs, and in most cases sympatric populations proved cleanly separable by features of male genitalia and tooth-counts of stridulatory files. Species groups were based mostly on comparisons of male genital structures and the results of DNA barcoding. Species are here characterized not only by their songs and morphology, but also by geographical, ecological, and seasonal distributions.

At a given temperature the pulse rate (PR) of the male's calling song is a key aid to identification. PR at 25°C has a narrow range of variation within a species and among the 13 species its mean value varies from 5 to 79 p/s. As in other crickets, pulse rates plotted as a function of temperature have a positive, linear trendline. When trendlines for 11 *Anaxipha* species are extrapolated downward, the temperature at $\hat{y}$=0 p/s is 2.7±2.2 (mean±SD) — *i.e.*, the lines tend to converge at about 3°C. This makes possible a simple formula for estimating the PR at 25°C from any *Anaxipha* calling song recorded at any temperature. Other aids to identifying species from their calling songs are the duration and regularity of breaks between pulse sequences and the relationship between PR and carrier frequency (CF). When CF is plotted as a function of PR, the relationship deviates noticeably from linear only in *vernalis*.

We propose that in *Anaxipha* spp., as well as in six other genera in four gryllid subfamilies, the synchrony of tooth impacts and the fundamental vibrations of the CF is maintained by the scraper moving continuously over evenly spaced file teeth — rather than by the much-studied (and well-established) catch-and-release mechanism of *Gryllus* spp. Our proposal is based on the high rates of change in CF with temperature and on differences in the teeth of the stridulatory files. The PR at 25°C of each of the 13 species is remarkable in the degree to which it predicts the mean values of these five characters: file tooth number, tooth density, file length, pulse duration, and pulse duty cycle (Fig. 17).

A neotype is designated for *Gryllus pulicaria* Burmeister (1838), the type species of the genus *Anaxipha*. With the e-version of this paper, extensive Supplementary Materials provide permanent access to data sets that are basic to our conclusions. These materials include detailed records of the specimens examined and of the more than 1300 recorded songs that were analyzed. Digitized versions of more than 450 of the recordings are archived in Cornell's Macaulay Library of Natural Sounds.

Key words

New species, type species, keys, male genitalia, DNA barcoding, calling songs, temperature effects, sound production mechanics, carrier frequency determination, forewing movement cycles, evolution of pulse rate

Introduction

Some 163 species of tiny brownish crickets are nominally in the trigonidiine genus *Anaxipha* (OSFO 2013), but Otte & Perez-Gelabert (2009, p. 127) suggest that the genus is "in serious need of revision" and that "the taxonomy of the Trigonidiinae as a whole is in a shambles." Species from around the world have been described in the genus *Anaxipha* and few have been transferred to other genera. Nearly all are from tropical or subtropical localities. Currently only four *Anaxipha* species have North American type localities, even though 70% of *Anaxipha* species are from the New World (Table 1). Caribbean *Anaxipha*, recently revised by Otte & Perez-Gelabert (2009), account for about 37% of the 114 New World species. Of the 38 new species of *Anaxipha* that Otte & Perez-Gelabert describe none occurs in North America and none occurs closer than Jamaica to southern Florida's Caribbean-like habitats.

North American *Anaxipha* commonly inhabit vegetation near the ground, where the males advertise their position (and their species) by their calling songs. These songs are remarkably loud and melodious for so small an insect and individuals are often numerous. This would seem to make them easy to collect but such is seldom the case. The plants they inhabit are often in dense or tangled stands and even when a male is calling from an isolated plant it may stop calling on approach and somehow escape the strokes of a sweep net. Naturalists who want to find all the cricket species in the habitats they study are likely to miss species of *Anaxipha* — unless they attempt to track down each distinctive cricket calling song. The first person to realize this and become intensely interested in North American *Anaxipha* was Bentley B. Fulton (1889-1960).

Fulton's studies of *Oecanthus*, *Nemobius*, and *Gryllus* (*e.g.*, 1925, 1931 and 1952) led to his renown by the mid 1960's as having demonstrated that the North American cricket taxonomists of his era, who had based their species concepts solely on studies of museum collections, had failed to recognize a substantial portion of the most commonly encountered U.S. species. In an account of Fulton's contributions to cricket taxonomy, Gurney (1964, p. 155) wrote that, Fulton's "ability to utilize songs in recognizing species and interpreting behavior was the outstanding key to his success" and opined (p. 156) that "Those at the forefront of scientific thought on evolution and speciation have used his conclusions in developing principles explaining the nature and relationships of species." Fulton's last paper (1956) was a revision of the North American species of *Anaxipha*.

In 1954, at Ohio State University, one of us (TW) was influenced by fellow graduate student R.D. Alexander to choose the acoustic behavior and systematics of tree crickets for his doctoral studies. At the time, Alexander was completing his doctoral studies on insect sound production in which he was among the first to use electronic

Table 1. Type localities of the 166 named, extant *Anaxipha* species (as listed by OSFO, May 2013).

	no. spp.	hemisphere %	world %
NEW WORLD			
North America (n. of Mexico)	4	3.5	2
Mexico	4	3.5	2
Central America	23	20.2	14
Caribbean	42	36.8	26
South America	41	36.0	25
New World total	**114**	**100**	**70**
OLD WORLD			
Africa s. of Sahara	21	42.9	13
Eurasia n. of Himalaylas	0	0	0
Indian Ocean (Mauritius)	2	4.1	1
Tropical Asia*	12	24.5	7
Australia & New Guinea	6	12.2	4
Pacific Ocean	8	16.3	5
Old World total	**49**	**100**	**30**

*Asia below the Himalayas, Phillippines, Malaysia, Indonesia except w New Guinea

devices for recording and analyzing insect sounds and the first to carefully compare the calls and calling behavior of more than 65 U.S. species of crickets and katydids (Alexander 1956). These studies later enabled Alexander to expand and put into formal nomenclature what Fulton had learned about North American *Gryllus* and *Nemobius* populations that had distinctive calling songs but were difficult to define morphologically. In 1955, TW accompanied Alexander during field work that included an opportunity to meet Fulton in his laboratory at North Carolina State. Because of worsening palsy, Fulton had retired in 1954. During our visit he was working on his 1956 *Anaxipha* revision, yet took time to help us collect in some of his favorite field sites.

In his revision Fulton reported new characters useful in identifying *Anaxipha* species. These included tiny teeth on the lower edge of tarsal claws, fringes of long hairs on tibial spines, and features of the male genitalia (which he dissected and illustrated by hand in spite of his palsy). Using these characters, Fulton described a new species, *A. litarena*, which he had discovered in coastal habitats of the Carolinas. Even so, he failed to resolve morphologically a "very puzzling situation" in regard to three "song types" of *A. exigua*. During the fall of 1928, his first year in North Carolina, Fulton learned that in Raleigh, what was morphologically *A. exigua* produced three distinctive calling songs (Fulton 1932). Much later, Fulton (1951) named these songs *triller*, *fast tinkle*, and *slow tinkle* and described their ecological distribution.

When TW was hired by University of Florida in 1957, he set out to emulate Fulton (1932) by quickly learning the calling songs of all crickets and katydids in the state that had employed him. This led to his finding several new species of *Anaxipha*. By 1964 TW had broadened the geographic extent of his ambition and had accepted R.D. Alexander's invitation to participate in a monograph covering all North American crickets and katydids. Though the planned monograph was later abandoned, preparing for it led TW to encounter, north of Florida, Fulton's puzzling situation of song types in *A. exigua*. Failure to solve the puzzle of the "*exigua* complex" led TW to put aside, in 1969, a manuscript on all North American *Anaxipha* including the new Florida species. When he retired in 2001, TW used the occasion to resume work on his *Anaxipha* manuscript, hoping to benefit from what he had learned about *A. exigua* and cricket systematics during the intervening years. Once more he failed to find a satisfying solution to the species classification of the *exigua* complex, and settled for including much of what he knew about North American *Anaxipha* species in the appropriate section of the openly accessible web site Singing Insects of North America (SINA 2014). Meanwhile, during the 1990s DF had become aware of multiple song-types within nominal *Anaxipha exigua* while assembling a collection of song recordings and photographs of crickets and katydids in their natural habitats for the mid-Atlantic region of the U.S. For the most part, these song-types seemed to match well with TW's species on SINA, and, in 2002, DF used email to share his data and conclusions with TW.

In October 2010, DF emailed TW that he had continued to study *Anaxipha* and had enough data to describe at least three new species. He included a graph in which a plot of pulse rate against carrier frequency unmistakably separated six song types of *Anaxipha* that he had studied in the mid-Atlantic states. These included the three species in the *exigua* complex that Fulton had recognized as song types and three species that Walker had also recognized but on the basis of far fewer recordings. Furthermore DF showed that Fulton's three song types in the *exigua* complex, plus one more, could be distinguished by the number of teeth in the stridulatory file, and he included a cladogram of his six song types based on amplified fragment length polymorphism (ALFP) of their DNA. With DF's encouragement and help, Dr. Tamra Mendelson, then at Lehigh University, had accomplished the AFLP work. DF wrote that he thought that Dr. Mendelson's work would be more publishable if the species were formally described and wanted to know when or if TW planned to describe the SINA species. We soon agreed that we should pool what we knew, decide what taxa should be recognized as species, and proceed to prepare a revision that was not to be delayed by puzzles left unresolved.

Our cooperation was fruitful and, by July 2012, we began drafting a manuscript about the 12 species we had recognized. In September we were confronted with a 13th species that was remarkably distinct from any previously known. We learned enough in the next five months to include it here.

Methods

Abbreviations used in this paper.—

Museums and collections of recorded songs and DNA:

ANSP	Academy Natural Sciences Philadelphia
BOLD	Biodiversity Institute of Ontario
FSCA	Florida State Collection of Arthropods
MHNG	Geneva Museum of Natural History
MLNS	Macaulay Library of Natural Sounds
NCSU	North Carolina State University
SWRC	Stroud Water Research Center
UMMZ	University of Michigan Museum of Zoology
WTL	Walker Tape Library, University of Florida

Collectors, recordists, etc. (3 of these are used only in SM):

BBF	Bentley B Fulton
DF and DHF	David H Funk
JDS	John D Spooner
JJW	James J Whitesell
REL	Robert E Love
TW and TJW	Thomas J Walker

Characteristics of calling songs:

CF	carrier (or dominant) frequency

p/s	pulses per second
PR	pulse rate
PD	pulse duration
PI	interval after a pulse (unless the pulse is the last in a pulse train)
PP	pulse period (=PD+PI)
Pdc	pulse duty cycle (=PD/PP)
PT	pulse train (a sequence of pulses produced at a uniform rate)
PTD	pulse train duration
PTI	pulse train interval
PTP	pulse train period
PTdc	pulse train duty cycle (=PTD/PTP)
WMC	wing movement cycle (during calling)

Supplementary materials.—Supplementary Materials [SM] items are accessible with the online version of *JOR* (http://www.bioone.org/loi/orth) but not with the print version because of their length or format (*e.g.*, active spreadsheets, videos). We have made extensive use of SM for a variety of reasons, but chiefly to make available the full datasets that are the basis for our conclusions. Examples include the 26 spreadsheets that contain the full records of our specimens and recordings of the 13 species we recognize and a PDF file that has the 70 images of male genitalia from which were picked the representative images for the 13 species that are in the in-print figures (Fig. 3A and Fig. 13). The contents of our SM are fully listed at the end of References.

References to specific SM items throughout this manuscript are by the name of the item (as seen in the list of SM items at the end of References).

The 26 individual spreadsheets from SMTbls_Specimens and SMTbls_Songs have been made into additional SM items in order to make the two that apply to each of the 13 species easily available for viewing to those browsing the species accounts online. (These 26 duplicate spreadsheets are omitted from the list of SM items at the end of References.)

Videos.—DF used a Nikon D90 DSLR equipped with a 50mm lens and a 13 mm extension tube to record at 24 frames per second a *calusa* male courting a female (SMVideo1_calusa). Later he imported the .avi file into Apple iMovie and slowed it to ¼ speed to produce a slow motion movie file (software essentially inserts three duplicates after each frame). This allows the viewer to more easily discern the close-hold-open wing movement cycles of the male (SMVideo2_calusaSloMo). An apparent artifact of this process was that, for many pulses in the video, the sound seems to coincide with the wing opening. Turning off the audio when interpreting the video eliminates this distraction. Subsequent frame-by-frame measurement of wing separation uncovered additional details of the wing movement cycles (SMFig_VideoAnalysis).

Song recordings.—Song recordings used in this study were made by TW in 1958 to 1973 and by DF in 1991 to 2012. TW used Nagra III or IV tape recorders in the field and a Magnecorder PT6 or an Ampex 351 recorder in the laboratory. Tape speed was 38.1 cm/s. Microphones were dynamic and had a flat frequency response of 1 to 18 kHz or higher. DF used a Sennheiser (Sennheiser Electronic Corporation, Old Lyme, CT) ME 66 Short Gun microphone throughout the study. Prior to 2007 recordings were made on a Sony (Sony Electronics, Inc., San Diego, CA) TC-D5M cassette recorder and later digitized with a Macintosh computer (sampling rate 44.1 kHz, 16 bit depth, file format AIFF). Beginning in 2007, recordings were made with a Roland Edirol R-09 Digital Recorder (Roland Corporation U.S., Los Angeles, CA) at a sampling rate of 44.1 kHz and a bit depth of 16 using a WAV file format.

Analyses of songs for pulse rate and carrier frequency.—DF analyzed his recordings using Canary 1.2.4 software (Bioacoustics Research Program, Cornell University, Ithaca, NY) or Audacity open source software (audacity.sourceforge.net).

TW used a Kay Sonograph audiospectrograph to determine pulse rate and carrier frequency of *Anaxipha* songs soon after they were tape recorded. Much later, for this paper, he used Cool Edit 2000 (Syntrillium Software) to analyze the digitized versions of his tapes, which by then had been archived in the Macaulay Library of Natural Sounds and accessible online at http://macaulaylibrary.org/. This means of analysis was occasionally used to confirm data points from the earlier analyses but its only extensive use was to characterize the phrasing of the pulse trains within the songs of those species that interrupted their calling songs with brief pauses. A small-scale comparison of the results of the two methods applied to the same *Anaxipha* songs revealed no large or biased differences in pulse-rate determinations and occasional non-trivial underestimates of carrier frequency.

Measurements of pulse durations and pulse duty cycles at 25°C.—Late in the writing of this paper we decided to have a Fig. 17, which would contain a series of six graphs displaying how evolutionary changes in pulse rate at 25°C affected three features of the stridulatory file and three features of the calling song. The two paragraphs below describe methods used by TW and DF to acquire the needed data.

Duty cycle by direct method.— This method took advantage of recordings previously selected for TW's pilot study of pulse-train phrasing. As described in SM_PTPilotStudy (with calculations and data in SMTbls_PTPilotStudy), for each species studied TW selected 4 or 5 recordings made close to 25°C from a single geographic area with no male represented by more than one recording. For the present study, TW selected one or more lengthy pulse trains from near the start of each previously used recording. (Only the *delicatula* recordings required selecting a second pulse train to provide enough qualifying pulses.) CoolEdit was then used to measure to the nearest ms the pulse duration and pulse period for the 2nd through 6th pulse in the pulse train. If the 6th pulse was the last pulse in the pulse train, the measurement continued with the 2nd pulse in the second pulse train. The Pdc was calculated as PD/PP. The data are in SMTbl_PDdataByDM.

Duty cycle by regression method.—This method took advantage of DF's practice of measuring and recording the durations of typical pulses for each digital recording as he logged it. Most recordings were field recordings and for most species only a few were made at 25±1°C. In order to estimate the PD at 25°C he regressed PD against temperature and used the regression formula to obtain the needed PD. For four species that had 4 to 34 recordings at 25±1°C he used those recordings to estimate the PD by taking the mean of these values (as in the direct method). The maximum discrepancy between that mean and the result of the regression method was 1.3 ms. To calculate the Pdc he used his estimate of PD and the reciprocal of PR at 25°C from Table 2 in this formula: Pdc = PD/(1/PR). [Details of the regression method are in SM_PDbyRegression and detailed data are in SMTbls_Data_PDbyRegress.]

CF temperature coefficients.—In the discussion of how carrier frequency is controlled in *Anaxipha* calling songs we found it useful to calculate

the rate of change of CF with temperature in the manner of Koch *et al.* (1988) — *i.e.*, by dividing the difference in CF at 20 and 30°C by the CF at 20°C. Most early literature relating to changes in CF with temperature had used pulse rate (which is linearly related to temperature) as a proxy for temperature. We continued that practice in order to make data from the early literature and our data on *Anaxipha* more directly comparable.

File characteristics.—Characteristics of the stridulatory file that are sometimes useful in separating closely related species of crickets include the number of file teeth, the length of the file, and the tooth density. TW and DF each measured these features but by different methods independently developed. Using procedures developed for studies of Oecanthinae (Walker 1962a, 1963), TW removed the right tegmen and slide-mounted it in Hoyer's medium, ventral surface up. Teeth were counted as they were mechanically moved past a line in the eyepiece of a compound microscope. Although the file curved, its length was determined with an eyepiece micrometer by measuring from the beginning of the first tooth (close to the hind margin of the forewing) to the end of the last. Some tegmina were later mounted on points with pinned specimens but most were left on the slides with labels keyed to "file slide" labels with the specimens. DF removed the right tegmen and slide-mounted it in either Euparal (permanent) or water (temporary). The tegmen was then photographed with a Nikon Labophot microscope. A single digital image was constructed from multiple fields (as necessary) using Adobe Photoshop CS3 software. File counts were made from the photograph and, starting at the hind margin, a small red dot was added every 10th tooth to facilitate counting (Fig. 3). Linear measurement was made from the first tooth (closest to hind margin) to the junction of the stridulatory vein and the harp vein. This measurement was expressed as length of cell 5 (*sensu* Otte 1994) and tooth density was estimated from this region in order to minimize errors attributable to straight-line measurement of the (slightly curved) stridulatory vein.

Tooth count, unlike file length and tooth density, was deemed directly comparable in the two methods, and was the only file feature used in our keys to species. However, the decision to plot file length and tooth density against pulse rate at 25°C, led DF to investigate how differences in our tooth density estimates could be reconciled. The species with the longest file on the most curved stridulatory vein (*i.e.*, the worst case) for which we both had measurements was *tinnulenta*. As a test, DF made measurements on the same individual using both techniques and found that reducing the value derived using TW's method by 8% gave a value comparable to that calculated using DF's technique. However, in species with shorter files this disparity decreased rapidly to zero. Thus, for the purposes of comparative analysis it was decided the error attributable to differences in methodology was too small to worry about and we pooled all our data without correction. In North American *Anaxipha*, tooth density varies (predictably) in different regions of the file, most conspicuously in species with ≤100 teeth. However, we made no attempt to quantify this for taxonomic purposes.

Genitalic dissection and photography.—Male genitalia were removed from pinned specimens that had been relaxed (or dissected from alcohol-preserved specimens) and cleared in hot 10% KOH. These were mounted in glycerin on a well slide and photographed in dorsal view using a Nikon Labophot trinocular microscope equipped with a Canon T1i digital SLR controlled with Canon EOS Utility software in Live View mode. Images taken at several focal points were composited in Adobe Photoshop CS3.

Morphological measurements.—Measurements made on specimens of interest were body length, hind femur length, and length of ovipositor. Body length was measured along the dorsal aspect of the specimen starting at the frons and, in males, ending at the tips of the forewings; in females, it also ended at the tips of the forewings unless the abdomen (exclusive of the ovipositor) protruded beyond the tips of the forewings. Then it ended at the base of the ovipositor. The length of the ovipositor was measured using the endpoints identified by Fulton (1956) and shown in Fig. 2E. All measurements were in millimeters and made with calibrated ocular micrometers.

In the species accounts, measurements are reported for holotypes and allotypes and, in a paragraph labeled "Measurements," we report the range of values found in series of specimens that were sometimes from a limited portion of the geographical range.

Presence or absence of long hindwings.—With the exception of two species restricted to south-most Florida, *Anaxipha* with hindwings that extend well beyond the forewings are rare in natural habitats. Among the other 11 species, such long-winged individuals (*macropters*) are nearly always encountered at or near artificial lights. Adults that have no hindwings that extend beyond the forewings are "short-winged," and, in most cases, they are *micropters*: that is, they had no or very short hindwings at the molt to the adult. However, in some cases short-winged crickets are macropters that have shed their long hindwings. These are *dealates*, rather than micropters — because they have lost their long hindwings by dealation (Walker & Masaki 1989). The metathoraxes of micropters and dealates are drastically different when viewed from above (Fig. 2G) but achieving this view may require lifting the forewings, an action that is damaging or destructive when attempted on a pinned specimen. Macropters and micropters of trigs sometimes differ in the presence of tympana (*e.g.*, Ingrisch 1977) and we found that to be the case in North American *Anaxipha*. Although all individuals have a well-developed posterior tympanum on each foretibia, macropters (and dealates) have conspicuous anterior tympana as well — as can be seen on the left foretibia of the macropter in Fig. 2G (right). This feature was used to assay the occurrence of dealates among short-winged specimens and the results are reported in the species accounts for the 11 species that have short-winged adults.

DNA barcoding.—DNA barcoding, the analysis of a standardized segment of the mitochondrial cytochrome *c* oxidase subunit 1 (COI) gene, was performed on representative specimens of all North American *Anaxipha* species recognized herein, as well as *Phyllopalpus pulchellus* and *Cyrtoxipha columbiana*. Tissues were sent to the Canadian Centre for DNA Barcoding for DNA extraction, polymerase chain reaction (PCR) and sequencing. PCR was performed using the PCR primers LCO1490_t1/HCO2198_t1 with M13 tails. Data is currently managed under project DHFC at Barcode of Life Data Systems (BOLD, Biodiversity Institute of Ontario, University of Guelph, Guelph, Ontario, Canada; boldsystems.org). Kimura-2-Parameter (K2P) distances were calculated using the BOLD 3.0 interface (Ratnasingham & Hebert 2007). Sequences were then analyzed and trees constructed using MEGA5 software (Tamura *et al.* 2011).

Deposition of specimens and recordings.—TW has curated the FSCA collection of Grylloidea and Tettigonioidea for many years and has donated to it all insect specimens he has collected. Nearly all tape recordings he made of crickets and katydids have been donated to the Macaulay Library of Natural Sounds of the Cornell Lab of Ornithology.

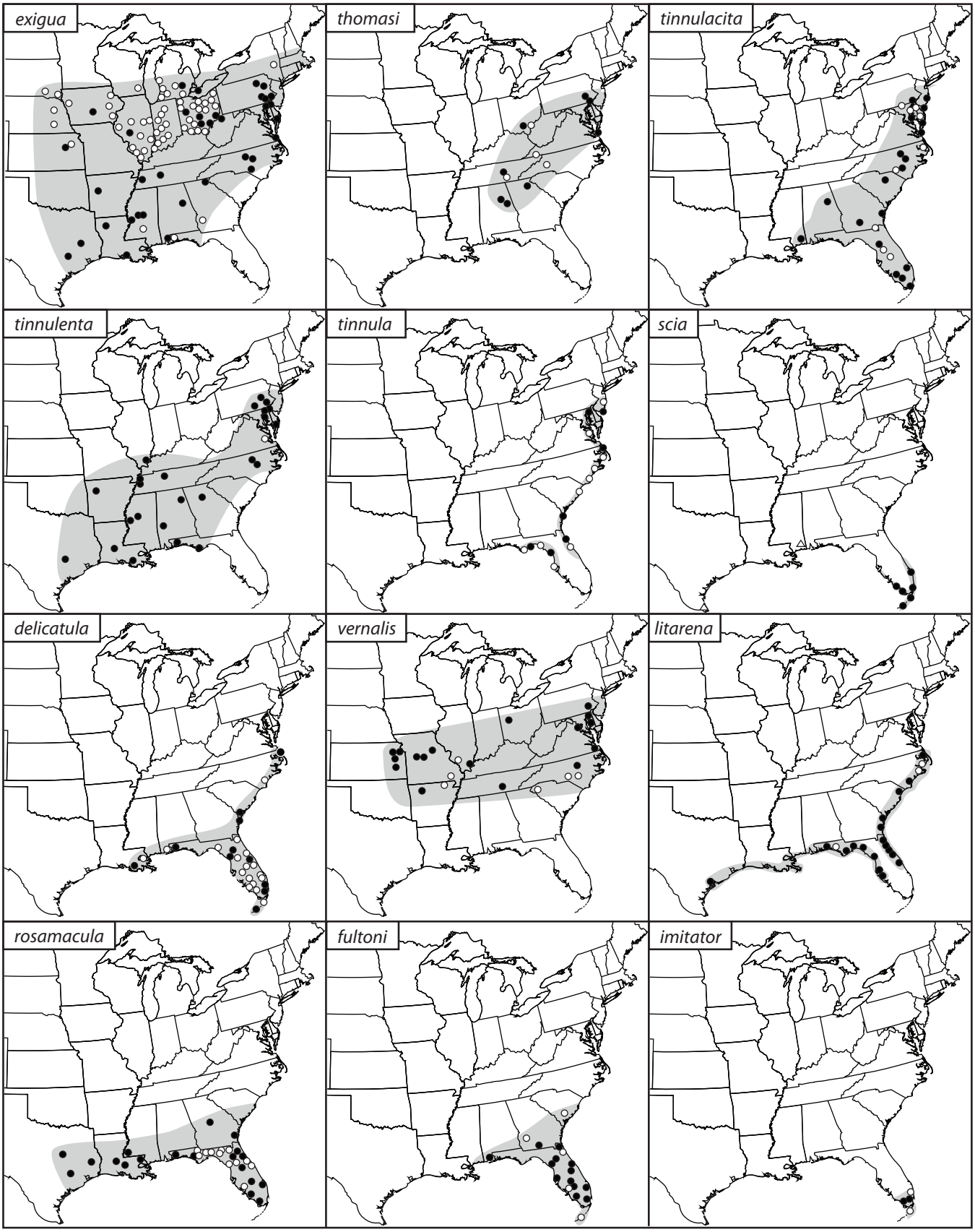


Fig. 1. Distribution of North American *Anaxipha* species. Shaded areas estimate general ranges. Filled circles are records based on recorded songs, examined specimens, or both. Open circles are less positively documented records. There is no map for *calusa* because it is known from a single small area. (See text for fuller explanation and SMTbls_MapData.xls for detailed data.)

Specimens (other than types) collected by DF reside in his personal collection except for DNA barcoded specimens, which are curated at the Stroud Water Research Center (SWRC). Sound recordings from barcode vouchers and types and others that are individually important to the conclusions of this paper will be deposited at Macaulay Library of Natural Sounds of the Cornell Lab of Ornithology.

Results

Type species of the genus Anaxipha.—In 1874 Saussure described the genus *Anaxipha* and included three species: *Gryllus pulicaria* Burmeister, *Trigonidium pallens* Stal, and ?*Gryllus pumilus* Burmeister. As first-named in Saussure's description, *G. pulicaria* Burmeister should be the type species of *Anaxipha*. In fact, Rehn (1905, p. 834) wrote that the genus "included *A. pulicaria* (Burmeister), *pallens* (Stål) and (?) *pumila* (Burmeister), of which *pulicaria* may be considered the type." However, Kirby (1906) made *Anaxipha pulicaria* (Burmeister) a synonym of *Anaxipha exigua* (Say) and designated *Acheta exigua* (Say, 1825) the type species of the genus. That designation was not questioned until 2007, when Mike Maehr noted that the type species of *Anaxipha* "needs verification" (OSFO 2012).

Saussure (1874) may not have seen specimens of *G. pulicarius* that were conspecific with the type material of that species. To verify that *G. pulicarius* was appropriate as the type species of Saussure's *Anaxipha*, we sought information about the type material of that species. OSFO (2013) lists the type as in "MLUH Halle" but, when all attempts to verify its existence there and at other museums that might house Burmeister's specimens proved fruitless, we decided to designate a neotype. The type locality of *G. pulicarius* is Jamaica, and it seemed highly likely that the species was among the eight species of *Anaxipha* that TW studied there and were later recognized by Otte & Perez-Gelabert (2009). Their exemplar of *Anaxipha pulicaria* (p. 139) is here designated the neotype of *G. pulicarius* Burmeister. This specimen is a tape-recorded male that TW identified as *A. pulicaria* because it was the Jamaican species most similar to the southern U.S. species that was long known by that name (but does not occur in Jamaica). The neotype (in FCLA) was collected at Worthy Park, St. Catherine Parish, 1200ft, 16 Nov 1968, by TW. Its file has 111 teeth and its recorded song is MLNS #114399. On their page 179, Otte & Perez-Gelabert (2009) provide eight images of the neotype including four of its genitalia.

Species accounts.—We recognize 13 North American *Anaxipha* species and characterize them in the following accounts. In the earlier literature or on the Web, 12 of these species have been known for many years, but seven of these 12 have lacked formal names until now. The accounts of the 13 species are arranged in a sequence that facilitates the explanation of the history of each species' recognition. The distribution maps of the 12 long-known species (Fig. 1) are arranged in the same sequence.

All new species are to be credited to Walker and Funk. For each species we propose a simple vernacular name to facilitate conversation and writing about the species in situations where scientific names would be off-putting. Otte (1994) proposed that trigonidiine crickets be called "trigs." Following him, we use that term as part of all vernacular names here proposed. In the accounts, we capitalize only the proper nouns in vernacular names, but we recognize that in some contexts all words in vernacular names are capitalized. Two to six color "portraits" of each species, taken by DF, are in SMFig_Portraits.

For the five species already formally named, species accounts begin with an explanation of how we associated an established name with one of the 13 North American *Anaxipha* taxa that we deem to be species. For the seven new species that were long known but not formally named, the accounts begin with the earlier status of the taxon, whether as a mistaken assignment to a named species or tentative recognition of a new species based on calling song, ecology, or morphology.

Fig. 2. Features of North American *Anaxipha* spp. A-C. Teeth on tarsal claws of representative species. A. *exigua*. B. *scia*. C. *tinnula*. D. Setal fringe on spine of hind tibia of *scia*. E. Lateral view of ovipositor of *tinnulacita* showing how length is measured. F. Courting *delicatula* male (viewed from beneath), showing ampulla of macrospermatophore (white sphere) and position of forewings during song production. G. Short-winged and long-winged females of *exigua* with all wings removed and with transverse white bars added to delineate pro-, meso- and metanotal areas. The micropter (left) has a small metanotal area and no anterior tympana. The macropter (right) has a large metanotal area and an anterior tympanum on each foretibia (*e.g.*, at arrow). H-J. Representative facial patterns of three species. H. *fultoni*. I. *exigua*. J. *delicatula*. [Photos by David Funk].

Anaxipha spp. are typically found in vegetation ranging from a few centimeters to about 2 m off the ground. The only other crickets likely to be confused with *Anaxipha* based on calls are some nemobiines. However, the latter always call from ground level, whereas *Anaxipha* are almost always found at least slightly above ground level.

Anaxipha exigua (Say 1825)

Say's trig

Figs 1, 2, 4, 5, 7-11, 13, 14, 17-19; Tables 2-6.

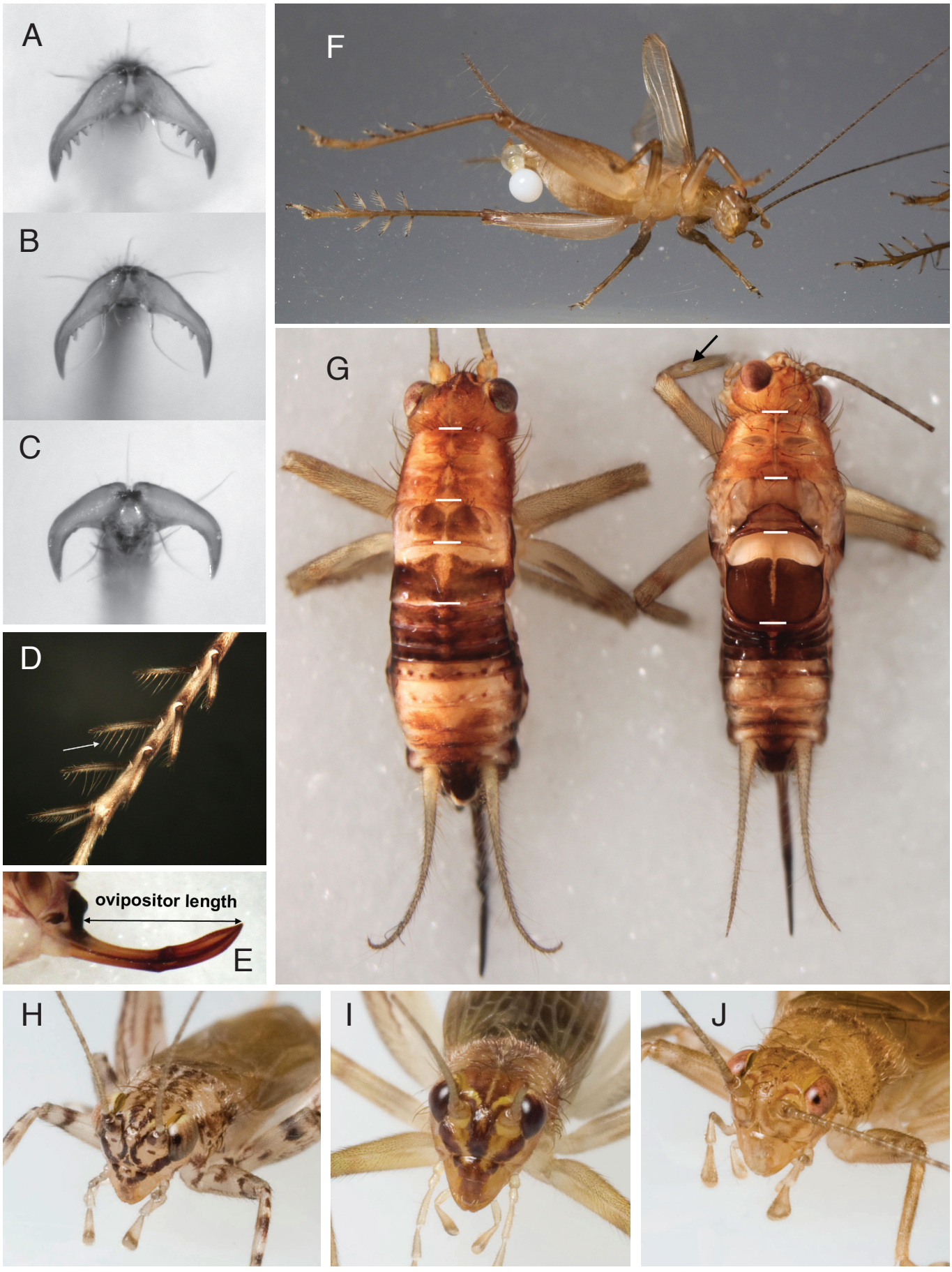
SMspecimens_exg; SMsongs_exg.

History of recognition.—The first species of North American *Anaxipha* was described by Thomas Say (1825) from a single male collected during an 1819 expedition across the Great Plains west to the Rocky Mountains (Sorensen 1995). Say reported that the specimen, which he described as *Acheta exigua*, was taken "near the village of the Konza Indians." Based on the original charts of the expedition, Rehn and Hebard (1912) concluded the site was "about eighty miles west of Kansas City, on the Kansas River, in Kansas." Among the features of *exigua* that Say noted were its small size and that it had "posterior thighs with a brown line on the exterior side." These were enough for Rehn & Hebard (1912, 1916) to decide correctly that Say's *exigua* was the largest, most boldly marked *Anaxipha* species known in North America.

Type specimen.—Say's type was lost or destroyed (Mawdsley 1993), but we see no reason to designate a neotype unless a song-recorded, molecularly studied male from close to the type locality becomes available.

Measurements.—Body length, ♂♂ 5.6-6.7mm, ♀♀ 5.8-8.0; hind femur, ♂♂ 4.3-5.4, ♀♀ 4.9-5.6; ovipositor, 2.4-2.6. (DF n=27 ♂♂, 17 ♀♀; PA and GA.)

Hindwings.—Macropters rare, of 99 ♂♂ and 48 ♀♀ examined 2 ♀♀ were macropterous when captured and one of these dealated in captivity; of the remaining 145 specimens 1 ♂ was a dealate; all others were micropters.



Seasonal occurrence.—Univoltine, with adults heard as early as late July and as late as the end of October.

Habitat.—On coarse weeds or woody plants, from near ground level to about 2 m above ground. Open woods to old fields and riparian areas, usually with at least partial shade. Often found with *thomasi* (under conifers) or *tinnulacita* and/or *tinnulenta* in other habitats.

Distinguishing features.—*A. exigua* can be distinguished from other North American *Anaxipha* by the following combination of characters: basal metatarsal segment shorter than the combined length of the 2nd and 3rd segments; spines of hind tibiae with a fringe of long hairs (as in Fig. 2D); hind femur with a broad dark stripe on the lateral face along the sulcus (Fig. 9A); stridulatory file with 100-135 teeth; song a continuous trill at ~44 pulse/s at 7.2 kHz (at 25°C); male genitalia as in Fig. 13A; ovipositor 2.4-2.6 mm, ratio of length of hind femur to ovipositor 2-2.4.

This is the continuously trilling species of the *exigua* group that has the highest pulse rate; its stridulatory file has the fewest teeth and lowest tooth-density of the complex.

***Anaxipha thomasi* new species**
Thomas's trig
Figs 1, 4, 5, 7-11, 13, 14, 17-19; Tables 2-6.
SMspecimens_thm; SMsongs_thm.

History of recognition.—The taxon long recognized as Say's *exigua*, we recognize as the *exigua* "complex," consisting of *exigua* and five additional species. These six species are most easily distinguished in the field by their calling songs but are also cleanly separable by more traditional means.

In the 1940's Edward S. Thomas of the Ohio State Museum pursued his interest in Ohio natural history by learning to identify calling crickets and katydids by their songs. By the early 1950's, Thomas had recognized that two song types occurred in Ohio among males that he morphologically identified as *A. exigua*. Furthermore he had learned that the song types were made by crickets of different size categories and different geographical and ecological distributions (Alexander 1956). As reported by Fulton (1956), the *exigua* of Thomas's larger race produced a trill and were heard abundantly in low ground throughout Ohio, whereas those that produced a fast tinkle were smaller; sang in dry uplands, usually associated with pines; and were not found north of Fairfield County, Ohio. The smaller race is here described as *thomasi*.

Holotype.—Male. Georgia: Rabun Co., Lakemont, 34.753158°N, -83.450846°W, coll. 11 Sep 2010, DFunk. (ANSP) Song recorded (R09_0488.WAV). BOLD sample ID: SWRC-Ae_179. GenBank Accession: KF670916. Body length 5.6mm, hind femur 4.2.

Allotype.—Female. Pennsylvania: Chester Co., Nottingham Park, 39.737065°N, -76.045836°W, coll. 15 Aug 2010, DFunk. (ANSP) BOLD sample ID: SWRC-Ae_151. GenBank Accession: KF670922. Body length 6.4mm, hind femur 4.75, ovipositor 2.1.

Measurements.—Body length, ♂♂ 5.5-5.9mm, ♀♀ 6.1-7.1; hind femur, ♂♂ 3.8-4.5, ♀♀ 4.3-4.8; ovipositor, 2.0-2.1. (DF n=14 ♂♂, 7 ♀♀; PA and GA.)

Hindwings.—No macropters known. Of the 19 ♂♂ and 9 ♀♀ short-winged adults examined, none was a dealate.

Other noteworthy specimens and song recordings.—Male, same locality as allotype: Song recorded (R09_0411.WAV, R09_0414.WAV [courtship]). BOLD sample ID: SWRC-Ae_150. (ANSP)

Seasonal occurrence.—Univoltine with adults appearing late summer into early fall.

Habitat.—On coarse weeds or woody plants beneath pines or other conifers, from several centimeters to about 2 meters above ground level. Often found with *exigua*.

Distinguishing features.—*A. thomasi* can be distinguished from other North American *Anaxipha* by the following combination of characters: basal metatarsal segment shorter than the combined length of the 2nd and 3rd segments; spines of hind tibiae with a fringe of long hairs (as in Fig. 2D); hind femur with a broad dark stripe on the lateral face along the sulcus (Fig. 9B); stridulatory file with 139-162 teeth; song a continuous trill at ~21 p/s at 7.8 kHz (at 25°C); male genitalia as in Fig. 13B; ovipositor 2.0-2.1 mm, ratio of length of hind femur to ovipositor 2.2-2.4.

This is the species of the *exigua* complex with the continuous trill that has the slowest pulse rate *or* the tinkle that is fastest; it is usually (always in DF's experience) found on or beneath pines or other conifers.

Origin of name.—Named for Edward S. Thomas, who first recognized this taxon as distinct from trilling *A. exigua*.

Note: Walker (2001-2013) listed this as "*Anaxipha* n.sp. D."

***Anaxipha tinnulacita* new species**
fast-tinkling trig
Figs 1, 2, 4, 5, 7-11, 13, 14, 17-19; Tables 2-6.
SMspecimens_tct; SMsongs_tct.

History of recognition.—B. B. Fulton, like E. S. Thomas (his contemporary), developed an interest in recognizing crickets and katydids by their calling songs. This interest fully developed after he became a professor of entomology at North Carolina State College in 1928 (Gurney 1964). North Carolina, with ecosystems ranging from montane to coastal, has a rich orthopteran fauna, yet by 1931 Fulton had developed a key to the state's crickets and katydids based on their calling songs (Fulton 1932). In that key *Anaxipha exigua* comes out in two places, one for the trilling song (=Say's *exigua*) and one for tinkling songs. Fulton notes that the tinkling song apparently occurs in two forms, the one (this species) having a tinkle rate about twice as fast as the other (*tinnulenta* n.sp.). Fulton (1951, 1956) later named the songs of his three "*exigua*" as trill, fast tinkle, and slow tinkle.

TW and DF independently encountered Fulton's three song forms of *exigua* and discovered that the three could be distinguished morphologically by the numbers of teeth in the stridulatory files (Fig. 11). Because only the trilling song occurs among populations of "exigua" as far north and west as the type locality of *exigua*, we concluded that Say's *exigua* corresponds to Fulton's triller song type. Our vernacular names for three of the six species of the *exigua* group preserve Fulton's original names for their songs.

Holotype.—Male. Pennsylvania: Chester Co., New London, 39.767099°N, -75.897706°W, coll. 9 Aug 2011, DFunk (ANSP). Song recorded (R09_0673.WAV). BOLD sample ID: SWRC-Ae_200. GenBank Accession: KF670936. Body length 6.7mm, hind femur 5.04.

Allotype.—Female, same locality as holotype, coll. as nymph 28 Jul 2011 and reared in lab, DFunk (ANSP). Specimen ID: SWRC-Ae_203. Body length 7.3mm, hind femur 5.0, ovipositor 2.5.

Measurements.—Body length, ♂♂ 5.9-6.5mm, ♀♀ 6.5-7.6; hind femur, ♂♂ 4.4-5.1, ♀♀ 4.8-5.8; ovipositor, 2.3-2.6. (DF n=18 ♂♂, 15 ♀♀; PA, MD and GA).

Hindwings.—Macropters rare, of the 41 ♂♂ and 28 ♀♀ examined, 3 ♀♀ were long-winged; none of the short-winged specimens was a dealate.

Other noteworthy specimens, song recordings and locality records.—A song recorded in a wax myrtle tangle in a longleaf pine savannah in George County, MS, was originally assigned to *thomasi*, but the locality proved more compatible with the known range of *tinnulacita* and the pulse rate of its song was closer to *tinnulacita* than to *thomasi*. As discussed under *scia*'s account, in south Florida *tinnulacita* is occasionally collected in mangrove, where it has anomalous color and tarsal claw dentition.

Seasonal occurrence.—Univoltine. In Florida, the earliest records of adults are in late June; whereas in the northeast, they are in early August.

Habitat.—On coarse weeds or woody plants from several centimeters to about a meter above ground level. Margins of woods to old fields and hedgerows as well as riparian areas. Often found with *exigua* and *tinnulenta*.

Distinguishing features.—*A. tinnulacita* can be distinguished from other North American *Anaxipha* by the following combination of characters: basal metatarsal segment shorter than the combined length of the 2nd and 3rd segments; spines of hind tibiae with a fringe of long hairs (as in Fig. 2D); hind femur with a broad dark stripe on the lateral face along the sulcus (Fig. 9C); stridulatory file with 176-213 teeth; song a continuous fast tinkle at ~13 p/s at 6.8 kHz (at 25°C); male genitalia as in Fig. 13C; ovipositor 2.3-3.3 mm, ratio of length of hind femur to ovipositor 1.7-2.3.

This species of the *exigua* group calls continuously with a pulse rate slower than *thomasi* and faster than *tinnula* and *tinnulenta*.

Origin of name.—From *tinnulus*, L., ringing, tinkling, and *citus*, L., quick; for its rapid, tinkling calling song.

Notes: We concluded that the fast-tinkling *Anaxipha* songs that Fulton (1956) reported from the lower foothills of the Blue Ridge Mountains were more likely *thomasi* than *tinnulacita* (Fig. 1). Walker (2001-2013) omitted this species from SINA because he could not reliably distinguish its song from the songs of crickets that he thought were *scia*.

***Anaxipha tinnulenta* new species**
slow-tinkling trig
Figs 1, 4, 5, 7-11, 13-15, 17-19; Tables 2-6.
SMspecimens_tlt; SMsongs_tlt.

History of recognition.—As mentioned in the previous species account, Fulton (1932) recognized three "song forms" of *A. exigua*. This is the species that produces the song that Fulton (1951, 1956) described as a "slow tinkle."

Holotype.—Male. Pennsylvania: Chester Co., New London, 39.767099°N, -75.897706°W, coll. 26 Aug 2009, DFunk (ANSP). Song recorded (R09_0211.WAV). BOLD sample ID: SWRC-Ae_102. GenBank Accession: HM399292. Body length 6.5mm, hind femur 4.8.

Allotype.—Female, same locality as holotype, coll. 1 Aug 2010, DFunk (ANSP). Specimen ID: SWRC-Ae_163. Body length 7.0mm, hind femur 4.6, ovipositor 2.4.

Measurements.—Body length, ♂♂ 5.8-6.5mm, ♀♀ 6.4-7.0; hind femur, ♂♂ 4.3-4.8, ♀♀ 4.6-5.4; ovipositor, 2.4-2.8. (DF n=20 ♂♂, 20 ♀♀; PA and MD).

Hindwings.—No long-winged specimen seen. Of the 46 ♂♂ and 17 ♀ short-winged specimens examined, 1 ♀ was a dealate; all others were micropters.

Seasonal occurrence.—Univoltine with adults appearing late summer into early fall.

Habitat.—On coarse weeds, herbs or woody plants from several centimeters to a meter above ground level. Often found with *exigua* and/or *tinnulacita*, but generally restricted to more open areas than either of those.

Distinguishing features.—*A. tinnulenta* can be distinguished from other North American *Anaxipha* by the following combination of characters: basal metatarsal segment shorter than the combined length of the 2nd and 3rd segments; spines of hind tibiae with a fringe of long hairs (as in Fig. 2D); hind femur with a broad dark stripe on the lateral face along the sulcus (Fig. 9D); stridulatory file with 253-309 teeth; song a continuous tinkle at ~5.1 p/s at 6.5 kHz (at 25°C); male genitalia as in Fig. 13D; ovipositor 2.4-2.8 mm, ratio of length of hind femur to ovipositor 1.8-2.0.

This member of the *exigua* group has the slowest calling song pulse rate and the stridulatory file with the most teeth and the highest tooth density. Often found in close proximity to *A. exigua* and *A. tinnulacita*, but generally more restricted to open-canopied habitats such as old fields and woods margins.

Origin of name.—From *tinnulus*, L., ringing, tinkling, and *lentus*, L., slow; for its slow, tinkling calling song.

Note: Walker (2001-2013) listed this as "*Anaxipha* n.sp. F."

***Anaxipha tinnula* new species**
tidewater trig
Figs 1, 2, 4, 7-11, 13, 14, 17-19; Tables 2-6.
SMspecimens_tnl; SMsongs_tnl.

History of recognition.—Based on a lack of teeth on the tarsal claws and short ovipositors, Fulton (1956) included specimens of this species from coastal New Jersey south to at least South Carolina under his concept of *scia*, a species that Hebard (1915) had described from a mangrove swamp in south Florida (see next species account). Fulton (1956) described the song of the North Carolina populations that he thought were *scia* but were actually this species as "a rapid tinkling like little bells, very much like the tinkling songs of *A. exigua*." Thus, when DF discovered that the type and allotype of *scia* were not this species of *Anaxipha* he became the first to recognize it as needing to be formally named and thereby solved TW's

dilemma of being unable to recognize *scia* by its song in Florida.

Holotype.—Male. Maryland: Kent Co., Still Pond, upper Codjus Cove, 39.335265°N, -76.118322°W, coll. 6 Sep 2009, DFunk (ANSP). Song recorded (R09_0239.WAV). BOLD sample ID: SWRC-Ae_105. GenBank Accession: HM399292. Body length 6.7mm, hind femur 4.8.

Allotype.—Female, same locality as holotype, coll. 29 Jul 2012, DFunk (ANSP). Specimen ID: SWRC-Ae_240. Body length 7.0mm, hind femur 5.4, ovipositor 2.0.

Measurements.—Body length, ♂♂ 6.4-6.7mm, ♀♀ 7.0; hind femur, ♂♂ 4.5-5.1, ♀♀ 4.8-5.4; ovipositor, 1.8-2.0. (DFn=20♂♂, 7♀♀; MD and NC.)

Hindwings.—One macropterous female is known (NC). Of the 51 short-winged adults examined, none was a dealate.

Other noteworthy specimens, song recordings and locality records.—At least 86 of the specimens Fulton (1956) recorded as *scia* were *tinnula* instead. These were collected by Fulton from tidal marshes at two sites along North Carolina's coast: Carolina Beach, New Hanover Co. (28M, 25F) and New Bern, Craven Co. (17M, 16F).

Of special note among specimens Fulton identified as *scia* were 1 male and 2 female collected by Morgan Hebard in Nevada's Amargosa Desert in Ash Meadows on Fairbanks Ranch, 24 Aug 1919. Notes by Hebard stated that "the crickets were found in a large colony in Tules (the western bull rush) around a large pool of strongly alkaline water. Individuals were near the surface of the water where the males were keeping up a continuous trilling . . . . They seek the thickest grasses and can be driven into the open . . . only with the greatest difficulty." Fulton wrote that the Nevada specimens did not differ from *scia* except in being "very pale" in general color and having "very conspicuous stripes on the hind femora." DF examined these ANSP specimens. Other than the more conspicuous stripe on the hind femora (as noted by Fulton), the Nevada specimens were indistinguishable from those found in Atlantic tidal marshes. From Hebard's verbal description the song may be similar to that of Eastern *tinnula*, but recordings will be needed to verify.

Seasonal occurrence.—Univoltine with adults appearing in late summer into early fall. (As early as late June in Florida).

Habitat.—Except for the Nevada population, known only from tidal marshes. Commonly found on cattails (*Typha*), pickerelweed (*Pontederia*) or cordgrass (*Spartina*). Specimens have been found with *delicatula* in cordgrass marshes of coastal NC, and within "earshot" of *tinnulacita* and *tinnulenta* near tidal margins in the northern part of its range.

Distinguishing features.—*A. tinnula* can be distinguished from other North American *Anaxipha* by the following combination of characters: basal metatarsal segment shorter than the combined length of the 2nd and 3rd segments; spines of hind tibiae with a fringe of long hairs (as in Fig. 2D); hind femur with a broad dark stripe on the lateral face along the sulcus (Fig. 9E); stridulatory file with 184-217 teeth; song a continuous tinkle at ~8.2 p/s at 6.4 kHz (at 25°C); male genitalia as in Fig. 13E; ovipositor 1.8-2.0 mm, ratio of length of hind femur to ovipositor 2.5-2.8.

This member of the *exigua* group has no teeth on its tarsal claws, a short ovipositor, a tinkle with a moderate pulse, and a stridulatory file with about 200 teeth; it is only known from tidal marshes, but often within "earshot" of *tinnulacita* and *tinnulenta* near the tidal margins; commonly found on cattails (*Typha*), pickerelweed (*Pontederia*) or cordgrass (*Spartina*).

Origin of name.—From *tinnulus*, L., ringing, tinkling; for its tinkling calling song.

Note: Walker (2001-2013) listed this species as "*Anaxipha* n.sp. E."

***Anaxipha scia* Hebard 1915**

mangrove trig

Figs 1, 2, 4, 6, 7, 9-11, 13, 14, 18, 19; Tables 2-6.

SMspecimens_sci; SMsongs_sci.

History of recognition.—The identity of this species caused us major confusion until DF found that individuals of the species that TW (2001-2013) had been calling *Anaxipha* n.sp. B were indistinguishable from Hebard's holotype and allotype of *A. scia*.

Holotype.—Female. Miami, Florida, in red mangrove swamp on edge of Brickell's Hammock, 16 Mar 1915, M. Hebard, Collr. (ANSP). Body length 4.7mm, hind femur 4.2, ovipositor 1.8.

Allotype.—Male, same data as holotype except for date (15 Mar 1915). Body length 6.2mm, hind femur 4.1, stridulatory file with 88 teeth, genitalia shown in SMFig_Genitalia.

Measurements.—Body length, ♂♂ 5.7-6.2mm, ♀♀ 4.8-5.2; hind femur, ♂♂ 3.8-4.2, ♀♀ 3.9-4.4; ovipositor, 1.7-1.9. (DF n= 1 ♀; FL) (TW n=6 ♂♂, 5 ♀♀; FL.)

Hindwings.—No long-winged specimen seen. Of the 15 ♂♂ and 10 ♀♀ examined that were short-winged, 1 ♂ was a dealate; all others were micropters.

Other noteworthy specimens, song recordings and locality records.—Fulton (1956) was first to report multiple new specimens of *scia* after the species was described in 1915. As noted above under *tinnula*, most of Fulton's "*scia*" were *tinnula* instead; however, these 8 specimens he reported from two sites in Florida are exceptions: 1F, Miami, 8 March 1919 (most likely taken by Hebard from the type locality, and previously noted by Blatchley 1920); 4M, 3F, Cortez Beach, Manatee Co.,4 Jan 1925 (TH Hubbell; by beating young mangrove seedlings and other vegetation beneath mangrove branches).

Between 1958-1971, TW and associates collected specimens and tape recorded the songs of *scia* from Collier, Monroe, Dade, and Palm Beach Counties in south Florida. In 2011, five live presumptive *scia* were collected by Lary Reeves in mangrove in Flamingo (Monroe Co.) and Matheson Hammock (Dade Co.) and sent by TW to DF. BOLD DNA analyses of the three from Flamingo formed a group distinct from other *exigua* group species but more similar to them than to other *Anaxipha*. DF recorded the song of a male among these three and found that it matched the song of *scia*. Morphology (stridulatory file tooth count, dentition of tarsal claw and ovipositor length) of these specimens was consistent with Hebard's types and thus all three were identified as *scia*. In the case of the two (males) from Matheson Hammock, one produced a song that matched that of *tinnulacita*; the other did not sing but both matched *tinnulacita* in file tooth count (but were atypical in color and claw dentition). These two were thus identified as *tinnulacita* with the anomalies tentatively ascribed to a local response to the salt-water environment.

See "Unresolved taxa" in Discussion for an account of *Anaxipha* males captured and recorded in George County, MS, and Cameron Co., TX, that had calling songs with pulse rates and carrier frequencies that would identify them as *scia* but differed in habitat and continuity of calling.

Seasonal occurrence.—Adults occur year-round as evidenced by records from every month except February, May, and September.

Habitat.—This species is known only from mangrove areas in south Florida and their immediate vicinity. It is particularly abundant in black mangrove (*Avicennia germinans)* where it occurs from near ground level to about a meter up and is sometimes easily collected by sweeping.

Distinguishing features.—*A. scia* can be distinguished from other North American *Anaxipha* by the following combination of characters: basal metatarsal segment shorter than the combined length of the 2nd and 3rd segments; spines of hind tibiae with a fringe of long hairs (Fig. 2D); hind femur with a rather indistinct dark stripe on the lateral face along the sulcus (Fig. 9F); stridulatory file with 82-91 teeth; song an intermittent trill at ~60 p/s at 6.1 kHz (at 25°C); male genitalia as in Fig. 13F; ovipositor 1.6-1.9 mm, ratio of length of hind femur to ovipositor 2.3-2.5.

This, the most darkly colored North American species (SMFig_Portraits), has a dark venter (http://entnemdept.ifas.ufl.edu/walker/Buzz/617a.htm) and is known only from mangrove; it is the only member of the *exigua* group that produces an intermittent trill rather than a continuous series of pulses; its pulse trains are more variable and often longer than those of *imitator* (Fig. 6C, D), the only other *Anaxipha* with an intermittent trill known from habitats adjacent to mangrove.

Anaxipha delicatula (Scudder 1877)

chirping trig

Figs 1, 2, 4-7, 9, 10, 11, 13-15, 17, 18, 19; Tables 2-6.

SMspecimens_dlc; SMsongs_dlc.

History of recognition.—Hebard (1924) noted that this name was available for the species to which Rehn and Hebard (1916) had assigned the name *A. pulicaria* (Burmeister). (He also noted that *A. pulicaria* was more appropriate to what we here describe as *A. fultoni*). Fulton (1956), after studying the genitalia of what Hebard would have called *delicatula*, concluded that two species were involved: this species and a new species that he named *A. litarena.* He failed to detect another new species among the populations he assigned to *delicatula*, in spite of the fact that the other new species (*vernalis*, described below) contrasted in its calling song to both *litarena* and *delicatula*. This was because, with the exception of a single series from one coastal locality, all the North and South Carolina specimens that he assigned to *delicatula* were *vernalis* instead.

Holotype.—Long-winged male. Fort Reed, Florida (now in Sanford, Seminole County, Florida), 23 Apr 1876, J.H. Comstock, collr. (MCZ) Body length 6.3mm, hind femur 4.5, stridulatory file with 73 teeth, genitalia shown in SMFig_Genitalia.

Measurements.—Body length: ♂♂ 6.2-6.8mm, ♀♀ 4.8-6.7; hind femur, ♂♂ 4.2-4.5, ♀♀ 3.9-4.6; ovipositor 2.6-3.3. (DF n=4 ♀♀; FL) (TW n=5 ♂♂, 5 ♀♀; FL.)

Hindwings.—Macropters sometimes frequent at light but adults collected elsewhere usually short-winged. Of 19 short-winged ♂♂ examined 11 were dealates and 8 were micropters. (No short-winged ♀♀ were examined.)

Seasonal occurrence.—In the vicinity of Gainesville, *delicatula* calls Feb to Oct with a strong peak in numbers in Mar to May (SINA 2013). In the Florida Keys TW has heard it as late as Nov and as early as Jan. At least two generations a year apparently occur in the latitudes of Florida. The four records of *delicatula* along the Atlantic coast north of Florida, each restricted to a single date, range from 12 Jun to 10 Sep. DF recorded and collected adults of this species near Corolla, NC on 19 Jul.

Habitat.—Fresh water marshes, including lizardtail (*Saururus*) and cattails (*Typha*); on herbaceous undergrowth in riparian areas; short-winged individuals found away from wet habitats may be macropters that have shed their wings. In North Carolina this species has been found in tidal marshes along with *tinnula*.

Distinguishing features.—*A. delicatula* can be distinguished from other North American *Anaxipha* by the following combination of characters: basal metatarsal segment shorter than the combined length of the 2nd and 3rd segments; spines of hind tibiae with a fringe of long hairs (as in Fig. 2D); hind femur without dark stripe on the lateral face along the sulcus (Fig. 9G); stridulatory file with 66-77 teeth; song a series of nearly regular chirps at ~79 p/s at 5.7 kHz (at 25°C); male genitalia as in Fig. 13G; ovipositor 1.3-1.6 mm, ratio of length of hind femur to ovipositor 3.0-3.3.

The chirps of the calling song of *delicatula* are more regular than in other species with broken trills; its ovipositor is very short and its HF/O ratio is very high (Fig. 10).

Anaxipha vernalis new species

spring trig

Figs 1, 4, 7-14, 17-19; Tables 2-6.

SMspecimens_vrn; SMsongs_vrn.

History of recognition.—Because of similarities in male genitalia, Fulton (1956) failed to distinguish this species from *A. delicatula*. The songs of the two species are strikingly different, but, as indicated above, the populations of "delicatula" Fulton studied in the field evidently did not include *delicatula* and were entirely *vernalis.*

Holotype.—Male. Pennsylvania: Chester Co., London Grove, 39.856248°N, -75.788021°W, coll. 5 Jul 2010, DFunk (ANSP). Song recorded (R09_0378.WAV). BOLD sample ID: SWRC-Ae_134. Genbank Accession: JF838447. Body length 6.7mm, hind femur 4.2.

Allotype.—Female, same data as holotype (ANSP). Specimen ID: SWRC-Ae_139. Body length 6.4mm, hind femur 4.3, ovipositor 1.5.

Measurements.—Body length, ♂♂ 6.4-6.8mm, ♀♀ 5.9-7.2; hind femur, ♂♂ 4.2-4.6, ♀♀ 4.3-4.7; ovipositor, 1.5-1.6. (DF n=5 ♂♂, 8 ♀♀; PA and MD.)

Hindwings.—No macropters known. Of the 25 short-winged adults examined, none was a dealate.

Seasonal occurrence.—Within its range, *vernalis* is the earliest *Anaxipha* to mature and may be heard calling from early May through early August.

Habitat.—Generally found within half a meter of the ground in open areas with vegetation dominated by tall grasses. Adults are often heard singing along roadsides and margins of marshes and are particularly difficult to capture.

Distinguishing features.—*A. vernalis* can be distinguished from other North American *Anaxipha* by the following combination of characters: basal metatarsal segment shorter than the combined length of the 2nd and 3rd segments; spines of hind tibiae with a fringe of long hairs (as in Fig. 2D); hind femur without dark stripe on the lateral face along the sulcus (Fig. 9H); stridulatory file with 102-112 teeth; song a more or less continuous trill at ~45 p/s at 5.6 kHz (at 25°C); male genitalia as in Fig. 13H; ovipositor 1.5-1.6 mm, ratio of length of hind femur to ovipositor 2.8-3.1.

During most of the calling season of this species, there is no other *Anaxipha* to be heard. However, by late July other species begin to call, including *exigua*, which produces a continuous trill with a pulse rate like that of *vernalis* but with a dominant frequency that is higher at every temperature (Fig. 8). Males of *vernalis* can be identified by features of the genitalia (Fig. 13) and the number of teeth in the stridulatory file (Fig. 11).

Origin of name.—From *vernalis*, L., of springtime; for its season of adult occurrence.

Note: Walker (2001-2013) listed this as "*Anaxipha* n.sp. G."

***Anaxipha litarena* Fulton 1956**
beach trig
Figs 1, 4, 6, 7, 9-11, 13, 14, 17-19; Tables 2-6.
SMspecimens_ltr; SMsongs_ltr.

History of recognition.—As explained above, Fulton (1956) used differences in the male genitalia to separate this species from *delicatula* (and from *vernalis*, a species he lumped with *delicatula*.) Fulton's paratypes of *litarena* from his own collection were from coastal habitats in North and South Carolina and Florida. However, the specimens he named as paratypes from the UMMZ collection were mostly from inland counties in north peninsular Florida. When TW began studying the *Anaxipha* from both coastal and inland counties of this same area, he soon recognized, on the basis of differences in calling song, that Fulton's *litarena* was restricted to coastal habitats and that there was an unrecognized inland species (described below as *rosamacula*) that seemed likely to account for Fulton's 40 UMMZ paratypes of *litarena* from inland localities. These were borrowed from UMMZ, and male genitalia and stridulatory files of five of them, from diverse localities, were examined. All were *rosamacula*.

Holotype.—Male. Carolina Beach, New Hanover County, North Carolina, on a shrub, *Iva*, growing on the first dune near the ocean; 12 Jun 1930, B. B. Fulton, collr. (USNM). Body length 7.1mm, hind femur 4.2, stridulatory file with 74 teeth.

Measurements.—Body length, ♂♂ 6.1-7.4mm, ♀♀ 5.0-6.5; hind femur, ♂♂ 4.0-4.4, ♀♀ 4.1-4.5; ovipositor, 1.5-1.6. (DF n=1 ♀; FL) (TW n=5 ♂♂, 5 ♀♀; FL.)

Hindwings.—No macropters known. Of the 59 ♂♂ and 22 ♀♀ examined that were short-winged, none was a dealate.

Seasonal occurrence.—In North Carolina, Fulton collected adults as early as 20 Apr and as late as 11 Sep; in Florida, the earliest record of adults is 19 Apr and the latest is 4 Sep. In both states the species seems to have been present in all intervening months, but the records are inadequate to reveal any generational peaks of abundance.

Habitat.—Occurs in a variety of open coastal habitats including forbs and grasses (frequently on *Distichlis spicata*) on tidal flats and behind dunes.

Distinguishing features.—*A. litarena* can be distinguished from other North American *Anaxipha* by the following combination of characters: basal metatarsal segment shorter than the combined length of the 2nd and 3rd segments; spines of hind tibiae with a fringe of long hairs (as in Fig. 2D); hind femur without dark stripe on the lateral face along the sulcus (Fig. 9I); stridulatory file with 65-77 teeth; song a series of short pulse trains, ~66 p/s at 5.9 kHz (at 25°C); male genitalia as in Fig. 13I; ovipositor 1.6-1.7 mm, ratio of length of hind femur to ovipositor 2.4-2.8.

This species is restricted to coastal areas, pulse trains of calling song are delivered at a nearly regular rate (Fig. 6B-1&2) with the intervals no longer than the pulse trains; male genitalia unique (Fig. 13I).

***Anaxipha rosamacula* new species**
pink-spotted trig
Figs 1, 4, 6, 7, 9-11, 13, 14, 17-19; Tables 2-6.
SMspecimens_rsm; SMsongs_rsm.

History of recognition.—In north Florida this species and *A. fultoni* (next account) are the first *Anaxipha* to mature each year. Both are abundant in a variety of near-the-ground habitats and their songs are similar. TW discovered that the songs were different only when he recorded songs of caged males at various temperatures and analyzed their pulse rates (Walker 1962b). By the time TW was preparing the manuscript for the 1962 paper, he could easily separate the two species by their appearance and he assigned names to the two based on Fulton's (1956) revision.

Holotype.—Male. Florida, Alachua Co., UF campus, 14May1970, TJW, JJW; song recorded WTL611-47, =MLNS125586. Body length, 5.7; hind femur, 4.0. (FSCA, in alcohol)

Allotype.—Female, Florida, Alachua Co., west Gainesville, 12May1961, Coll#1, TJW, JJW; sweeping weeds in hammock area. Body length, 5.3 (to tips of forewings, 4.7); hind femur, 4.4; ovipositor, 1.7.

Paratypes.—Male (TJW-118), Florida, Collier Co., US 41, Midway Campground (25.8508°N, 80.9890°W), 05Jan2013, L. Reeves; song recorded 17.6-26.6°C (n=4; details in SMsongs_ros). BOLD sample ID: SWRC-TJW_118. GenBank Accession: KF670909. Body length, 6.1; hind femur, 4.3; file teeth, 92. (SWRC, in alcohol). Female, (TJW-76), Florida, Alachua Co., UF-NATL, gridblock E5, 01Apr2011, TJW; BOLD sample ID: SWRC-TJW_76. GenBank Accession: KF670910. Hind femur, 4.51; ovipositor, 1.75. (SWRC, in alcohol)

Measurements.—Body length, ♂♂ 5.6-6.5mm, ♀♀ 4.4-5.5; hind femur, ♂♂ 3.4-4.2, ♀♀ 3.8-4.5; ovipositor, 1.4-1.7. (DF n=1 ♀; FL) (TW n=6 ♂♂, 5 ♀♀; FL.)

Hindwings.—No macropters known. Of the 18 ♂♂ and 6 ♀♀ examined that were short-winged, none was a dealate.

Other noteworthy specimens, song recordings and locality records.—BOLD, SWRC-TJW-76, Alachua Co., FL. Fulton's paratypes of *litarena* that were verified as being this species *rosamacula* include three from widely separated localities in Alachua Co., FL (Fairbanks, Newberry, and Warburg Lake), two from St. Tammany Par., LA, and one from Macon, GA.

Seasonal occurrence.—Records of calling at Gainesville, FL, show a pronounced peak in March and April but drop to low numbers for the rest of the year (Walker 2013). Some of this drop surely results from the quiet songs of *rosamacula* becoming increasingly difficult to identify as louder and more raucous species join the insect chorus. The continued presence of the species throughout the year suggests at least two additional generations annually.

Habitat.—Calls within *ca* 1m of the ground in a wide variety of terrestrial habitats, including open roadsides and the undergrowth of closed forest, from xeric to hydric. The calls issue from species of herbaceous and low woody plants and from vines. This species and *fultoni* often occur in mixed populations, where their calls may be hard to distinguish initially.

Distinguishing features.—*A. rosamacula* can be distinguished from other North American *Anaxipha* by the following combination of characters: basal metatarsal segment shorter than the combined length of the 2nd and 3rd segments; spines of hind tibiae with a fringe of long hairs (as in Fig. 2D); hind femur without dark stripe on the lateral face along the sulcus (Fig. 9J); stridulatory file with 74-93 teeth; song a trill that is briefly broken at irregular intervals, ~66 p/s at 6.3 kHz (at 25°C); male genitalia as in Fig. 13J; ovipositor 1.4-1.8 mm, ratio of length of hind femur to ovipositor 2.4-2.8.

The calling song of this species is likely to be confused only with that of *fultoni* but most gaps between pulse trains are noticeably shorter (Fig. 6E, F); male genitalia are distinctive (Fig. 13J).

Origin of name.—From *rosa*, L., rose, and *macula*, L., spot; for the pink markings evident on fresh specimens.

Notes: Walker (1962) incorrectly identified this species as *Anaxipha pulicaria*, and Walker (2001-2013) listed it as "*Anaxipha* n.sp. C."

***Anaxipha fultoni* new species**

Fulton's trig

Figs 1, 2, 4, 6, 7, 9-11, 13, 14, 17-19; Tables 2-6.

SMspecimens_flt; SMsongs_flt.

History of recognition.—This is the species to which Rehn and Hebard (1916) assigned the name *A. vittata* (Bolivar) and that Fulton (1956), following Hebard (1924) assigned the name *A. pulicaria* (Burmeister). However, the type locality of *A. pulicaria* is Jamaica, and based on TW's specimens and recorded songs from Jamaica, Otte & Perez-Gelabert (2009, p. 139) fixed its identity as a species different from the one described here. Most of the specimens that Fulton (1956) identified as *A. pulicaria* were likely *A. fultoni*, with the others being *A. rosamacula*.

Holotype.—Male. Florida, Alachua Co., w. Gainesville, 12May1961, coll#1, TJW, JDS; roadside weeds in hammock area song; recorded 17.0-27.5°C, WTL612-4a,b,c,d,e,f,h=MLNS128380, 128399, 128404, 128419, 128439, 128462, 128506. Body length, 5.2; hind femur, 3.7. (FSCA, in alcohol).

Allotype.—Female. Florida, Alachua County, University of Florida campus, 25Mar1959, coll#1, TJW. Body length, 4.5; hind femur, ca. 3.5; ovipositor, 1.45. (FSCA).

Paratypes.—Male (TJW-46). Florida, Alachua Co., C.R. 346 at River Styx (29.5170°N, 82.2227°W), 26Apr2011, L. Reeves; song recorded 18.9-19.8°C (n=6; details in SMsongs_ful). BOLD sample ID: SWRC-TJW_46. GenBank Accession: KF670896. Hind femur, 3.9; file teeth, 97. (SWRC, in alcohol). Female, (TJW-58), Florida, Levy Co., Gulf Hammock (on US 19) (29.2535°N, 82.7248°W), 29May2011, L. Reeves; BOLD sample ID: SWRC-TJW_58. GenBank Accession: KF670897. Hind femur, 3.50; ovipositor, 1.43. (SWRC, in alcohol)

Measurements.—Body length, ♂♂ 5.2-6.6mm, ♀♀ 4.3-5.0; hind femur, ♂♂ 3.3-3.9, ♀♀ 3.5-3.6; ovipositor, 1.3-1.5. (DF n=3 ♀♀; FL) (TW n=6 ♂♂; 5 ♀♀; FL.)

Hindwings.—Macropters are sometimes frequent at light but adults collected elsewhere are usually short-winged. Of the 12 ♂♂ and 5 ♀♀ examined that were short-winged, 1♀ was a dealate; all others were micropters.

Other noteworthy specimens, song recordings and locality records.—BOLD, SWRC-TJW-46, 58, 71, 72 from Alachua and Levy Co., FL. Fulton (1956) reports a male from Edisto Beach, S.C. and notes that Rehn and Hebard (1916) reported a female from Albany, GA.

Seasonal occurrence.—Records of calling at Gainesville, FL, are from every month with largest numbers in March to May, with a suggestion of a much smaller second peak in August to October (Walker 2013).

Habitat.—Like *rosamacula*, this species is commonly heard in a broad range of terrestrial habitats, usually calling from perches no more than *ca* 1 m up. More often than *rosamacula*, it has been collected in coastal habitats—though not tidal ones.

Distinguishing features.—*A. fultoni* can be distinguished from other North American *Anaxipha* by the following combination of characters: basal metatarsal segment shorter than the combined length of the 2nd and 3rd segments; spines of hind tibiae without a fringe of long hairs; hind femur without dark stripe on the lateral face along the sulcus (Fig. 9K); stridulatory file with 97-112 teeth; song a trill that is broken at irregular intervals, ~43 p/s at 6.2 kHz (at 25°C); male genitalia as in Fig. 13K; ovipositor 1.3-1.5 mm, ratio of length of hind femur to ovipositor 2.4-2.7.

The calling song of *fultoni* is likely to be confused only with that of *rosamacula* but most gaps between pulse trains are noticeably longer (Fig. 6E, F); this is the only species other than *imitator* and *calusa* that lacks setal fringes on the spines of the caudal tibia (Fig. 2D); male genitalia distinctive (Fig. 13K).

Origin of name.—Named in honor of B. B. Fulton, author of the first revision of North American *Anaxipha*.

Notes: Because this species was more boldly marked than *rosamacula*, Walker (1962b) incorrectly identified this species as *Anaxipha imitator*. Walker (2001-2013) listed it as "*Anaxipha* n.sp. A."

Anaxipha imitator (Saussure 1878)

Cuban trig

Figs 1, 4, 6, 7, 9-11, 13, 14, 17-19; Tables 2, 3, 5, 6.

SMspecimens_imt; SMsongs_imt.

History of recognition.—This species occurs in southernmost Florida, where it has been identified as *A. imitator* ever since Hebard (1915) reported its occurrence at Brickell's Hammock in Miami. We confirmed the use of *imitator* for this species by soliciting photographs of Saussure's syntypes and here designate a lectotype.

Lectotype.—Female (MHNG). John Hollier, MHNG, reported that a "definite" female syntype and two probable ones were in that collection. He sent photographs of the three to TW, who judged all three to be conspecific with presumptive *Anaxipha imitator* specimens from Dade County, Florida. On this basis we selected the "definite" syntype as lectotype. When he is notified that this revision is in press, Hollier will label the specimen as lectotype. Hollier (email, 2 Aug 2011) reported that the labels already on the pin of the lectotype were "[female symbol] Cuba, Mr H. d. Sauss." [handwritten on ruled white card with "Cuba" printed]; "Cyrtox. imitator Sss." [handwritten on green paper]; "Syntypus" [printed on red paper]. Hollier noted that the fact that the name was underlined probably indicates "that the specimen was reviewed by Saussure for the Biologia Centrali-Americana, since the type specimens of the species described there all have the name underlined, whilst the vast majority do not."

Measurements.—Body length, ♂♂ 5.3-6.2mm, ♀♀ 4.6-5.6; hind femur, ♂♂ 3.7-4.1, ♀♀ 3.6-3.8; ovipositor, 1.2-1.3. (DF n=1 ♀; FL) (TW n=5 ♂♂, 5 ♀♀; FL.)

Hindwings.—Only macropters are known and these are apparently not attracted to artificial lights.

Seasonal occurrence.—Adults are present year round (specimens from every month except Feb, Oct, and Dec).

Habitat.—Understory of hardwood hammocks where it is an active flier, landing on herbaceous plants, the leaf litter, and the lower branches of trees; occasionally collected in adjacent habitats.

Distinguishing features.—*A. imitator* can be distinguished from other North American *Anaxipha* by the following combination of characters: basal metatarsal segment about 1.5× the combined length of the 2nd and 3rd segments; spines of hind tibiae without a fringe of long hairs; hind femur without dark stripe on the lateral face along the sulcus (Fig. 9L); stridulatory file with 97-112 teeth; song a trill that is broken at irregular intervals, ~45 p/s at 6.8 kHz (at 25°C); male genitalia as in Fig. 13L; ovipositor 1.3-1.4 mm, ratio of length of hind femur to ovipositor 2.6-2.9.

A. imitator is restricted to tropical hardwood hammocks, a rare and often much-disturbed habitat of the four south-most Florida counties. When encountered, identification is no problem because no other small North American species has a dark lateral stripe extending from its eye to the tip of its folded wings (SMFig_Portraits). In the field, it may be recognized by its song (Fig. 6D) and by its active running and flying about.

Anaxipha calusa new species

Calusa trig

Figs 3-7, 10, 11, 14, 17-19; Tables 2, 3, 5, 6.

SMspecimens_cls; SMsongs_cls.

History of recognition.—This species was discovered by Lary Reeves on 18 Sep 2012 as he was seeking to identify crickets by their calls in bushes along US 41 at Midway Camp Ground, Collier County, Florida (25.8508°N, 80.9890°W). He succeeded in capturing alive an immature male and an adult macropterous female that he suspected were of the species whose call had attracted his attention. When the two specimens were given to us for identification, we thought that the adult female might be *imitator* but when the male juvenile matured, it was much more boldly patterned than any *Anaxipha* known to occur in North America (Fig. 3B), and it produced a unique tinkling calling song in which the pulses were produced during calling at very slow, but variable, rates. Returning to the same site on 4 Jan 2012 Reeves collected three males and two adult and two juvenile females. He also surveyed other areas by listening for their distinctive calls and found it to be common in cypress stands all along the Loop Road, which is largely in Dade County.

Although we had no doubt that the species was new to North America, we knew it might have been described from elsewhere. Because it was widespread in a wilderness area, we guessed that it was most likely either a previously missed Florida endemic or the result of a long-ago introduction from the Caribbean. If the latter and the introduction had been by natural means, the likely place of origin would be Cuba. In his *Entomofauna Cubana*, Zayas (1974) listed these three *Anaxipha*: *vittata* (Bolivar 1888), *poeyi* (Bolivar 1888), and *imitator* (Saussure 1878); *calusa* matches Zayas's concept of none of the three. If *calusa* were a named species from elsewhere in the Caribbean, Otte & Perez-Galabert (2009) should have included it. It is not evident among the 42 species of *Anaxipha* they list and illustrate.

Holotype.—Male (TJW-103). Florida, Collier Co., Midway Campground along Rt 41 (25.8508°N, 80.9890°W) 18Nov2012, Lary Reeves; song recorded 15.1-22.5°C (n=9; details in SMsongs_cal), BOLD sample ID: SWRC-TJW-103. GenBank Accession: KF670876. Body length, 7.4; hind femur, 5.29. (FSCA, in alcohol)

Allotype.—Female (TJW-104). Florida, Collier Co., Midway Campground along Rt 41 (25.8508°N, 80.9890°W) 18Nov2012, Lary Reeves; Body length, 7.1; hind femur, 5.34; ovipositor, 2.25. (FSCA, in alcohol)

Measurements.—Body length, ♂♂ 7.1-8.4mm, ♀♀ 6.7-7.1; hind femur, ♂♂ 5.3-5.9, ♀♀ 5.3-5.8; ovipositor, 2.2-2.3. (DF n=3 ♂♂, 4 ♀♀; FL.)

Hindwings.—The seven adults examined (including two reared from nymphs) were macropters and none shed their wings in captivity.

Other noteworthy specimens, song recordings and locality records: No other specimens or records that are certainly *calusa* are known other than from Dade and Collier Counties but specimens similar to it are known from greenhouses in Ontario, Northern Nicaragua, and Costa Rica. These are described by DF in SM_AcalusaRelatives. A recording of 38 s or more from each of the three song-recorded *calusa* males are at http://entnemdept.ifas.ufl.edu/walker/Buzz/636a.htm. These and all other *calusa* recordings will soon be archived at MLNS.

Seasonal occurrence.—Adults known from September and January; may occur year round.

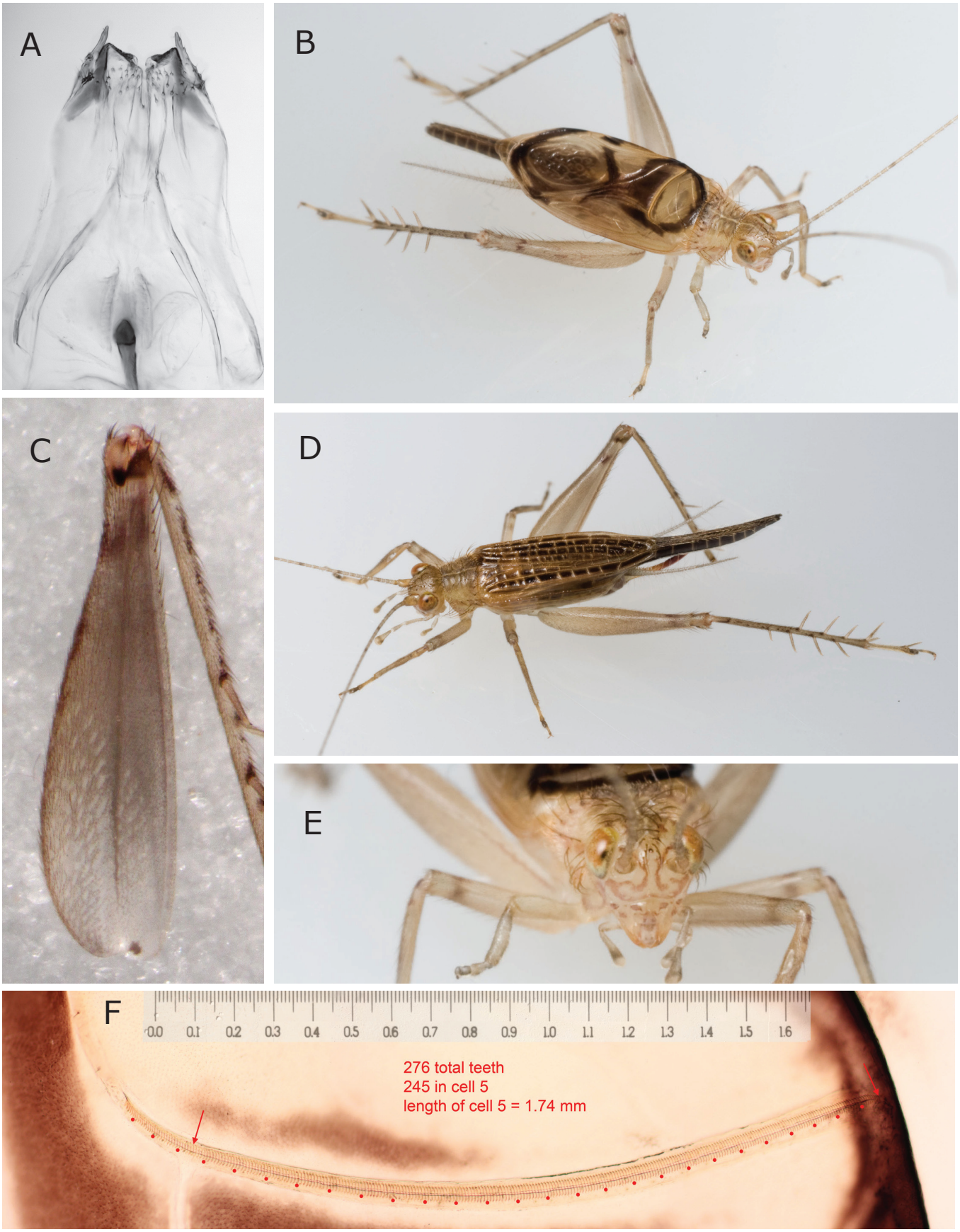


Fig. 3. *A. calusa* n. sp. A, B, E, genitalia and two views of male holotype; D, allotype; C, F, anterior face of hind femur and stridulatory vein of paratype; F, A red dot marks each additional 10 teeth; the red arrow marks the junction of the harp vein with the stridulatory vein. [Photos by David Funk].

Table 2. Pulse rate as a function of temperature in the calling songs of North American *Anaxipha*. The trendlines in this table were selected for possible use in arriving at a mean value of Tŷ=0. Criteria for their selection included avoiding effects of possible geographical variation, favoring recordings of caged individuals to increase the likely accuracy of ambient temperature data, maximizing the number of individuals contributing, and favoring high r^2 values. (I.D.=insufficient data)(All trendlines considered are in SMTbl_PRtrendlines.)

Song	Trendlines for p/s vs C				Tŷ=0*	p/s@25C	Males from
Species	n	b	a	r^2	(-a/b)		
Continuous trills or tinkles							
vernalis	138	2.050	-6.378	0.943	3.1	45	MD, PA, VA
exigua	125	2.090	-8.698	0.767	4.2	44	DE, MD, PA
thomasi	32	0.924	-1.986	0.638	2.1	21.1	Pennsylvania
tinnulacita	173	0.467	1.514	0.865	-3.2	13.2	DE, MD, PA
tinnula	22	0.354	-0.627	0.898	1.8	8.2	Kent Co., MD
tinnulenta	136	0.245	-1.061	0.790	4.3	5.1	DE, MD, PA
calusa	25	0.376	-3.238	0.813	I.D.[a]	6.2	Collier Co., FL
Intermittent trills or chirps (see Fig. 6)							
delicatula	27	3.952	-19.380	0.958	4.9	79	Florida
rosamacula	52	2.973	-8.627	0.963	2.9	66	Florida
litarena	40	3.032	-9.440	0.935	3.1	66	Florida
scia	30	2.708	-8.078	0.916	3.0	60	Florida
imitator	8	3.211	-34.925	0.928	I.D.[b]	45	Dade Co., FL
fultoni	22	1.953	-6.346	0.981	3.2	42	Alachua Co., FL
					mean value of (-a/b) = 2.7; SD = 2.2; n = 11.		

* Tŷ=0 is the temperature at which the expected value of y reaches zero when the trendline for a species is extrapolated downward; -a/b calculates its value.

[a] The calling song of *calusa* is a continuous tinkle but because the PR never quite stabilizes, PR at any temperature cannot be measured as precisely as in other species. Recordings were made in a limited range of temperatures with none higher than 25°C.

[b] The trendline for *imitator* is based on 3 caged and 5 field recordings between 21-28°C.

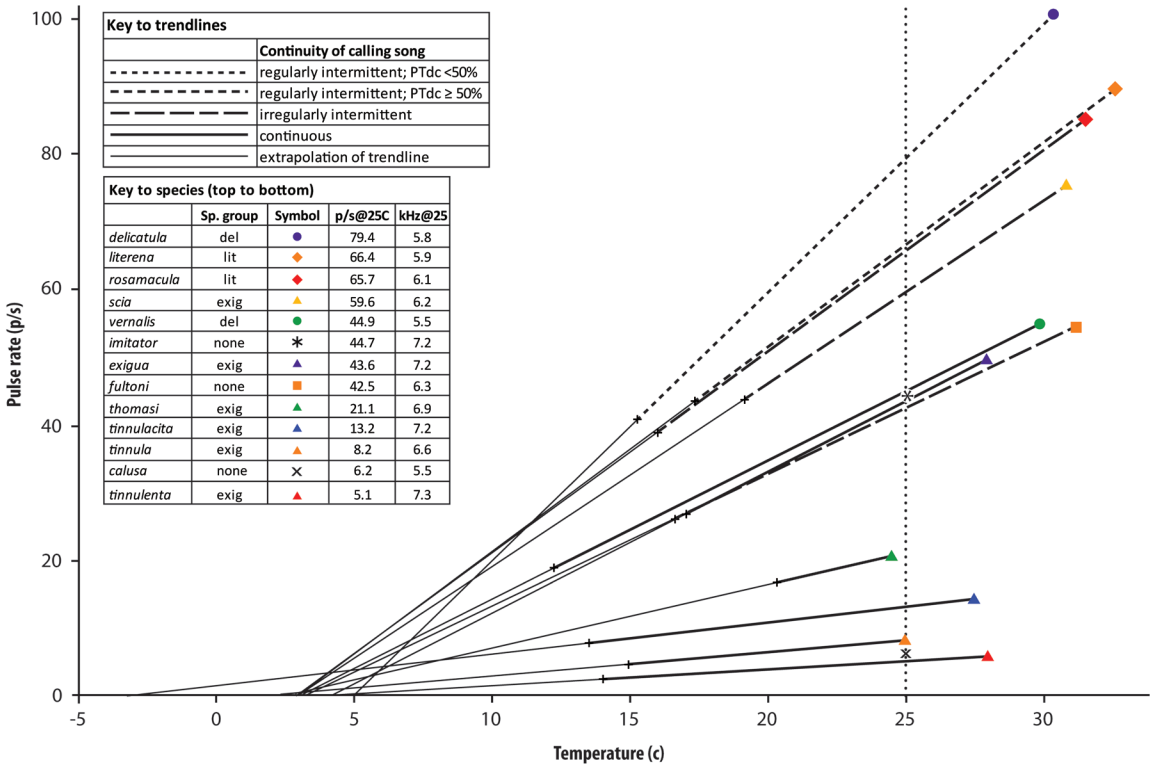


Fig. 4. Pulse rates and song continuity as aids in identifying North American *Anaxipha* by their calling songs. The upper lengths of the sloping lines are trendlines showing PR as a function of temperature. The vertical dotted line crosses these lines at 25°C, showing that interspecific differences in pulse rates are often substantial. The continuities of the trendlines reflect important differences in the continuities of the calling songs (see upper key). When the trendlines are extrapolated downward to an expected PR of 0, they tend to converge at 3°C, making it possible to estimate a trendline from any single recording of an *Anaxipha* calling song, provided the caller's ambient temperature is known. Data for *imitator* and *calusa* are insufficient to establish a trustworthy trendline, but their estimated pulse rates at 25°C are indicated by symbols on the vertical dotted line. (See text for details.) Formulas for trendlines are in Table 2. SMFig_PRvsTempAll shows all PR data for each of 12 species.

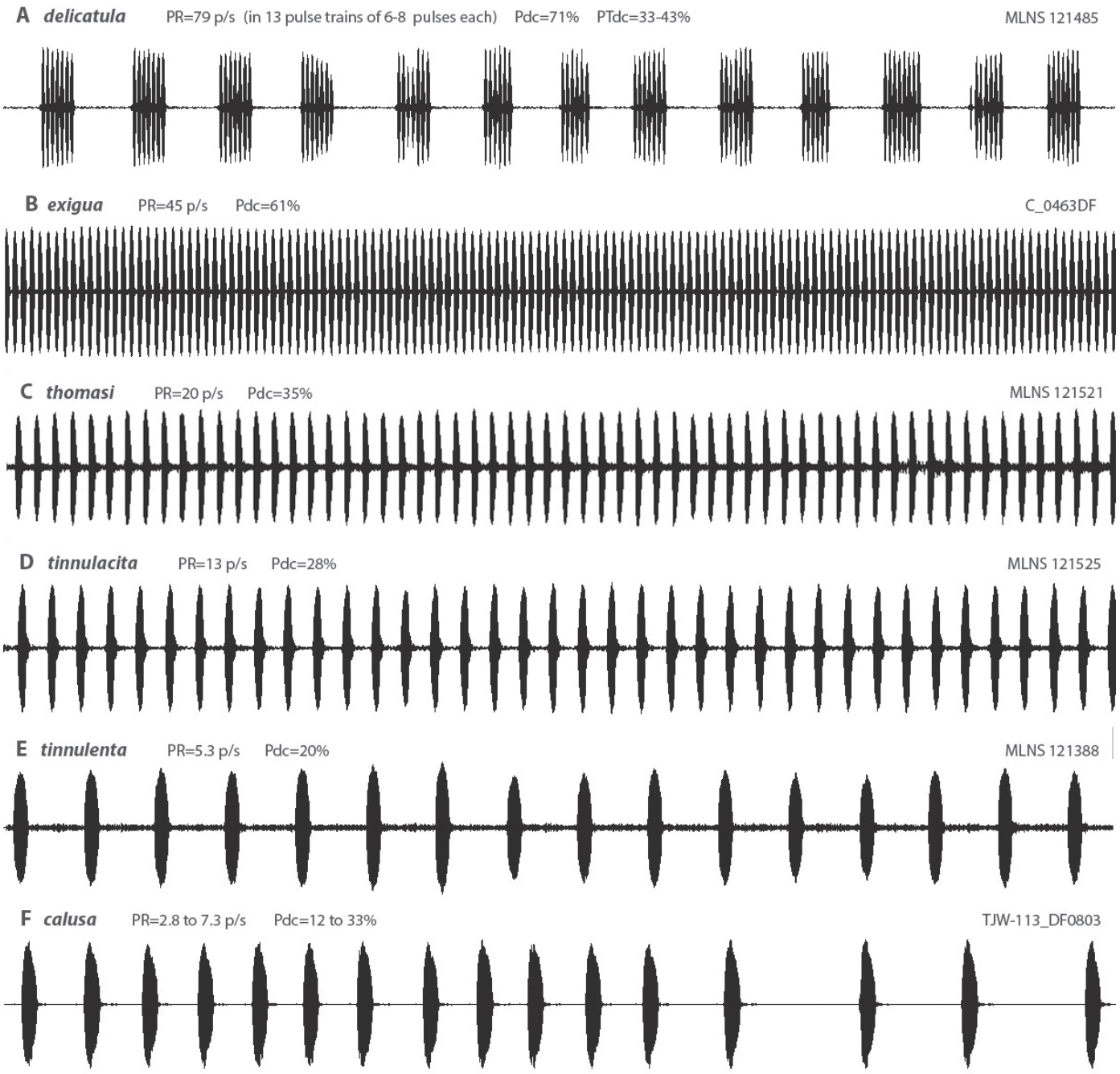


Fig. 5 A-F. Waveforms of 3-s samples of calling songs of six species at *ca* 25°C that show the range of pulse rates (p/s) and pulse duty cycles (Pdc) in North American *Anaxipha*. The songs from which these samples were taken have been described as: A. regularly broken trill, B. continuous trill, C. slow-pulsed trill or very fast tinkle, D. fast tinkle, E. slow tinkle, F. irregular tinkle.

Habitat.—Known only from an extensive area dominated by small cypress trees (*Taxodium* sp.) and their associates. For photographs of the vegetation in the immediate vicinity of the type locality go to http://entnemdept.ifas.ufl.edu/walker/Buzz/636a.htm .

Distinguishing features.—*A. calusa* can be distinguished from other North American *Anaxipha* by the following combination of characters: basal metatarsal segment about 1.5× the combined length of the 2nd and 3rd segments; spines of hind tibiae without a fringe of long hairs; hind femur without dark stripe on the lateral face along the sulcus (Fig. 3C); stridulatory file with about 276 teeth (Fig. 3F); song a slow, rather irregular tinkle (Fig. 5F), ~6.2 p/s at 5.4 kHz (at 25°C); male genitalia as in Fig. 3A; ovipositor 2.2-2.3 mm, ratio of length of hind femur to ovipositor 2.3-2.6.

As illustrated by the year of its discovery, this is the least likely to be encountered *Anaxipha* in North America. But once encountered it is the easiest to recognize — by its bold markings or by its tinkling song that never quite settles on an unvarying pulse rate.

Origin of name.—In 1513, when Spaniards first came to southwest Florida, they encountered the Calusa, a native people with a complex society who successfully resisted subjugation for nearly two centuries.

Note: Walker (2013-2014) listed it as "*Anaxipha* n.sp. I."

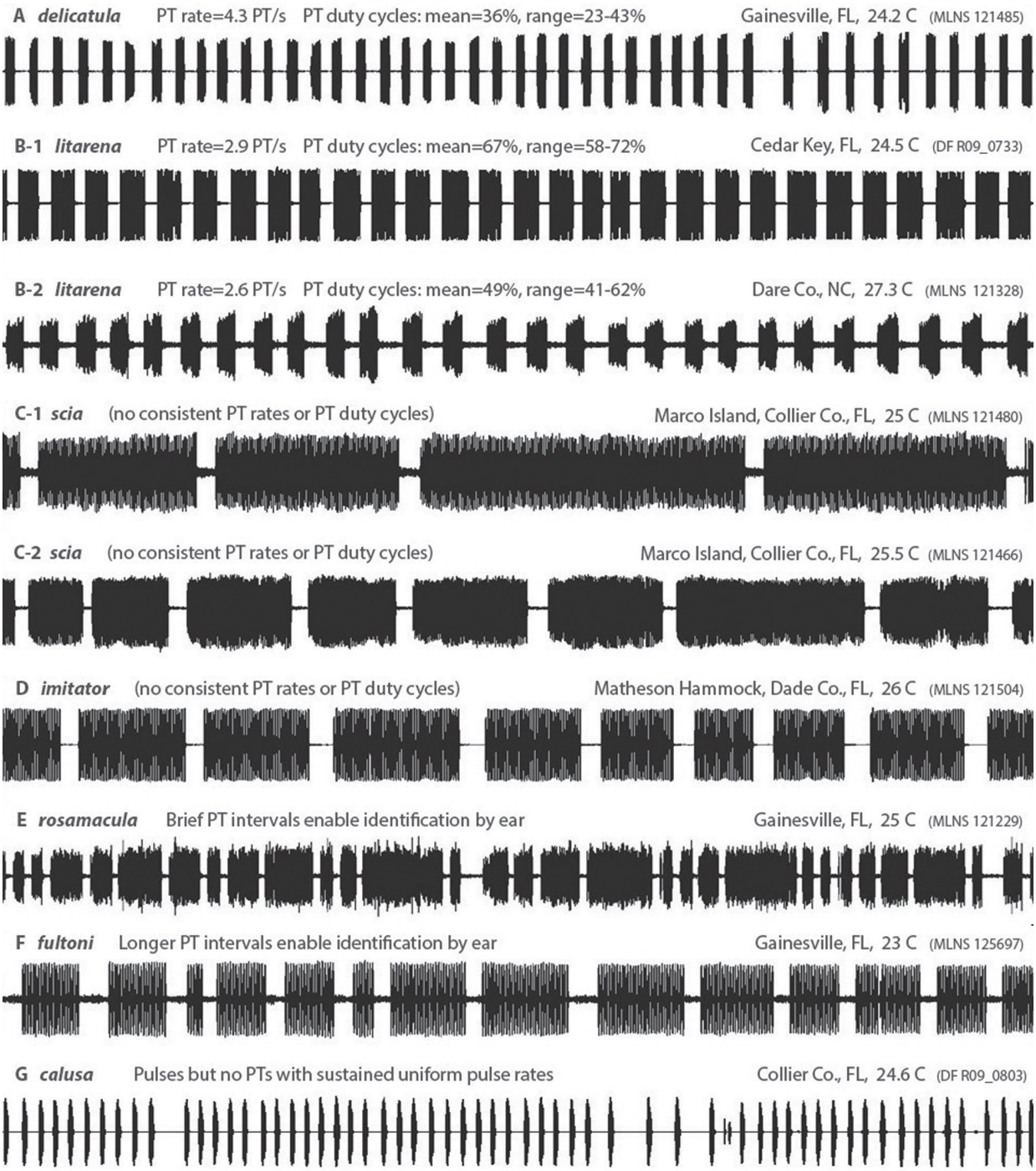


Fig. 6 A-G. 10 s samples of waveforms illustrating differences in pulse train phrasing. A, B-1, B-2, In *delicatula* and *litarena* the PTs are shorter and more uniform than in the other species. C and D, In *scia* and *imitator* the PT intervals are fairly uniform but the pulse trains are much longer and less uniform that in *delicatula* and *litarena*. E and F, In both *rosamacula* and *fultoni* pulse train phrasing is highly variable but brief intervals between most PTs distinguish the song of *rosamacula* from that of *fultoni*. G, The song of *calusa* has an indefinite pulse rate and hence no well-defined pulse trains.

Discussion

Unresolved taxa.—After dark, on 12 Aug 1964, TW stopped in a grassy, longleaf pine area along US 98 in George County, MS, and collected two male *Anaxipha* from tall grass in an open weedy area. Five nights later, in Cameron County, TX, on tall grass in a freshwater marsh next to Texas 345, he recorded two *Anaxipha* males and captured three others. The songs of the five males collected at these two sites were later recorded. None of the recordings could be distinguished from those of Florida *scia* on the basis of pulse rate or carrier frequency. However, the habitats of these crickets were in contrast to the mangrove habitats of *scia* in Florida and their calling songs were essentially continuous rather than broken for brief periods at irregular intervals. When DF studied the genitalia of the two males from Mississippi and of two of the males from Texas, he concluded that the genitalia of the MS and TX pairs differed from one another and that those from the MS males differed from those of *scia*. On the basis of genitalia, the MS pair belonged to the

delicatula group and the TX pair belonged to the *exigua* group. (SM has images of the genitalia and other details about these crickets.) File tooth counts for the MS specimens were 96 and 85; for the TX ones, 84 and 88.

Species identification by calling song

Introduction.—The ease of identifying *Anaxipha* species by their songs contrasts with the difficulty of identifying many of the species by morphological means. In fact, when geographic locality and habitat are taken into account, the local species are usually easy to distinguish by ear. Careful morphological studies of adult males have made identifying dead specimens of all species possible but often only after manipulating the specimen and examining the results with a quality microscope. When identification by song requires the analysis of a recording, advances in electronics have led to digital cameras with video modes that will do the recording. When electronic analysis of the recorded song is needed, an online PC will do the job if combined with free software and instructions on how to use it (Capinera *et al.* 2004).

Necessary terminology.—The basic unit of *Anaxipha* calling songs is a *pulse*, the sound made when the *scraper* on the edge of one forewing engages the *file* on the underside of the other forewing during a portion of a *wing movement cycle*. These cycles occur at uniform rates for brief to prolonged periods, producing *pulse trains*. The *pulse rate* (PR) during a pulse train (PT) is an important character, because it is species specific (though temperature sensitive). At 25°C, the mean PRs of North American *Anaxipha* species range from 5 to 79 *p/s* (Fig. 4). Within a pulse train, each pulse has a *pulse duration* (PD) and is followed by a *pulse interval* (PI). The PD plus the PI is a *pulse period* (PP). The proportion or percent of the PP that is occupied by the PD is the *pulse duty cycle* (Pdc). See Fig. 5 for 3 s waveforms of calling songs that illustrate the full range of pulse rates and duty cycles.

The calling songs of *Anaxipha* are musical in quality because their pulses and pulse trains are nearly pure in *frequency*, with the *carrier frequency* (CF) of the song being characteristic of the species but, as with PR, temperature sensitive. At 25°C, the mean carrier frequencies of the 13 species range from 5.5 to 7.3 kHz (inset of Fig. 4).

The calling songs of species that produce pulse trains that usually last 4 s or longer are said to be *continuous* and if the PR is high enough to make the individual pulses hard to detect, the effect is termed a *trill* (Fig. 5B). If the PR is so slow that each pulse is easily distinguished, the song can be rendered as a continuing *tink, tink, tink, tink* and described as a *slow tinkle* (Fig. 5E). In between are *fast tinkles* (Fig. 5D) and *slow-pulsed trills* (Fig. 5C).

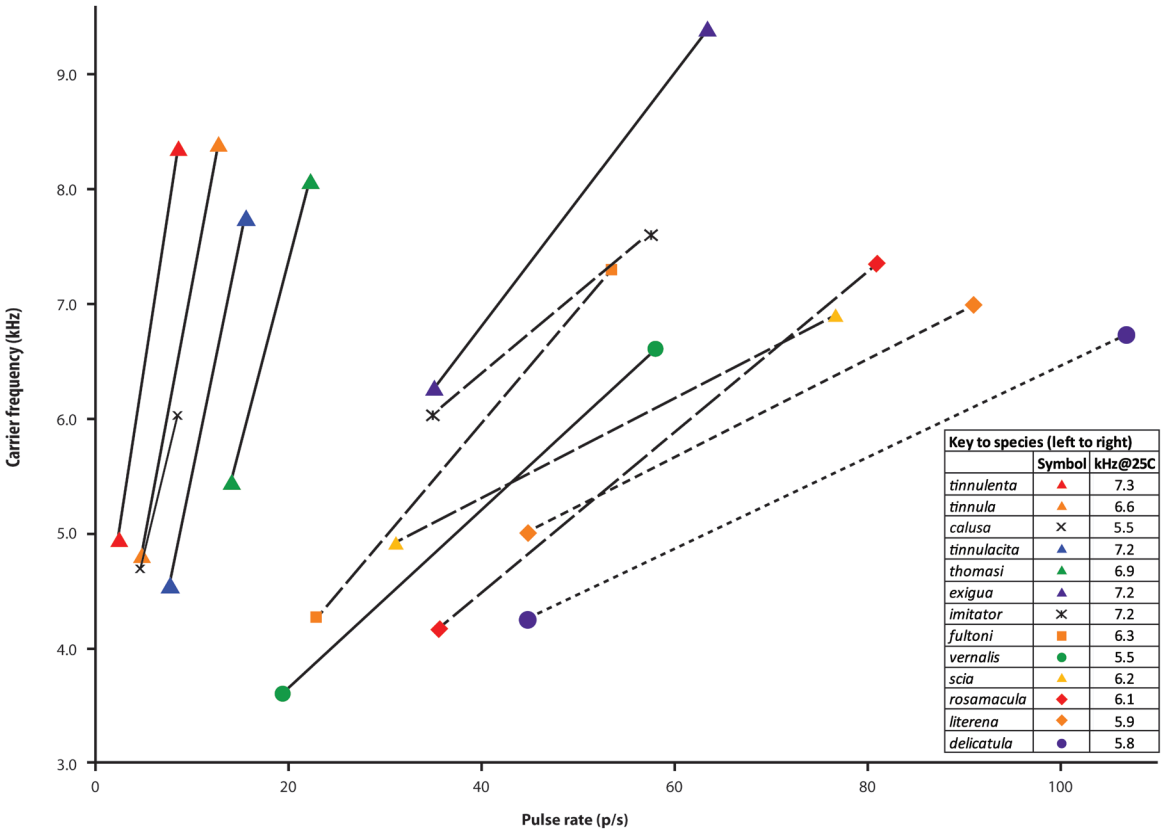


Fig. 7. Trendlines for carrier frequency plotted as a function of pulse rate in North American *Anaxipha*. The bottom end of each line is the expected kHz of the lowest recorded PR for the species and the top end is the expected kHz for the highest recorded PR for the species. The y-axis span of each line (*i.e.*, max kHz-min kHz) thus depends not only on the range of temperatures at which recordings were made but also on the rate of change of kHz with PR. The lines for *calusa* and *imitator* have the least spans (1.5 and 1.6 kHz) but are based on recordings made over a range of only 9.5 and 6.4°C. The continuities of the trendlines reflect important differences in the continuities of the calling songs (see key in Fig. 4). Lines for species of the *exigua* group end in triangles; for the *delicatula* group, in circles; for the *litarena* group, in tipped squares. Lines for species without sister species in the region end in a square (*fultoni*) or open symbols (*calusa* and *imitator*). In the key, species are listed in the left-to-right order of their trendlines. Formulas for trendlines are in Table 6. Only for *delicatula* do the data appear nonlinear (see Fig. 8).

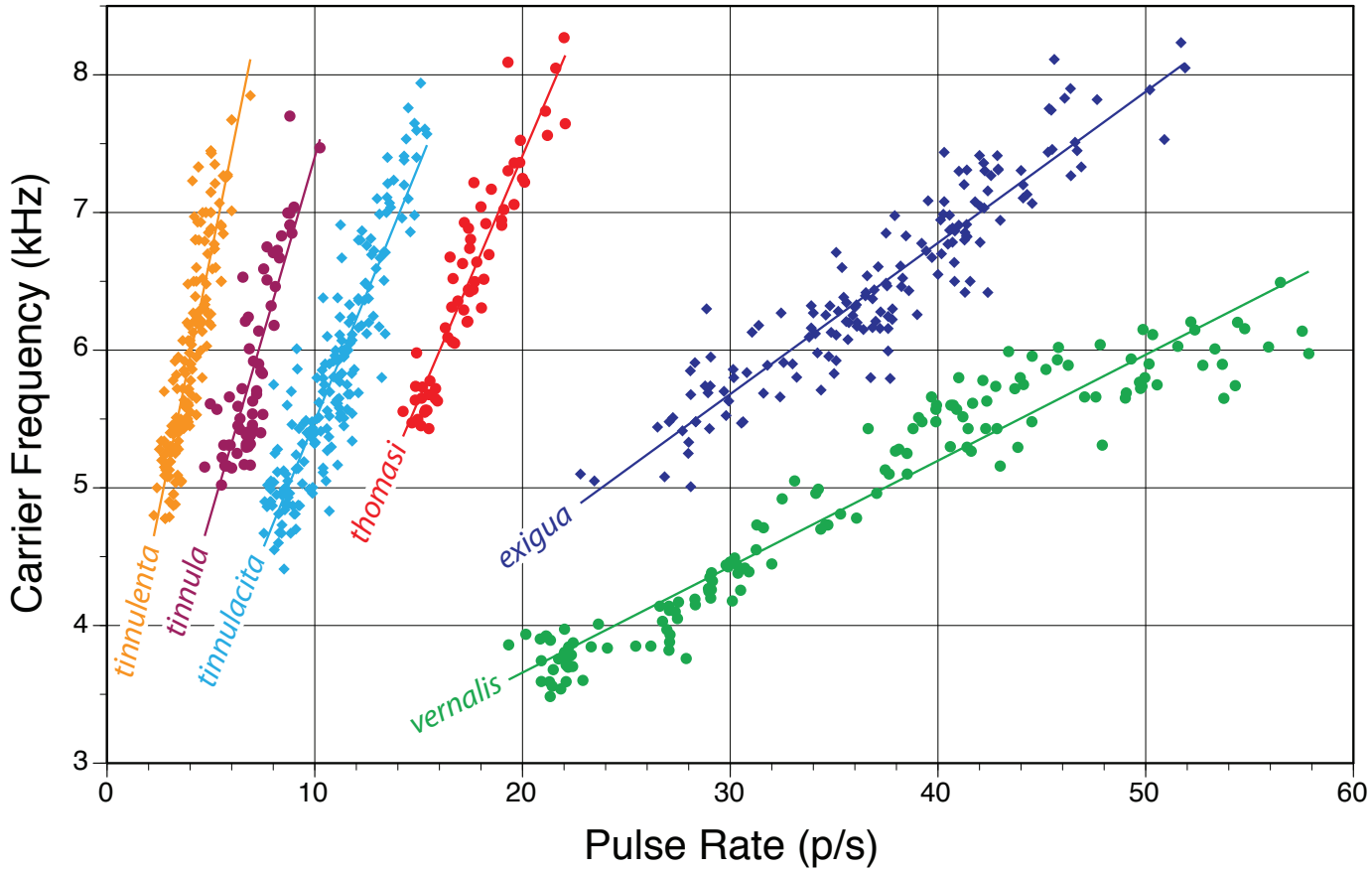


Fig. 8. Carrier frequency *vs* pulse rate pairs as an aid to identifying six *Anaxipha* species that produce continuous calling songs — with no need that the temperature of the calling male be known! The data points are from DF recordings of the six species (n= 792). Nearly all are from the mid-Atlantic states but a few are from Georgia (details are in SM).

Pulse rate.—At every temperature at which calling occurs, pulse rate (PR) is a valuable means of identifying *Anaxipha* species. Because the downward extrapolated PR *vs* °C trendlines tend to converge at 0 p/s (Fig. 4, Table 2), the differences in PR between species with similar rates will be greater at higher temperatures. Knowing the PR without knowing the temperature of the caller is practically useless, because, except for a large gap between trillers and tinklers, the active space in Fig. 4 is pretty well filled with lines. For example, a calling song with a PR of 45 p/s and no temperature data would only eliminate five of the 13 North American *Anaxipha* species. The pulse rates of the four species with tinkling songs that occur in the same geographical area can usually be distinguished by ear (with subjective adjustments for temperature), but accurate PR determinations at carefully measured temperatures are required in many cases for the species that trill and cannot be distinguished by whether the trill is continuous or intermittent.

Using pulse rates to identify calling songs that were recorded at temperatures other than the standard 25 °C can be done by plotting them on a copy of Fig. 4 and connecting each point to 3 °C, but it can be done quicker and more accurately by using a spreadsheet-based application (SMTbl_PRcalculator).

Those wishing to record and analyze *Anaxipha* songs and lack access to specialized audio equipment and software may find help in the section on Sound Production in the field guide by Capinera *et al.* (2004).

Pulse-train phrasing.—All species that interrupt their pulse trains too frequently to be considered to have continuous calling songs have rapid pulse rates (42 to 79 p/s at 25 °C). For these six species, the phrasing of the pulse trains is an important aid to identification (Fig. 6A-F) but the six species fall into three pairs with the members of each pair sometimes difficult or impossible to identify by PT phrasing alone.

The A, B-1, and B-2 waveforms in Fig. 6 illustrate that *delicatula* and *litarena* have songs that are repetitions, at a nearly uniform rate, of pulse trains of nearly uniform lengths. In *delicatula* the PT rate is nearly always faster, the PT durations are usually shorter, and the PT intervals are relatively longer. This causes the pulse train duty cycle (PTdc) to be less than 50%. In *litarena* the PT rate is usually slower, the PT duration usually greater, and PTdc usually greater than 50%. In Florida the PT phrasing seems always to be useful in separating the two species by ear but this may not be the case in coastal North Carolina.

The 10 s song samples in Fig. 6E, F illustrate how *rosamacula* and *fultoni* may be distinguished by ear by their calling songs. In *rosamacula* nearly all intervals between pulse trains are momentary, whereas in *fultoni* few if any PT intervals would be so interpreted.

Even when samples are taken from the same locality and within a narrow range of temperatures, intraspecific and intra-individual variation in PT phrasing in these six species is so great that an attempt to quantify the phrasing and to statistically analyze the interspecific differences proved too complex to continue (SM_PTpilotStudy).

Carrier frequency.—In *Anaxipha*, as in most crickets, the CF of the calling song increases markedly with ambient temperature. Fig. 7 shows this effect but does so by using PR as a proxy for temperature.

This is valid because PR is linearly related to temperature (Table 2), and useful because it allows the CF of a recorded song to be used for identification even when temperature was poorly measured or not measured at all. The six species in Fig. 8 are five members of the *exigua* group plus *vernalis*. All six have continuous calling songs that are cleanly separated based on kHz/PR data pairs alone. The four species with the slowest pulse rates are very similar in their dominant frequencies but are well separated by their pulse rates. The two species with the highest pulse rates have almost identical PR *vs* temperature relationships but at any PR have discrete ranges of carrier frequencies.

Air temperature measurements in the field may be a poor indicator of what an individual cricket, whether a signaler or the receiver of a signal, is experiencing. For example, species of the *exigua* group often bask in sunlight, especially late in the season when air temperatures may be low, with the result that an individual's body temperature may be significantly higher than ambient air. The fact that all six northeastern species can be distinguished by the relationship between PR and CF, as illustrated in Fig. 8, suggests the crickets themselves may use that relationship to distinguish each other. A possible case in point is that *exigua* and *vernalis* have overlapping seasons of calling and call at essentially the same PR (Fig. 4). They also have the greatest differences in their CF: 1.7 kHz at 25°C (inset of Fig. 4). Of relevance here is that recent work by Mhatre & Robert (2013) has demonstrated that the tympanal ears of a tree cricket have previously unsuspected abilities to actively amplify and adaptively tune to conspecific carrier frequencies.

Key to species based primarily on calling song (for recorded songs and live males)

The following key will enable the identification of captive *Anaxipha* species by their song. Under field conditions, when the singer is not definitely known to be an *Anaxipha*, several other, unrelated, cricket species could mistakenly 'key' to an *Anaxipha* species. For example, in the mid-Atlantic region, the songs of several common *Allonemobius* species can be confused with some of the continuous-calling *Anaxipha*. The pulse rate and carrier frequency of *Allonemobius allardi* is very similar to that of *Anaxipha tinnulacita*. Similarly, *Al. tinnulus* could be confused with *An. tinnula* or *tinnulenta*, or *Al. walkeri* with *An. thomasi*. However, *Allonemobius* species nearly always call from ground level, while most *Anaxipha* call from just above to about 2m above ground level. Also, there are distinct differences in habitat preferences: most *Allonemobius* prefer low open grassland such as pasture or lawn while *Anaxipha* tend toward taller, mixed vegetation. Confusion is most likely in transitional areas such as field to woods.

1. Song continuous (pulse trains often lasting 4s or longer) 2
1′. Song intermittent (pulse trains interrupted frequently but briefly) 8
2(1). Pulse rate at 25°C greater than 40 3
2′. Pulse rate at 25°C less than 25 4
3(2). Calling season May until early August; carrier frequency *ca* 5.5 at 25°C (or see Fig. 8) ..... *vernalis*
3′. Calling season late July until end of October; carrier frequency *ca* 7.2 at 25°C (or see Fig. 8) ..... *exigua*

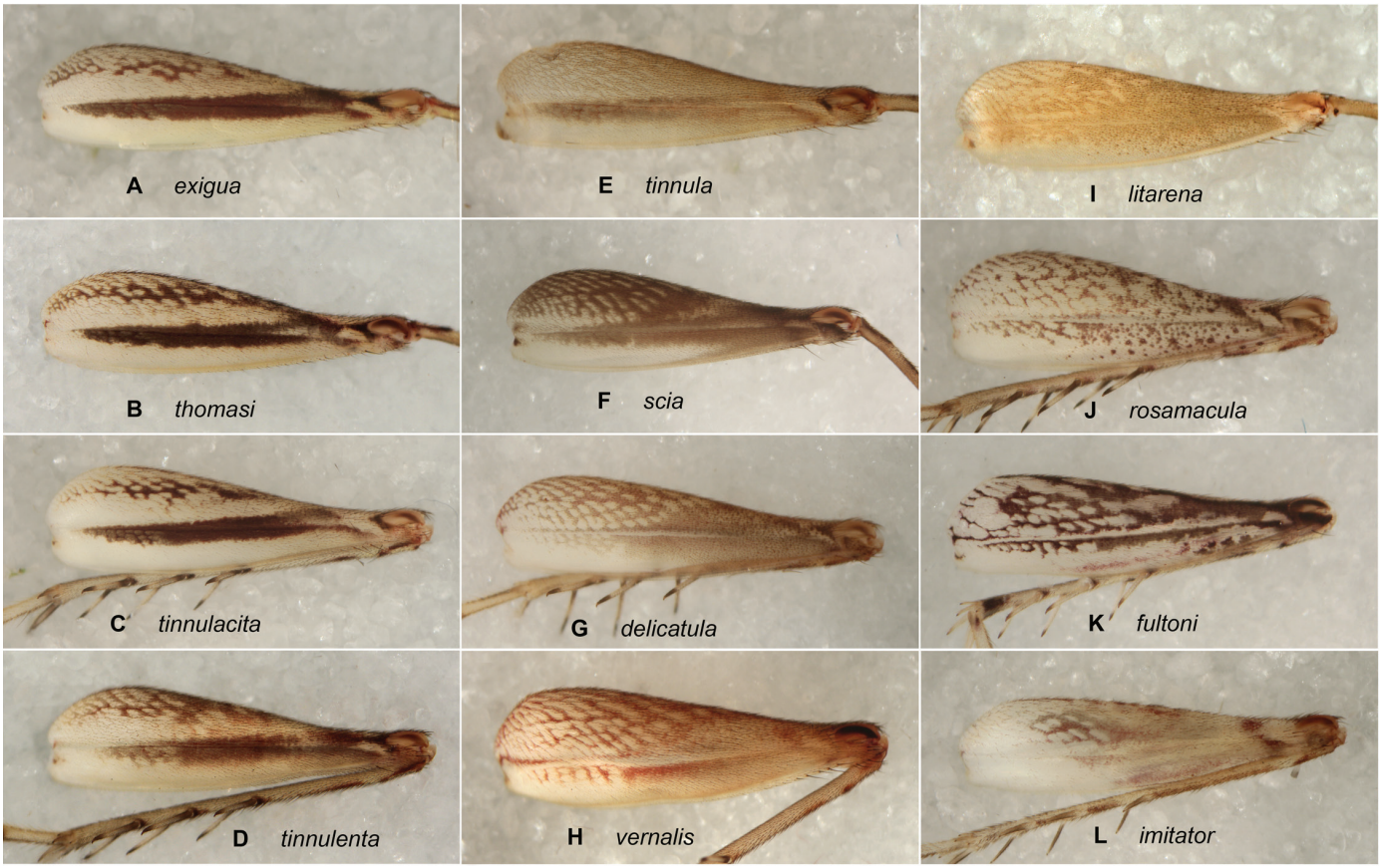


Fig. 9. A-L. Representative femoral stripes of 12 North American *Anaxipha* species. (Images not at a common scale.) Similar view of *calusa* femur is in Fig. 3C. Photos by David Funk.

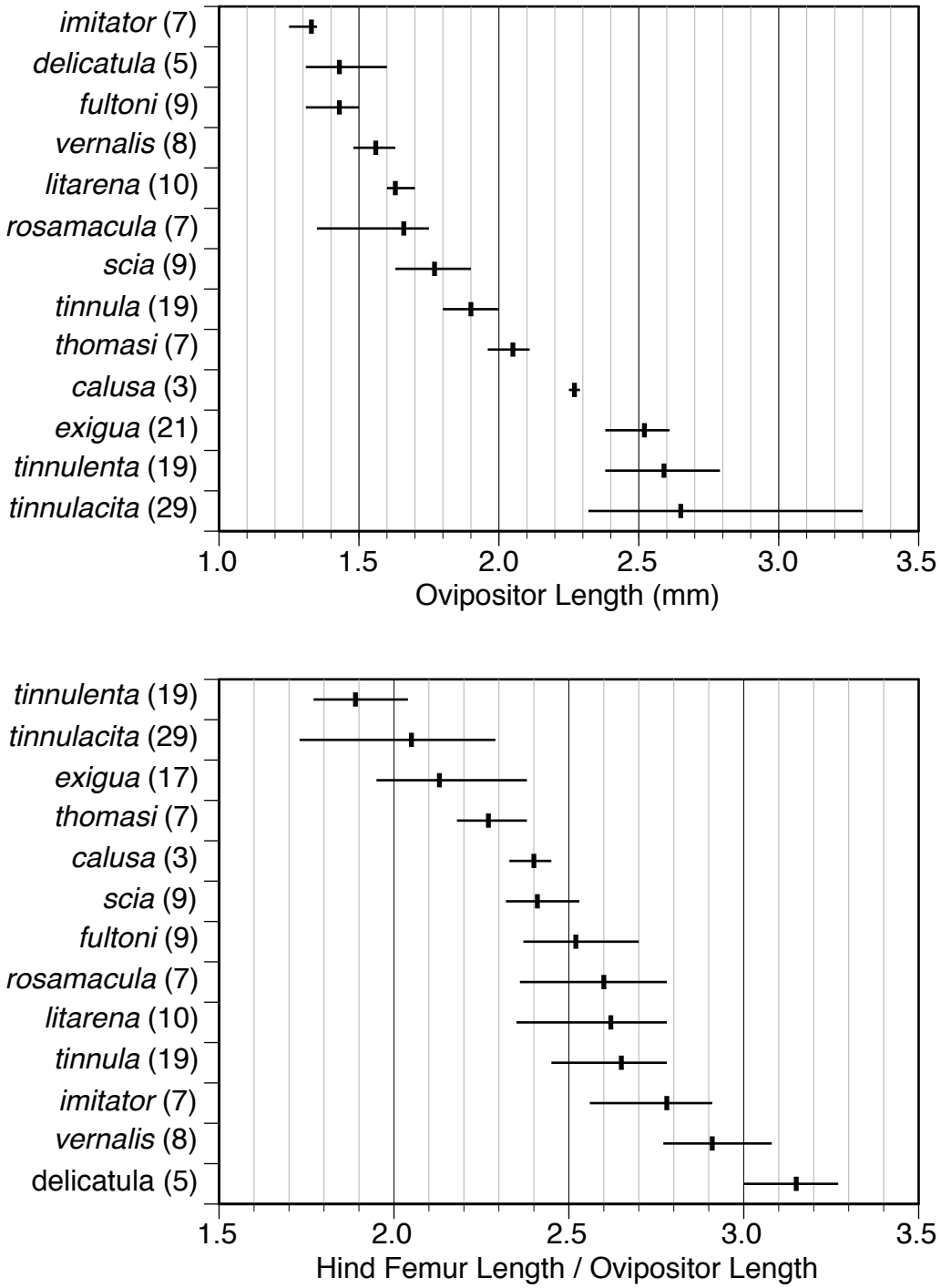


Fig. 10. Range and mean of two ovipositor-related characters of North American *Anaxipha*. Number of individuals measured is in parentheses.

4(2′). Pulse rate at 25 °C >10 (individual pulses hard to detect) 5
4′. Pulse rate at 25 °C <10 (individual pulses easy to detect) 6
5(4). Pulse rate at 25 °C greater than 17; calling from or near pines . . . . . *thomasi*
5′. Pulse rate at 25 °C less than 17; not known to call from pines . . . . . *tinnulacita*
6(4′). Pulse rate at 25 °C greater than 6.5; tidal marsh habitats . . . . . *tinnula*
6′. Pulse rate at 25 °C less than 6.5; inland and freshwater habitats 7
7(6″). Occurring only north of peninsular Florida . . . . . *tinnulenta*
7′. Occurring only in south peninsular Florida. . . . . *calusa*
8(1′). Restricted to mangrove and hardwood hammocks of s. Florida 12
8′. Not occurring in these habitats 9
9(8′) Pulse train durations irregular (Fig. 6E-F) 10
9′ Pulse train durations fairly uniform (Fig. 6A-D) 11
10(9). Most pulse train intervals ≥0.2s; PR at 25 °C *ca* 42 . . . . . *fultoni*
10′. Few pulse train intervals ≥0.2s; PR at 25 °C *ca* 66 . . . . . *rosamacula*

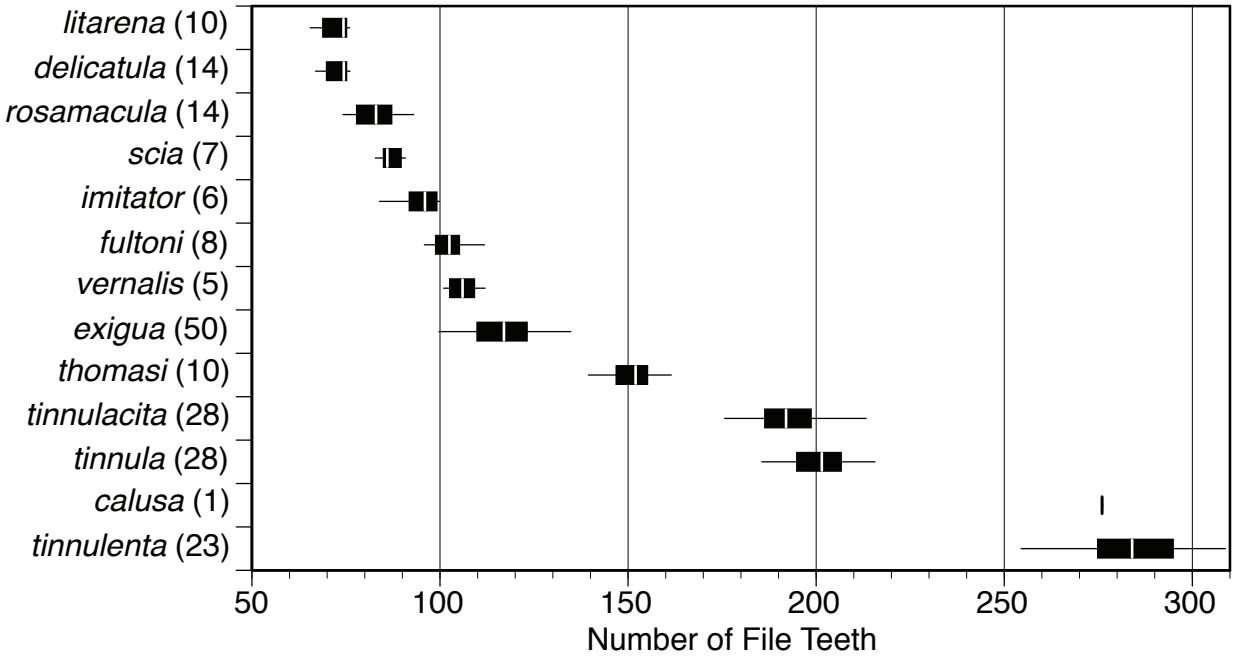


Fig. 11. Box plots of the number of teeth in the stridulatory files of North American *Anaxipha*. For each species, the vertical white line is the median value, the black box shows the 2nd and 3rd quartiles, and the horizontal black line shows the range of values. The number after each species name is the sample size. (Detailed data are in SMTbl_StridFiles.)

11(9′). Pulse rate at 25 °C *ca* 79; PTdc seldom more than 50% . . . . . *delicatula*

11′ Pulse rate at 25 °C *ca* 66; mean PTdc more than 50% . . . . . *litarena*

12(8). Mangrove tidal areas; pulse rate at 25 °C *ca* 60 . . . . . *scia*

12′ Subtropical hardwood hammocks; pulse rate at 25 °C *ca* 45 . . . . . *imitator*

Species identification based primarily on morphology

Easy to observe characters.—The presence of a conspicuous dark stripe on the lateral face of the hind femur (Fig. 9A-F) identifies an *Anaxipha* individual as being a member of the *exigua* group. This stripe is easily seen in live or freshly killed individuals, but may be obscure in older, pinned material.

Most *Anaxipha* have rather conspicuous teeth on the tarsal claws (although a high quality stereomicroscope at 50× or higher may be required to observe them). In one species (*tinnula*) these teeth are absent and the surface of the claw is smooth or only slightly roughened Fig. 2C). In another species (*scia*) the teeth are present but small (Fig. 2B). With the exception of some *tinnulacita* individuals from mangrove habitat in southern Florida, all other North American *Anaxipha* have well developed teeth on the claws as in Fig. 2A.

On the six large spines on the distal half of the hind tibia there is, in most North American *Anaxipha* species, a fringe of long hairs arranged in a single line on the side nearest the tibia (Fig. 2D). This fringe is absent in *fultoni*, *imitator* and *calusa*. In some instances, especially older museum specimens of species that have the fringe, many of these hairs may have been broken off. However, there is almost always some remnant of them.

The length of the ovipositor varies among species and can be useful in distinguishing females (Fig. 2E shows method of measurement). Measuring the length of the ovipositor relative to the length of the hind femur is a good way to normalize for overall body size (Fig. 10).

The importance of macropters to identification is that in *imitator*

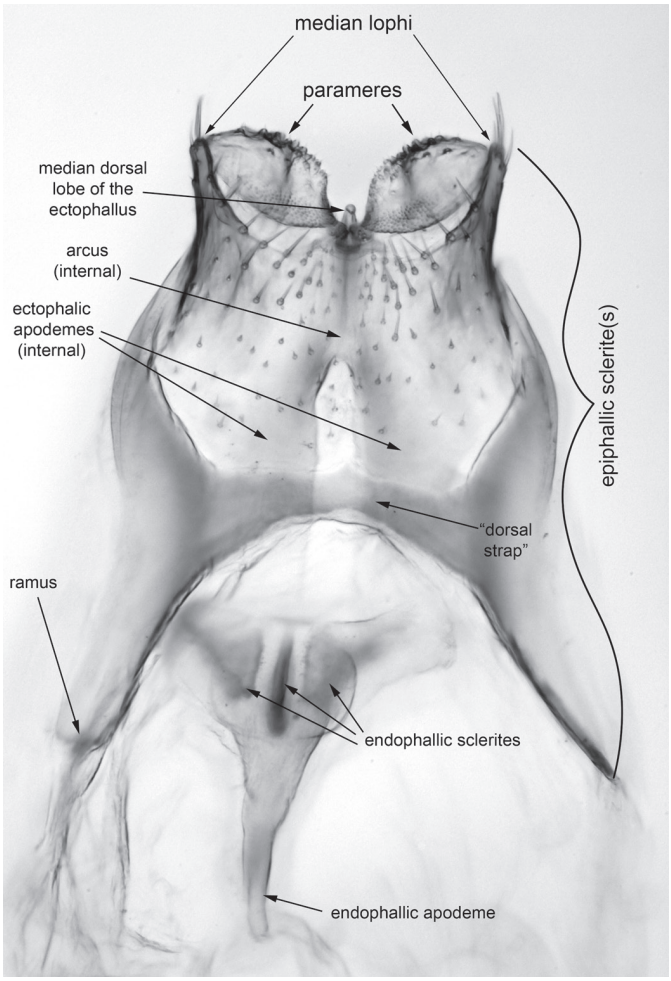


Fig. 12. Male genitalia (dorsal view) of *Anaxipha vernalis* with pertinent structures labeled. Terminology follows that of Desutter (1987).

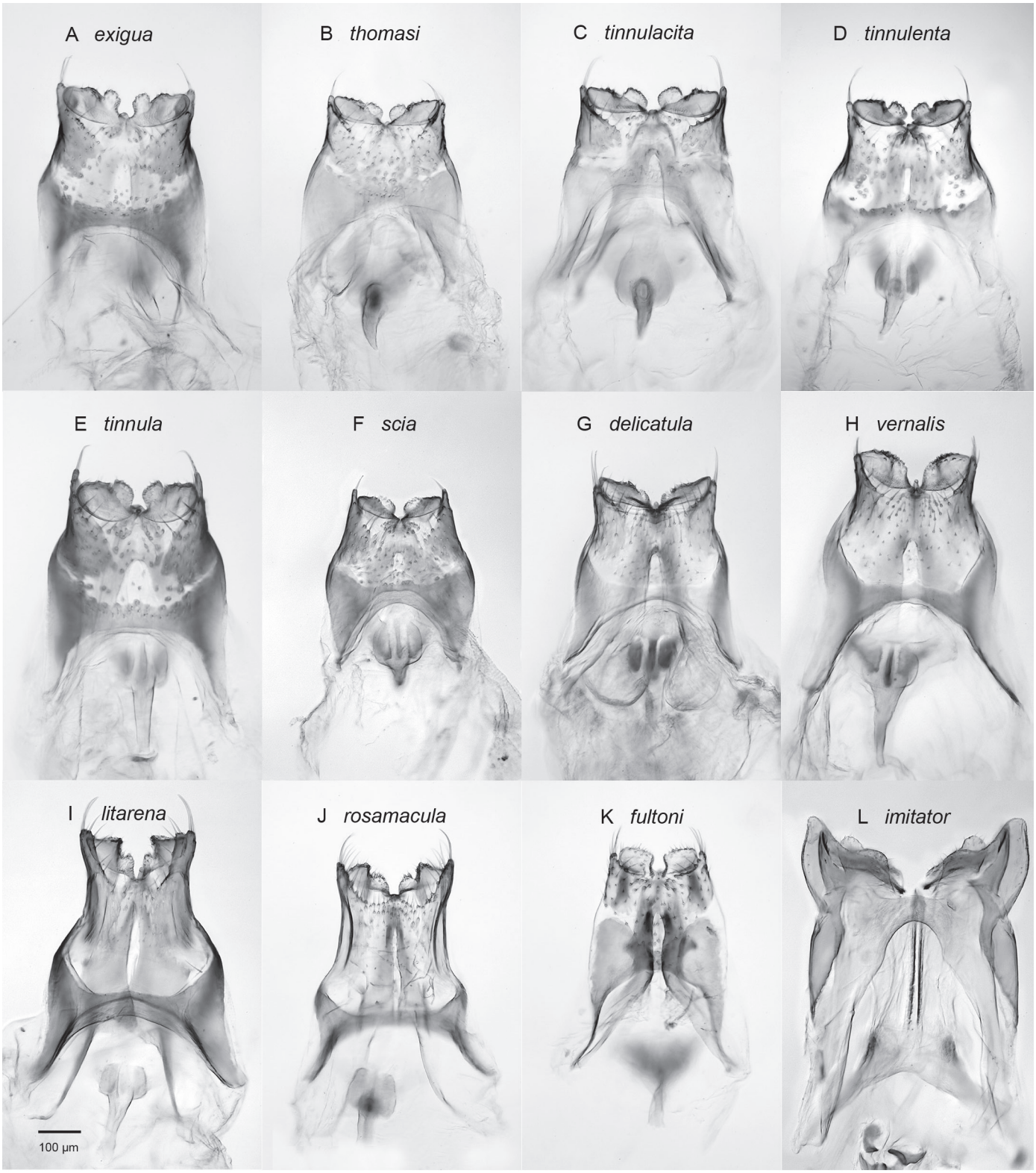


Fig. 13 A-L. Representative male genitalia of North American *Anaxipha* species (for *calusa;* see Fig 3A). All images at scale at lower left. A-F. *exigua* group. G-H. *delicatula* group. I-J. *litarena* group. K. *fultoni*. L. *imitator*. Fig. 3A shows genitalia of *calusa*. (Additional images are in SMFig_Genitalia.)(Preparations and photos by David Funk.)

and *calusa* only macropters are known and that in *delicatula* and *fultoni* they are sometimes numerous at light but rarely collected otherwise.

Stridulatory file characters.—The number of teeth on the stridulatory file is an important character for distinguishing many *Anaxipha* species — perhaps the only way to reliably distinguish most members of the *exigua* group in the absence of calling song data. Enumeration requires removal of the right forewing, making at least a temporary slide mount and observation under a compound microscope at ≥100×. Fig. 11 illustrates the distribution of tooth counts among the North American species.

Male genitalia.—Characters of the male genitalia are useful for identification to at least the level of species group (Figs 12, 13). They are best observed following dissection and clearing with KOH. For the purposes of illustration, we made temporary slide mounts and photographed under a compound microscope in dorsal aspect. However, in practice it is best to view specimens from several angles in liquid under a good stereomicroscope because some structures (especially the parameres) sometimes distort or rotate. It is a good practice to evert the genitalia of freshly killed males which often obviates the need for dissection. When dissection and clearing are necessary, removal is much easier (and less destructive) if the genitalia are already everted.

Key to species based primarily on morphology

1. Basal segment of hind tarsus ≤1× as long as the other two combined. Spines of hind tibiae with or without a fringe of long hairs (Fig. 2D). Lophi of male genitalia narrow and pointed in dorsal view, bearing stout setae at their apices (Fig. 13A-K). Usually micropterous. Distribution not limited to southern tip of FL 2
1′. Basal segment of hind tarsus distinctly longer (about 1.5×) than the other two combined. No fringe of long hairs on the spines of the hind tibiae. Lophi of male genitalia without stout setae at their apices; either broad and flat, resembling cat's ears in dorsal view (Fig. 13L) or narrow and pointed (Fig. 3A). Always macropterous. Distribution limited to southern FL 12
2(1′). Hind femur usually with a broad dark stripe on the lateral face along the sulcus (Fig. 9A-F). Stripe usually with margins entire (obscure in *scia*) and sharply contrasting against background (may be faint in *tinnula*). Parameres on male genitalia with distinct median lobes that protrude caudally as far or further than the remaining portion of parameres (Fig. 13A) . . . . . *exigua* group 3
2′. Hind femur without a broad dark stripe along the sulcus on lateral face but sometimes (in *fultoni*) with a narrow line having jagged margins or a row of confluent spots. Parameres on male genitalia without distinct median lobes, or if lobes present (Fig. 13I–J), protruding well short of the remaining portion of parameres 8
3(2). Stridulatory file on male right tegmen with about 87 teeth (range 82 to 91). Stripe on hind femur with indistinct margins (Fig. 9F). Length of ovipositor 1.6-1.9 mm. Tarsal claws with small teeth (Fig. 2B). Song an intermittent trill (Fig. 6C). Distribution limited to mangrove areas of southern coastal FL . . . . . *scia*
3′. Stridulatory file with ≥100 teeth. Stripe on hind femur with distinct margins (Fig. 9A-E). Tarsal claw dentition variable. Length of ovipositor usually >1.9 mm. Song a continuous trill (or tinkle). Distribution not limited to coastal mangrove 4
4(3′). Tarsal claws without teeth (Fig. 2C). Stridulatory file with about 200 teeth (range 184-217). Length of ovipositor 1.8-2.0 mm. Ratio of length of hind femur to ovipositor (HF/O) 2.4-2.8. Stripe on hind femur often faint. Distribution limited to tidal marshes from NJ to northern FL. Song a tinkling trill at a pulse rate of 8 p/s at 25°C. . . . . *tinnula*
4′. Tarsal claws usually with distinct teeth (Fig. 2A; lacking in some *tinnulacita* from coastal south FL). Stridulatory file variable. Length of ovipositor usually >2.0 mm. If ovipositor <2.0 mm, HF/O <2.4. Stripe on hind femur always distinct. Distribution not limited to tidal marshes. Song variable 5
5(4′). Stridulatory file with about 150 teeth (range 139-162). Length of ovipositor <2.2 mm. Song a continuous trill; pulse rate 21 p/s at 25°C. Found only on or under pines. . . . . *thomasi*
5′. Stridulatory file with <135 or >175. Length of ovipositor >2.3 mm. Pulse rate of song >40 or <15/s at 25°C. Not restricted to pine habitat 6
6(5′). Stridulatory file with about 117 teeth (range 100-135). Song a fast trill, pulse rate 44 p/s at 25°C . . . . . *exigua*
6′. Stridulatory file with >175 teeth (range 176-309). Pulse rate of song <15 p/s at 25°C 7
7(6′). Stridulatory file with about 190 teeth (range 176-213). Song a fast tinkling; pulse rate 13 p/s at 25°C . . . . . *tinnulacita*
7′. Stridulatory file with about 280 teeth (range 253–309). Song a slow tinkling; pulse rate 5 p/s at 25°C . . . . . *tinnulenta*
8(2′). No fringe of long setae on the spines of the hind tibia. Parameres of male genitalia without median lobes; lateral areas of epiphallus unsclerotized; dorsal strap broad with distinctively shaped area of sclerotization (Fig. 13K). Pale, with sharply delineated pattern of dark brown on head, pronotum and legs (Fig. 2H) . . . . . *fultoni*
8′. Spines of hind tibia bearing a row of long, thin setae on the side nearest the tibia (Fig. 2D). Parameres with (Fig. 13I, J) or without (Fig. 13G, H) median lobe; epiphallus with strong lateral sclerotization; dorsal strap narrow. Straw-color to pale brown, with more or less obscured brownish or pinkish pattern 9
9(8′). Parameres with distinct, recessed median lobes (Fig. 13 I-J). Ratio of length of hind femur to ovipositor (HF/O) <2.8 (*litarena* spp. group). 10
9′. Parameres without median lobes (Fig. 13G-H). HF/O >2.75 . . . . . (*delicatula* group) 11
10(9). Sclerotized baso-lateral area of epiphallus narrower; distinct ridge at base of lophi (Fig. 13J). Stridulatory file with about 83 teeth (range 74-93). Markings on body often pinkish. Range, inland habitat from southeastern TX to southern SC . . . . . *rosamacula*
10′. Sclerotized baso-lateral area of epiphallus broader; without distinct ridge at base of lophi (Fig. 13I). Stridulatory file with about 72 teeth (range 65-77). Range, coastal habitat from TX to NC exclusive of southern FL. . . . . *litarena*

11(9′). Stridulatory file with about 73 teeth (range 66-77). Song consisting of more or less regular chirps; pulse rate 79 p/s at 25°C. Ovipositor shorter relative to hind femur, HF/O >3.0. Range southeastern LA through FL and north to NC along the Atlantic coast . . . . . *delicatula*

11′. Stridulatory file with about 106 teeth (range 102-112). Song a continuous trill; pulse rate 44 p/s at 25°C. Ovipositor longer relative to hind femur, HF/O <3.1. Range eastern KS to the mid-Atlantic states. . . . . *vernalis*

12. Side of body in both sexes with a broad dark brown stripe extending from eye across lateral field of pronotum, tegmen and exposed portion of folded wing (SMFig_Portraits). No obvious tegminal maculation in male. Lophi of male genitalia broad and flat, resembling cat's ears in dorsal view (Fig. 13L). Stridulatory file with about 94 teeth (range 84-100). Length of ovipositor <1.4 mm . . . . . *imitator*

12′. Without a broad dark brown lateral stripe as above. Male with distinctive dark maculation on tegminae (Fig. 2B). Lophi of male genitalia narrow and pointed, extending well beyond parameres (Fig. 3A). Stridulatory file with about 276 teeth (Fig. 3F). Length of ovipositor >2.0 mm . . . . . *calusa*

Relationships among species

Mating and mating tests.—When DF first became interested in crickets and their calling songs he soon saw the remarkable courtship and mating that generally follows when a female cricket is attracted to a calling male (Alexander & Otte 1967). This led him to observe carefully what he saw and to start making notable photographs of the details. His initial studies were of the larger species in his area — the oecanthines *Oecanthus* spp. and *Neoxabea bipunctata*; the eneopterines *Orocharis saltator* and *Hapithus agitator*; and the nemobiines *Allonemobius fasciatus* and *allardi* (results for oecanthines and *Orocharis* reported in Funk 1989). Later he did an exhaustive study, in microscopic detail, of the mating behavior and reproductive structures of the trigonidiine *Phyllopalpus pulchellus* (SM_PhyllopalpusMating). Thus when DF became aware that he had in abundance, in the area that he lived, the four inland *Anaxipha* species of the *exigua* group that Fulton (1956) could not distinguish morphologically, he thought he might learn something of their reproductive isolation by studying the details of their mating behavior and comparing the results of intra and interspecific pairings.

The pattern of *Anaxipha* mating as observed in the laboratory for six of the 13 North American species is that courtship is initiated following antennal contact between a male and a female. (It is presumed that such a female will usually have been attracted to the male's vicinity by his calling song.) Courting males sing and this song does not differ in pulse rate or dominant frequency from the male's calling song (although the phrasing may be different). If a female remains attentive, the male soon extrudes a small spermatophore. After a maturation period (generally 10 to 20 minutes) he encourages the female to mount him whereupon he inserts the sperm tube into her genital opening, leaving the ampulla hanging free. She then dismounts taking the spermatophore with her and the male then extrudes a second, much larger spermatophore (Fig. 2F). This pattern of producing an initial spermatophore with a very small ampulla, followed by a second spermatophore with a much larger ampulla, seems to be the norm for trigs generally. For the Hawaiian trig, *Laupala pacifica*, deCarvalho and Shaw (2005) have termed these two types micro- and macro-spermatophores. *Anaxipha* males have not been observed to produce a macrospermatophore without having first transferred a microspermatophore. In *Phyllopalpus pulchellus* the ampullae of microspermatophores contain no sperm, while those of macrospermatophores contain many (up to 35,000; SM_PhyllopalpusMating). A similar situation probably exists in *Anaxipha*. If a female remains attentive after receiving a macrospermatophore, the male will usually produce a second microspermatophore, followed by another macrospermatophore. DF has not observed more than two of each type transferred in a single bout in *Anaxipha*, but up to three rounds were observed in *Phyllopalpus*.

It is common in the mid-Atlantic region for as many as three *exigua*-group species to be found in very close proximity (*i.e.*, within centimeters of each other). Although the rather large differences in calling song are presumed to minimize long-distance attraction between heterospecifics (first barrier to hybridization), individuals in these habitats are still likely to encounter one another if only by chance. Since antennal contact alone can result in the initiation of courtship of conspecifics, DF decided to test whether encounters by heterospecifics in the lab might result in courtship, spermatophore production and/or mating.

In mating tests among the four inland species of the *exigua* group, DF tried all possible pairings one or more times. In 8 of 16 attempted heterospecific pairings males sang following antennal contact, but in only two cases was a spermatophore produced. These two pairings went to the stage of microspermatophore transfer and involved males of *thomasi* and females of *tinnulenta* and *tinnulacita*. Unlike the other three species, *thomasi* is strongly restricted to pines. In our experience, the only other *exigua*-group species found in this habitat along with *thomasi* is *exigua*. Of the eight conspecific pairings attempted, six resulted in spermatophore production but only two were allowed to continue through spermatophore transfer (SMTbl_MatingTests).

Relationships among species as revealed by morphology.—The 13 North American *Anaxipha* species recognized herein can be divided into six groups based on morphology, three of which are monotypic.

Anaxipha imitator and *calusa* are the only North American species with the basal segment of the hind tarsus distinctly longer than segment 2+3 combined, a condition shared with some (most?) other Neotropical species. The male genitalia are quite different from other North American species. Both lack the stout terminal setae present in other North American species (Fig. 13L); in other respects *imitator* and *calusa* show little resemblance to each other.

Like the remaining North American species, *fultoni* has a shortened first segment of the hind tarsus, but the spines of the hind tibiae lack the distinctive row of long, fine setae that characterize the remaining species (Fig. 2D). The shape and pattern of sclerotization of the epiphallus is also distinct (Fig. 13K).

The remaining three groups are distinguished primarily by differences in the male genitalia and coloration of the hind femur. Members of the *exigua* group, which includes *exigua*, *thomasi*, *tinnulacita*, *tinnula*, *tinnulenta* and *scia*, all have very similar male genitalia with distinct median lobes on the parameres that protrude caudally as far or further than the remainder of the paramere (Fig. 13A-F). *Exigua*-group species generally have a distinct dark stripe on the hind femur (Fig. 9A-F). This stripe usually has distinct margins (obscure in *scia*) and contrasts strongly with the background coloration (but may be faint in *tinnula* and tends to fade in older pinned specimens of all species). Males of *exigua*-group species can be distinguished

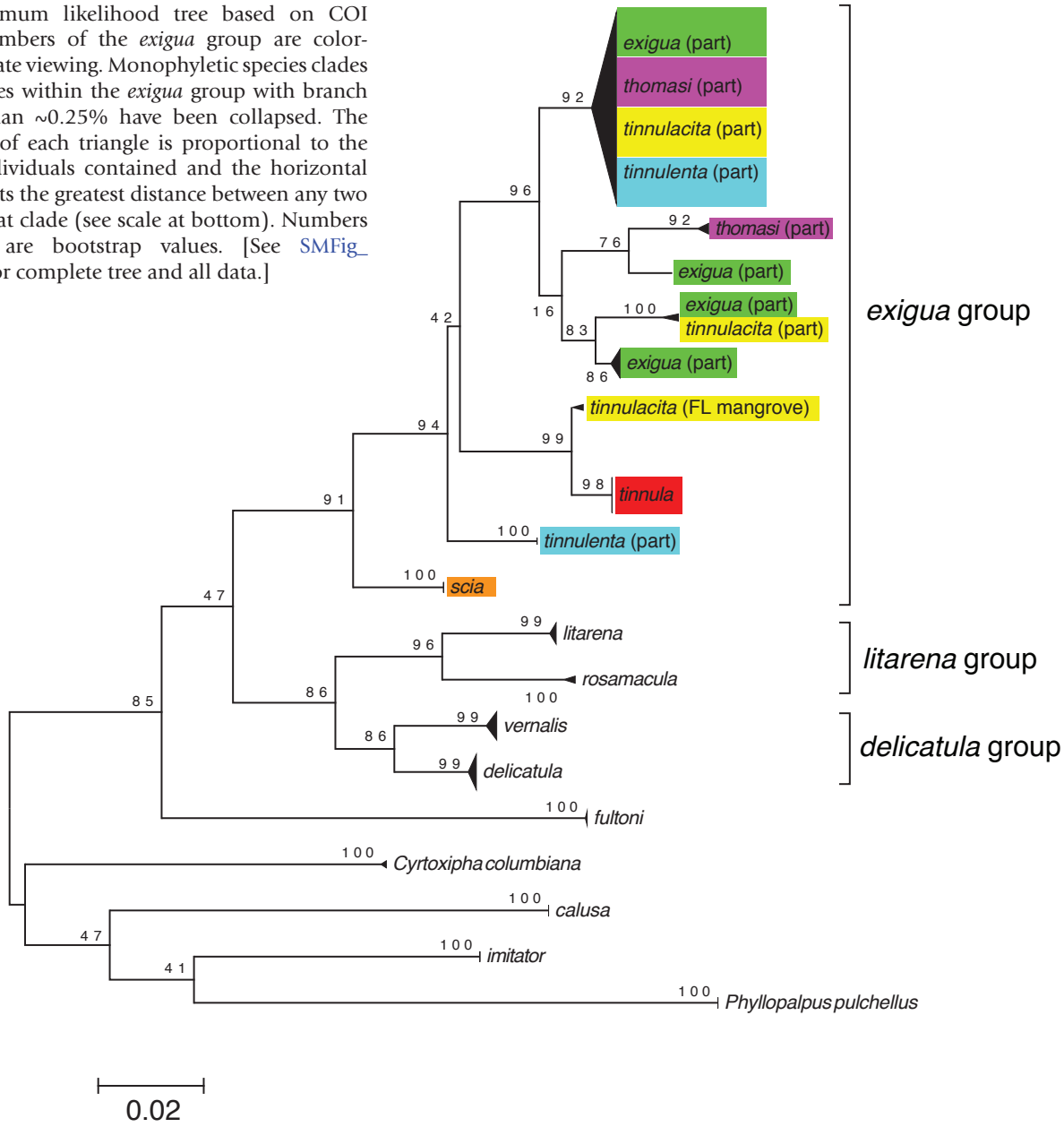


Fig. 14. Maximum likelihood tree based on COI sequences. Members of the *exigua* group are color-coded to facilitate viewing. Monophyletic species clades as well as clades within the *exigua* group with branch lengths less than ~0.25% have been collapsed. The vertical extent of each triangle is proportional to the number of individuals contained and the horizontal extent represents the greatest distance between any two members of that clade (see scale at bottom). Numbers on branches are bootstrap values. [See SMFig_MaxLikliTree for complete tree and all data.]

by calling song and the number of teeth on the stridulatory file. Females of some species can be distinguished by ovipositor length and tarsal claw dentition, but no reliable characters have been found to distinguish those of *exigua*, *tinnulacita* and *tinnulenta*.

The *litarena* group includes *litarena* and *rosamacula*. Male genitalia have a distinctive shape, with recessed median lobes on the parameres (Fig. 13I-J). Males can be distinguished by the number of teeth on the stridulatory file and minor differences in the genitalia. Females may be separated by differences in body coloration.

The *delicatula* group includes *delicatula* and *vernalis*. The male genitalia lack distinctive median lobes on the parameres but otherwise resemble those of the *exigua* group. Males of the two can be distinguished by the number of teeth on the stridulatory file (Fig. 11) and females, in most cases, by the relative length of the ovipositor (Fig. 10).

Identification and relationships among species based on DNA barcoding.—DNA barcoding involves the sequencing of short, standardized gene regions to aid in species identification and discovery. The term barcoding gene loosely describes a fragment of DNA that has low sequence divergence within species but high divergence among species, from which unknown samples can be placed accurately into species groups simply by calculating their pairwise genetic distances (Hebert *et al.* 2003).

A 658-bp region of the mitochondrial cytochrome c oxidase I (COI) is currently the most commonly used gene for barcoding animals and major efforts are underway to construct reference libraries of sequences for known species (Ratnasingham & Hebert 2007). Many studies have shown that intraspecific differences in COI sequences typically fall in the range of 0-2%, whereas interspecific comparisons are usually characterized by >5% divergence. The use of COI for accurate species identification depends on the existence of this "barcoding gap". Some studies have shown more than 95% of species in test assemblages possess distinctive COI sequences (*e.g.*, Hebert *et al.* 2003).

COI was sequenced for 132 of our specimens including representatives of all 13 of the North American *Anaxipha* plus two other North American trigs, *Phyllopalpus pulchellus* and *Cyrtoxipha columbiana*. Table 3 shows minimum and maximum intra- and

Table 3. Summary of intra- and inter-specific K-2P distances calculated from COI sequences. (Complete data are in SMTbls_COIspecimens.)

Species	(Species group)	Number of individuals sequenced	Geographic coverage (state)	Minimum intraspecific distance (%)	Maximum intraspecific distance (%)	Minumum interspecific distance (%)	Closest species
exigua	(*exigua*)	20	PA,GA	0	3.8	0.31	*thomasi*
thomasi	(*exigua*)	18	PA,GA	0	4.8	0.15	*tinnulenta*
tinnulacita	(*exigua*)	18	PA,MD,FL	0	5.46	0	*tinnulenta*
tinnula	(*exigua*)	10	MD,NC	0	0.15	0.77	*tinnulacita*
tinnulenta	(*exigua*)	16	PA,MD	0	5.48	0	*tinnulacita*
scia	(*exigua*)	3	FL	0	0	5.78	*tinnula*
litarena	(*litarena*)	6	FL	0	0.48	4.26	*rosamacula*
rosamacula	(*litarena*)	2	FL	0.37	0.37	4.26	*litarena*
vernalis	(*delicatula*)	8	PA,MD	0	0.31	4.8	*delicatula*
delicatula	(*delicatula*)	10	NC,FL	0	0.62	4.8	*vernalis*
fultoni	(*fultoni*)	4	FL	0	0.15	11.75	*rosamacula*
calusa	(*calusa*)	3	FL	0	0	13.08	*exigua*
imitator	(*imitator*)	3	FL	0	0	12.27	*rosamacula*

minimum inter-specific Kimura-2-Parameter (K2P) distances. For 10 of the 15 species maximum intraspecific distances were less than 0.7% while minimum interspecific values were >4%, thus barcoding might enable accurate identification of these species. However, most members of the *exigua* group were not resolved by COI. For *tinnula*, only two haplotypes were found (differing by 0.15%), but minimum interspecific distance was only slightly higher (0.77%). For *exigua*, *thomasi*, *tinnulacita* and *tinnulenta* minimum interspecific distances were considerably *lower* than maximum intraspecific comparisons. In the case of *tinnulacita* and *tinnulenta*, individuals were found with identical haplotypes.

Three types of trees were constructed using MEGA5 software: Neighbor-joining, Maximum Likelihood and Maximum Parsimony. In all trees, *Phyllopalpus pulchellus*, *Cyrtoxipha columbiana* and *Anaxipha imitator* and *A. calusa* appeared strongly differentiated from each other and from the remaining *Anaxipha* species. Branching topology differed among methods but in each case confidence was low, as indicated by low bootstrap values. However, these trees reinforce the idea that *Anaxipha* as currently recognized is likely polyphyletic. For the remaining North American *Anaxipha* species the three methods rendered similar results. The Maximum Likelihood tree (based on the method of Tamura & Nei 1993) is illustrated in Fig. 14. *Anaxipha fultoni* is well differentiated from the remaining *Anaxipha*. The *delicatula* and *litarena* groups are well supported, as is the exigua group. Within the *exigua* group, *scia* appears to be well differentiated from the other *exigua* group species, and the 10 *tinnula* specimens form a coherent group, but COI relationships among the remaining *exigua* group specimens are not consistent with the species concepts presented in this paper. These include *exigua*, *thomasi*, *tinnulacita* and *tinnulenta* (all previously included under *exigua*). K2P distances among species in this group are quite small — in a few cases individuals we consider different species have identical COI haplotypes. Conversely, there is considerable diversity within our species. Thus, all four appear polyphyletic in this tree.

The inability to resolve closely related species using COI is not unique to the *Anaxipha exigua* group. A similar situation has been documented in other insect taxa (*e.g.*, blow flies; Whitworth et al. 2007). One of us (DF) has discovered identical COI haplotypes in specimens belonging to different but closely related species of the nemobiine cricket genera *Allonemobius* (*allardi* and *walkeri*) and *Eunemobius* (*carolinus* and *melodius*) (unpublished; sequences public and available at BOLD). Shaw (2002) reported that mitochondrial markers gave a misleading picture of evolution in Hawaiian *Laupala* (Trigonidiinae) when compared to nuclear DNA and morphological evidence, and that some patterns of mtDNA variation were likely the result of persistent interspecific hybridization during the history of this group. Hurst and Jiggins (2005) suggested that cases such as these might be the result of endosymbiont-driven introgression. Endosymbionts such as *Wolbachia* are common in crickets generally (although they have yet to be documented in *Anaxipha*). As a rule, these microorganisms are transmitted vertically and thus are in linkage disequilibrium with maternally-inherited mtDNA in their hosts. New infections among populations (by occasional movement of hosts) or even between sibling species (via hybridization events) can result in indirect selection on mtDNA, leading to major changes in the patterns of mitochondrial diversity. The direction of these changes depends on the direct effects of endosymbionts (*e.g.*, cytoplasmic incompatibility, male-killing).

Indirect selection on mtDNA resulting from endosymbionts is predicted to result in patterns similar to what we observe in *Anaxipha*, that is, COI barcoding effectively places individuals to genus and separates more distantly related congeners, but may fail to resolve very closely related sympatric species. Preliminary AFLP (amplified fragment length polymorphism) data taken by Tamra Mendelson (unpublished) using nuclear DNA from a subset of our specimens suggests that each of our *exigua* group species really is monophyletic. Any future attempts to assess phylogenetic relationships between closely related *Anaxipha* species and populations from molecular data should include nuclear markers.

Mechanics of sound production in *Anaxipha*

Introduction.—Terminology and information about cricket sound production that was essential to identifying *Anaxipha* species by their calling songs was introduced in an earlier section. These eight features of song production in *Anaxipha* were not needed there but are basic to the subject of this section.

(1) Unlike those cricket taxa whose sound mechanics have been most thoroughly studied, which usually call from the ground and hold their wings at an angle of about 45° to the body axis when calling, *Anaxipha* species usually call from foliage and hold their forewings approximately perpendicular to the body axis while calling (Fig. 2F and SMvideo1_calusa). This near-perpendicular position of the wings during calling is also characteristic of other crickets that call from foliage (Eneopterinae, Oecanthinae) and permits the calling cricket to position itself at the edge of a leaf (or in a leaf

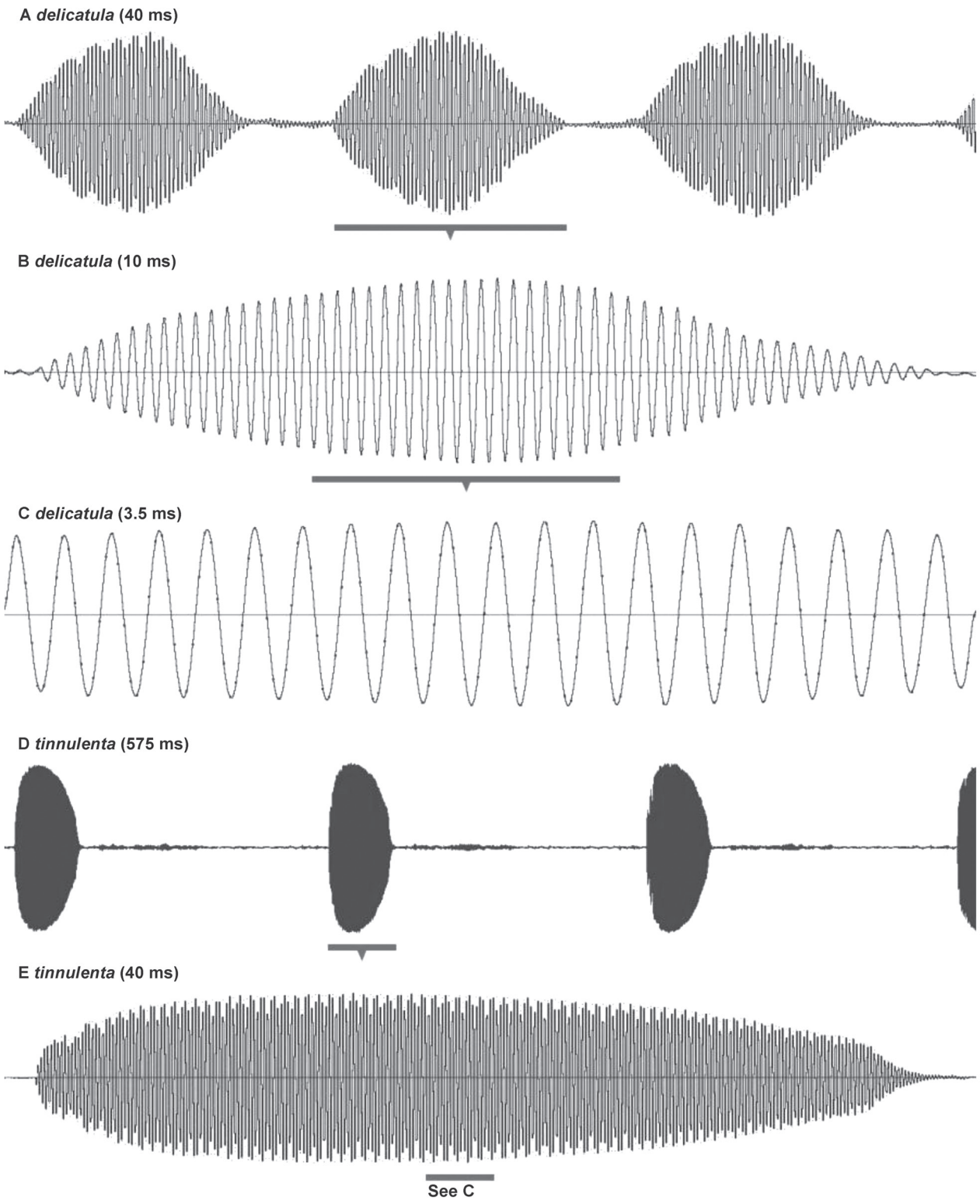


Fig. 15. Waveforms in calling songs of the *Anaxipha* species with the highest and lowest pulse rates (both at about 25°C). Duration of each waveform is to the right of the species name. Horizontal bars with arrows beneath waveforms show the portion of each waveform that is expanded by the waveform below. A-C, *delicatula* (MLNS 121494), 76 p/s, 5.64 kHz. A, Three pulse periods B, One pulse. C, Twenty fundamental vibrations. D-E, *tinnulenta* (R09_0756DF), 5.4 p/s, 6.94 kHz. D.Three pulse periods. E, One pulse. The bar beneath this wave form is 2.9 ms, the duration of the waveform that would produce 20 sine waves, the equivalent of C. (Note that waveforms A and E are the same duration.)

notch or a leaf hole) and call with the dorsal surfaces of the wings continuing the plane of the leaf, a behavior that increases the power output and range of the song (Forrest 1982, 1991).

(2) In most crickets, including *Anaxipha*, but with exceptions in Mogoplistinae and Gryllotalpidae (Masaki *et al.* 1987, Forrest 1987), the right forewing is nearly always above the left when the wings are at rest.

(3) Both male forewings generally have files, and when the files of the two wings differ, the file of the right wing (the wing on top at rest) is the better developed one and is the one that functions in sound production (Masaki *et al.* 1987).

(4) Each pulse in a cricket calling song corresponds to a wing closure — *i.e.*, when the distal portions of the raised wings move mesad; wing opening is silent or nearly so (Pierce 1948 and all later authors).

(5) The teeth of cricket stridulatory files project toward the anal margin of the wing. Thus when the scraper is engaged with the file during wing closure, the scraper is moving "against the grain" of the teeth and the resistance to moving is greater than it would be if the file were engaged during wing opening (Walker & Carlysle 1975).

(6) Pulses in cricket calling songs are nearly pure tones — *i.e.*, their waveforms are nearly sinusoidal, showing no evidence of strong overtones (Fig. 15) (Pasquinelly & Busnel 1954, Dumortier 1963, and all later authors).

(7) The instantaneous frequency during a calling song pulse may remain almost constant or change slowly (usually downward) during the main portion of the pulse (audiospectrograms in Leroy 1966 and in SINA 2014).

(8) During the main portion of the pulse, impacts of the scraper on the file teeth are synchronous with the fundamental oscillations of the song and hence with the principal vibrating areas of the wings (Kreidl & Regen 1905 according to Dumortier 1963, Pierce 1948, Walker 1962b, Dumortier 1963, Nocke 1971, Elliott & Koch 1985, Montealegre-Z *et al.* 2011).

Synchronization of forewing oscillations and file tooth impacts.—How insects as small as crickets can produce sounds that are nearly pure in frequency has long been of interest and talented researchers have studied the problem using increasingly sophisticated physical and electronic methods (*e.g.*, Nocke 1971, Sismondo 1979, Koch *et al.* 1988, Bennet-Clark 1999, Bennet-Clark & Bailey 2002, Montealegre-Z *et al.* 2009, Mhatre *et al.* 2012, Robillard *et al.* 2013). Most of these authors relied on crickets that are easily reared or otherwise conveniently available for laboratory studies and few were concerned with the effects of temperatures on the frequencies produced. In the following account we briefly review the history of these studies and the background for our conclusion that CF control in *Anaxipha* is different from that of most crickets previously studied yet probably similar to CF control in most crickets.

Currently the most widely accepted means of CF control in crickets, and the best substantiated one, is that the resonances of certain membranes in the forewings control the toothstrike rate (which corresponds to CF) via some sort of escapement mechanism that releases one file tooth at a time. Early adapters of this idea were Pasquinelly & Busnel (1954), who proposed that during calling, the raised forewings of *Oecanthus pellucens* acted like the prongs of a tuning fork. Specifically, they conjectured that the resonant frequency of the forewings in that species controls the movement of the scraper during its engagement with the file and, that during each fundamental vibration of this tuning fork, the file and scraper move slightly apart, allowing a tooth to be released, and return, catching the next tooth. Decades later, using *Gryllus campestris*, Koch *et al.* (1988) explored this proposed mechanism in convincing detail, showing that as the forewings close during the production of a pulse, the motion momentarily stops and reverses as each successive file tooth is struck. In exploring the effect of temperature on stridulation in that species, they showed that between 20 and 30° C the wing closing speed, tooth impact rate, and CF were nearly constant, whereas the rates at which chirps and pulses were produced were strongly temperature dependent. Koch *et al.* (1988) concluded that their results fit a "clock escapement model" but not a "cog-rattle" model, which they described as a system in which the scraper impacts a resonant structure but is driven along the file unrestrained by an escapement mechanism. The tooth strike rate is free to vary with the temperature because "no mechanical feedback occurs between oscillator and wing movement; *i.e.*, the wing motion is *not* controlled by the harp motion." This would allow CF to vary substantially with temperature.

Walker (1962b) studied the effects of temperature on the songs of 19 species of crickets — including 10 species of *Oecanthus* but representing five subfamilies. In attempting to explain substantial changes in CF as a function of pulse rate in 18 of these 19 species (SMTbl_CFTempCoefs), he rejected the escapement model (as formulated by Pasquinelly & Busnel 1954) and proposed that the forewings act like the sounding board of a musical instrument in that they can be made to vibrate at a range of tooth impact frequencies (*i.e.*, a cog-rattle model)

Sismondo (1979) was first to measure the resonances of the forewings of a cricket with a wide range of temperature-dependant CFs in its calling song. The species was *Oecanthus nigricornis*, and he used live males and ingenious techniques to make repeatable measurements of a remarkably diverse set of phenomena associated with CF determination. For example, he demonstrated the modes of vibration produced in each forewing by stroking its file with an artificial scraper, and he compared the effects on CF of gradual changes in ambient temperature with the effects of a sudden decrease of 12°C or more. Significantly, he showed that the forewings had free resonances that ranged between 1.0 and 6.9 kHz, that the usual CF of the *O. nigricornis* calling song changed from 3.0 to 4.6 kHz over a range of 15 to 32°C, and that between 3.8 and 4.6 kHz the resonances formed "a virtually continuous series." His summary stated that "the concept of a resonator with continuously variable tuning is supported."

More than 30 years later, using state-of-the-art technology, Mhatre *et al.* (2012) extensively studied the resonances of the wings of *Oecanthus henryi*. With laser Doppler vibrometry they measured the resonances of the five major vibrating areas of the left and right forewings of five males at 18, 22, and 27°C and reported that they "vibrated maximally and most coherently in response to sound between 2.5 and 4.5 kHz at all temperatures." When they studied the effect of aspect ratio on the resonances of plates that resembled the shape and structure of the wings of *O. henryi*, they found that changing the aspect ratio beyond the range of natural wings of *O. henryi* changed the deflection modes from their more efficient states in the real wings. Unlike Sismondo (1979), who concluded that different cells of the forewings became the dominant resonators at different temperatures, Mhatre *et al.* (2012) showed that wing cells did not resonate independently from one another but formed a single wing-shaped plate with different modes of vibration at different temperatures.

To summarize, the forewings of two species of *Oecanthus* have been studied and found to have resonances that could be driven by continuously varying tooth-strike frequency. Sismondo's techniques for determining resonances in *O. nigricornis* were so imprecise com-

Table 4. Temperature coefficients for pulse rates and carrier frequencies between 20 and 30°C (based on detailed data in SMTbl_CFTempCoefs).

Subfamily	Species	Source	Temp. coef. PR	Temp. coef. CF
From literature				
GRY	*Gryllus campestris*	Koch *et al.* 1988, Table 1		0.07
GRY	*Gryllus rubens*	Walker 1962b, Fig. 14	0.66	0.05
ENE	*Orocharis*, 5 species	Walker 1969a, Fig. 12	0.40-0.59	0.23-0.36
ENE	*Antillicharis oriobates*	Walker 1969a, Fig. 12	0.49	0.29
OEC	*Oecanthus*, 10 species	Walker 1962a, b, 1963	0.55-0.70	0.23-0.41
TRG	*Cyrtoxipha*, 4 species	Walker 1962b, 1969b	0.64-0.95	0.30-0.51
NEM	*Pictonemobius ambitiosus*	Walker 1962b, Figs 6, 14	0.59	0.24
NEM	*Eunemobius carolinus*	Walker 1962b, Figs 6, 14	0.51	0.34
		Range of values (excluding *Gryllus* spp)=	0.40-0.95	0.23-0.51
From data derived from trendline formulas in Tables 2 and 5				
TRG	*tinnulenta*	Tables 2 and 5	0.64	0.23
TRG	*tinnula*	Tables 2 and 5	0.55	0.28
TRG	*tinnulacita*	Tables 2 and 5	0.43	0.32
TRG	*thomasi*	Tables 2 and 5	0.56	0.49
TRG	*fultoni*	Tables 2 and 5	0.60	0.37
TRG	*exigua*	Tables 2 and 5	0.63	0.38
TRG	*vernalis*	Tables 2 and 5	0.59	0.33
TRG	*scia*	Tables 2 and 5	0.59	0.29
TRG	*rosamacula*	Tables 2 and 5	0.58	0.40
TRG	*litarena*	Tables 2 and 5	0.59	0.25
TRG	*delicatula*	Tables 2 and 5	0.66	0.33
		Range of values for *Anaxipha* =	0.43-0.66	0.23-0.49

pared to those used to study *O. henryi* that it seems highly likely that the differences in results are entirely technique related. However, it should be noted that the wings of *O. henryi* are unusually elongate for the genus, a conclusion supported by the aspect ratios of the forewings (length/dorsal width) of six eastern U.S. species having a range of 2.07 (*O. latipennis*) to 2.80 (*O. angustipennis*) (Fulton 1915, Plates IV & V) and four Indian species having a range of 2.78 (*O. bilineatus*) to 3.20 (*O. henryi*) (Metrani & Balakrishnan 2005, Table 1).

Currently then, there is convincing evidence that in certain grylline crickets, CF is determined by a clockwork-like escapement mechanism in which the resonant frequency of wing membranes (especially the harp) control the tooth-strike rate. This results in the CF being little affected by changes in temperature. However, all other crickets that have been carefully studied for temperature effects on CF have proved to be tree-cricket-like rather than field-cricket-like in this respect.

Grylline species, such as those of *Gryllus* and *Teleogryllus*, are among the most robust and sclerotized of crickets and are adapted to singing from the ground. On the other hand, *Oecanthus* species sing from vegetation and are among the most delicate of crickets. None of these three taxa seems especially likely to be representative of the prototypical system for producing the nearly pure frequencies characteristic of cricket calling songs. Cricket taxa that seem more

Table 5. Carrier frequencies in the calling songs of North American *Anaxipha*. (Plots of trendlines and all source data are in SMTbls_Songs.) (I.D.=insufficient data.)

Song	Trendlines for kHz vs p/s				No. states	PR based on Table 2		kHz at est. PR	
Species	n	b	a	r^2		p/s@20C	p/s@30	kHz@20C	kHz@30C
Continuous trills or tinkles									
vernalis	156	0.078	2.112	0.825	9	34.6	55.1	4.8	6.4
exigua	195	0.110	2.441	0.840	13	33.1	54.0	6.1	8.4
thomasi	79	0.328	0.837	0.809	7	16.5	25.7	6.2	9.3
tinnulacita	253	0.405	1.486	0.811	10	10.8	15.5	5.9	7.8
tinnula	86	0.449	2.711	0.726	5	6.5	10.0	5.6	7.2
tinnulenta	196	0.548	3.711	0.776	13	3.8	6.3	5.8	7.2
calusa	25	0.376	-3.238	0.813	1	I.D.	I.D.	4.8	6.3
Intermittent trills or chirps (see Fig. 6)									
delicatula	57	0.040	2.470	0.753	2	59.7	99.2	4.9	6.4
rosamacula	89	0.070	1.696	0.814	5	50.8	80.6	5.2	7.3
litarena	60	0.043	3.082	0.651	4	51.2	81.5	5.3	6.6
scia	48	0.058	2.700	0.741	1	46.1	73.2	5.4	6.9
imitator	8	0.072	3.537	0.867	1	I.D.	I.D.	5.7	7.8
fultoni	64	0.099	2.018	0.854	3	32.7	52.3	5.3	7.2

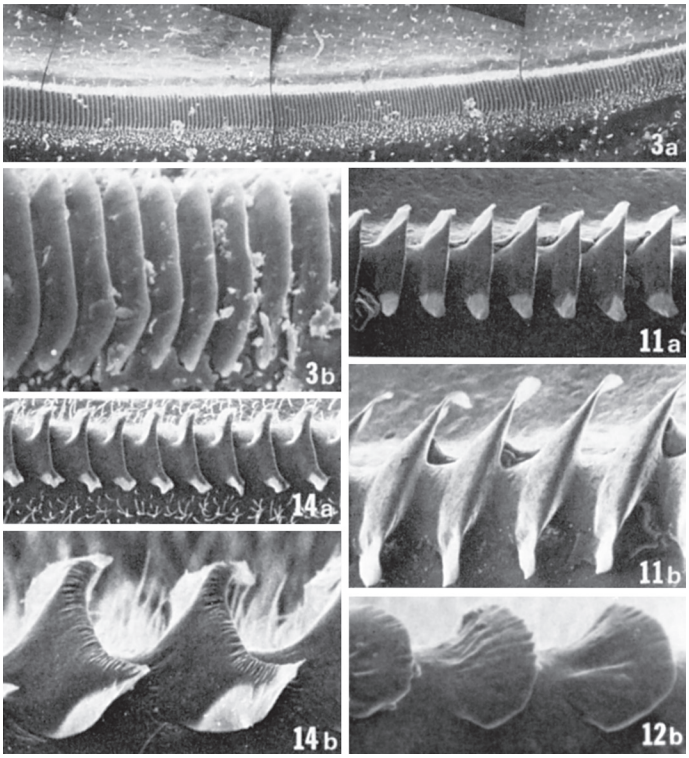


Fig. 16. SEM images of selected segments of the stridulatory files of four crickets from three subfamilies (from Walker & Carlysle 1975) 3. *Anaxipha latipennis* (Trigonidiinae). 11. *Gryllus ovisopis* (Gryllinae). 12. *Anurogryllus arboreus* (Gryllinae). 14. *Amphiacusta* sp. (Phalangopsinae). The (a) image for each species is from the central portion of the file; whereas (b) images are enlargements of a small number of the teeth. The *A. latipennis* file had 485 teeth; its (a) image shows about a quarter of the teeth. For *A. arboreus* (Gryllinae), the source paper has both an (a) image and a second close-up image.

likely to have species that use prototypical means to produce pure frequencies include Nemobiinae, Trigonidiinae and a group of closely related subfamilies currently lumped with the Eneopterinae (OSFO 2014).

These subfamilies make up the majority of the cricket fauna of the moist tropics and most sing with their wings in a near-perpendicular position. Song production in these neglected groups deserves careful study by modern methods. In our opinion, published data (top section of Table 4) suggest that all these groups have CFs that vary enough with temperature and pulse rate to question the hypothesis that the resonances of one or a very few wing cells control tooth-strike rate. The data for *Anaxipha* (Table 5 and bottom section of Table 4) are more extensive than for any other "neglected group" and are consistent with earlier data from the literature (Table 4). In all cases the coefficients for CF seem large enough to reject the clock escapement theory of CF control. If the control of CF in *Anaxipha* spp. is by the rate of file tooth impacts ("cog-rattle" control of Koch *et al.* 1988), their files (and those of *Oecanthus*) might be expected to contrast with the files of *Gryllus* spp. This is because files used in escapement control must bring the scraper to a stop before it is allowed to move forward again. In their detailed study of wing movements during calling in *G. campestris*, Koch *et al.* (1988, Fig. 3B) showed that at each file tooth impact the scraper comes to a complete stop and must "move a bit backwards to escape from locking position." In contrast, files that function to control CF by tooth impact rate need to have teeth that allow the scraper to move continuously forward as it impacts successive teeth. Nearly 40 years ago, Walker &

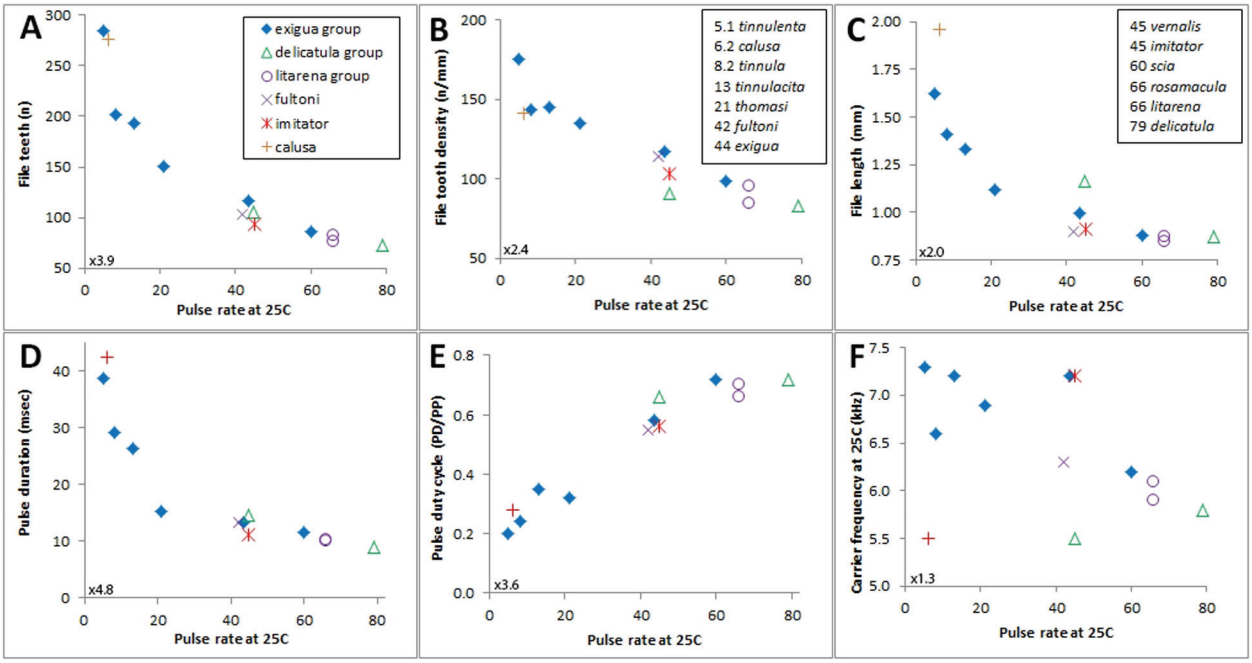


Fig. 17. These graphs show three morphological characters and three calling song characters plotted as functions of calling song pulse rate for 13 *Anaxipha* species. A. Number of teeth in the stridulatory file. B. File tooth density. C. File length. D. Pulse duration. E. Pulse duty cycle. F. Carrier frequency. Because the x-axis is the same for all graphs, the 13 species are always in the same left to right order and can be identified by the sequence of pulse rates and species as listed in the text boxes of B and C. The range of values for each of the six characters graphed is expressed by dividing the highest value by the lowest value. The results varied from a high of ×4.8 in D to a low of ×1.3 in F; each such multiplier is displayed at the intersection of the axes. (The multiplier for PR values is ×15.5!) Sources of data: Tables 2, 6, Fig. 7, SMTbl_StridFiles.

Table 6. Pulse durations and pulse duty cycles for Fig. 17.

		PR@25C	Direct method[a]			Regression method[b]				
Species group	Species	from Tbl 2	n	PD (ms)	Pdc	n	PD (ms)	Pdc	State(s)	Data from
exig	*tinnulenta*	5.1				52	38.7	0.2	PA, MD	DF
none	*calusa*	6.2	2[c]	42.5	0.28				FL	DF
exig	*tinnula*	8.2				25	29.3	0.24	MD,NC	DF
exig	*tinnulacita*	13.2				71	26.3	0.35	PA,MD,DE,FL	DF
exig	*thomasi*	21.1				42	15.2	0.32	PA, GA	DF
none	*fultoni*	42	4	13.3	0.55				FL	TW
exig	*exigua*	44				83	13.3	0.58	PA, MD	DF
del	*vernalis*	45				81	14.7	0.66	PA, MD	DF
none	*imitator*	45	4[d]	11.1	0.56				FL	TW
exig	*scia*	60	5	11.5	0.72				FL	TW
lit	*litarena*	66				17	10	0.66		DF
lit	*rosamacula*	66	4	10.2	0.70				FL	TW
del	*delicatula*	79	4	8.9	0.72				FL	TW

[a]Details of data acquired by the direct method, as used by TW, are in SMTbl_PDbyDirectMethod,
[b]Details of data acquired by the regression method, as used by DF, are in SM_PDbyRegression and SMTbls_DataforPDbyRegression.
[c]All other recordings at temperatures below 24°C.
[d]These recordings at 26, 27, 27, and 27°C.

Carlysle (1975) sought correlations between the structure of cricket file teeth and the parameters of the songs produced. They studied the files of 24 species of crickets selected for their taxonomic and calling song diversity. They found no correlations, but now, looking at the 28 scanning electron micrographs of file teeth they published, we find that the files of only three species seem especially adapted to stopping the scraper at each tooth. The files of these three have deep pockets between sturdy teeth into which the scraper might fit. Should this occur, the forewings would need to temporarily reverse directions in order to continue closing. The file teeth of these three species share an additional noteworthy feature not evident among Walker & Carlysle's other SEM images — *i.e.*, they have very thin, lateral extensions that, hypothetically, might function to dampen the shocks of the repeated sudden stops during wing closures (Fig. 16). The three species are two unidentified *Amphiacusta* spp (Phalangopsinae) and *Gryllus ovisopis* (Gryllinae). (Although *G. ovisopis* has no calling song, *Gryllus* that call have similar file teeth.)

The 10 genera, from five subfamilies, with files that do not seem as well adapted to stopping wing closure at every tooth impact are these: (After each genus is the number of SEMs that Walker & Carlysle used to illustrate the files of that genus.) *Anurogryllus* (Gryllinae) (3), *Allonemobius* (3), *Eunemobius* (2), *Hapithus* (3), *Anaxipha* (2) (see also Fig. 16), *Cyrtoxipha* (2), *Phyllopalpus* (2), *Orocharis* (3), *Oecanthus* (4), and *Neoxabea* (1).

Wing movement cycles during calling.—In most crickets the wing movement cycle (WMC) for each pulse is a wing closure (C), with the scraper and file engaged, followed by a wing opening (O), with the scraper and file making scant if any contact. The forewings would be expected to move more slowly during C than during O because the resistance to movement is greater. This is probably always the case, but instances in which the PI is longer than the PD make it necessary to either suppose that the wings move more slowly during a near frictionless O than in a file-engaged C or that at least one hold (H), with no movement along the file, has been added. Among our 13 species, these five seem likely to have an H in their WMC: *thomasi* (approximate Pdc at 25°C: 35%), *tinnulacita* (28%), *tinnula* (22%), *calusa* (21%), and *tinnulenta* (20%). All but *calusa* are in the *exigua* group, which is distant from that species group in both morphology and genetics (Figs 3, 14).

If only one H is added per WMC the sequence becomes either C-H-O- or C-O-H-. Determining which is the case requires monitoring wing position at intervals sufficiently brief to detect the H. Pierce (1948, Fig. 93) used a 50 frames per second film camera to reveal that the WMC in *Allonemobius allardi*, has the sequence C-O-H- with the H being about as long as the C and O combined. Walker *et al.* (1970) used an ultra-high-speed camera to make films of calling crickets and katydids at a thousand or more frames per second (*e.g.*, Walker & Dew 1972, Morris & Walker 1976). *Allonemobius sparsalus*, one of several crickets filmed, was selected as a subject because its song consists of triplets of pulses, with the pulses within the triplets and the triplets themselves produced at a regular rate (http://entnemdept.ufl.edu/walker/buzz/536a.htm). When the film was

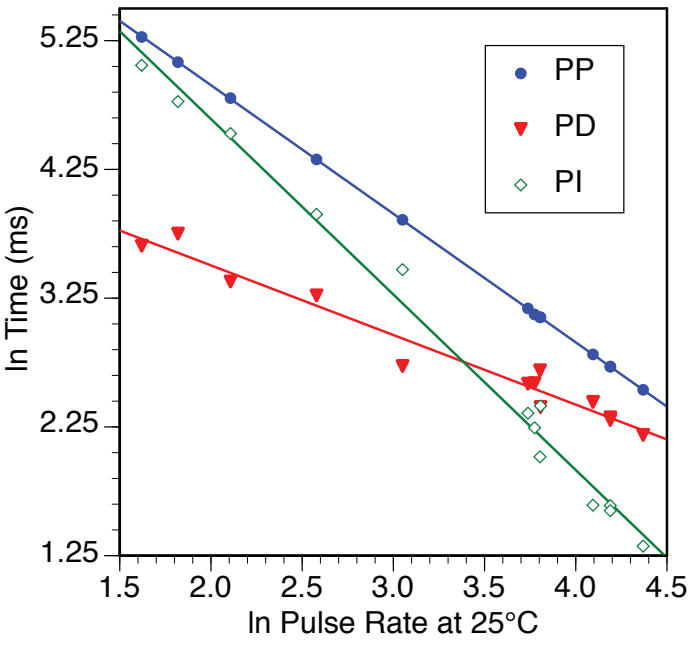


Fig. 18. Log/log plots of pulse period, pulse duration and pulse interval against pulse rate at 25°C, for 13 species of *Anaxipha*. Trendlines: pulse duration = -0.541(PR) + 4.586 (r^2, 0.96); pulse interval = -0.136(PR) + 7.368 (r^2 = 0.99).

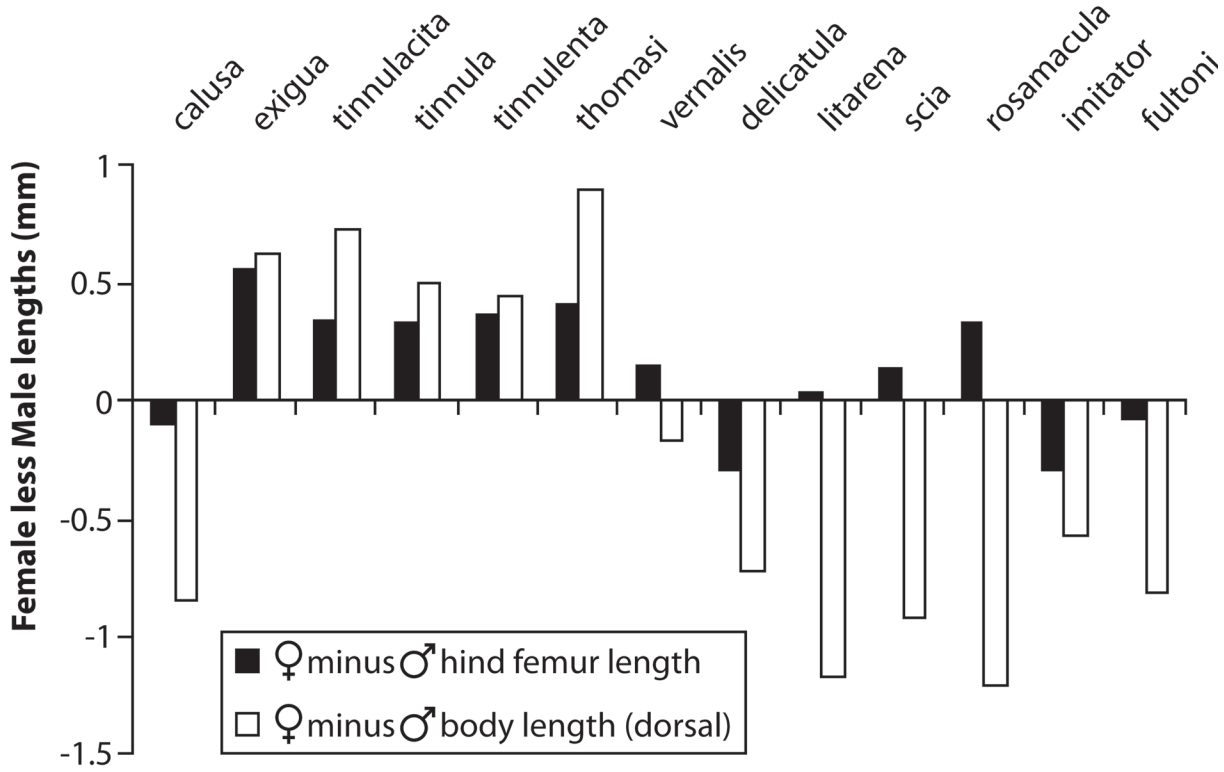


Fig. 19. Sexual differences in length of hind femur and in dorsally measured body length in 13 *Anaxipha* spp. Species are arranged, left to right, in approximate* descending order of body mass based on femoral lengths. Tabular data for this figure are in SMTbls_HFandBLmeasurements.xlsx.

*The summed average femoral lengths of male and female *thomasi* and *vernalis* were 8.81 and 8.85mm, which seemed close enough to a tie to excuse moving *thomasi* next to its four closest relatives.

analyzed using the same techniques as in the examples cited above, an H was revealed between the triplets while the wings were in the O position making the sequence for three pulses and a pause C-O-C-O-C-O-H- rather than O-C-O-C-O-C-H- (SM_WMCsparsalsus). These two examples from nemobiines suggest that any *Anaxipha* with a Pdc low enough to have an H in its WMC would likely have a C-O-H- sequence. However, when DF made and slowed a video of *calusa*, we agreed that the sequence was O-C-H- (SMvideo2_calusaSloMo) and that generalizing from nemobiine WMCs would not be justified. We await a definitive determination of the WMC of an *exigua*-group tinkler.

A recent study of eneopterine crickets of the tribe Lebinthini (Robillard *et al.* 2013) documented WMCs in *Lebinthus* n. sp. that were markedly more complex than any previously reported for crickets and were suggestive of some of the ones known in phaneropterine katydids (Walker & Dew 1972, Heller 1990). The song consisted of short trains of pulses produced within a WMC, with successive pulses within a WMC initially increasing in intensity. Each song consisted of 15 or more WMC of this pattern: O-(H-) C-H-C-H-...C-H- with each C-H- unit producing a pulse and the number of C-H- units gradually increasing from a few to >10. The (H-) occurred only in the first few WMCs of a song.

Evolution of pulse rates among North American species of Anaxipha.— The 13 species of North American *Anaxipha* provide an unusual opportunity to examine the relationship of calling song pulse rates to changes in the stridulatory files and in other features of the calling song. This is because the range of pulse rates is extraordinarily wide (5.1 to 79 p/s at 25°C) and the genetic relationships among the species are well established — through concordant molecular and morphological studies. The genetic relationships of certain species are extremely close, as in the case of the five species of the *exigua* group that cannot be distinguished by COI analysis or male genitalia; and in others extremely distant, as in the cases of *calusa* and *imitator*, which are likely to be placed in other genera in the future.

In Fig. 17, three features of the stridulatory file and three features of the calling song are plotted as functions of pulse rate at 25°C. Pulse rate is in the position of an independent variable for these graphs because of its demonstrated importance to cricket females in distinguishing the songs of conspecific males from those of other species. In Fig. 17A-C, number of file teeth, file length, and file tooth density have general trends that apply to all species groups over the full range of pulse rates. This is not unexpected because, all other things being equal, producing faster and slower pulse rates should be facilitated by changes in the file in the directions that the trends indicate. As faster pulse rates evolve, pulse duration may be constrained by the shorter pulse period, and shorter pulses are facilitated by shorter files. Conversely, when slower pulse rates evolve, longer pulses seem to be favored, as evidenced by Fig. 17D, which shows a strong relationship for all species between PR and PD. Longer pulses are facilitated by longer files and/or higher tooth densities, and they could be constrained by physical limitations to the length of the file and the density of teeth thereon. An advantage of longer pulses over shorter ones in the attraction of conspecific females might result from more easy detection by listening females, or from increased likelihood that they would interfere with females detecting pulses produced by rival males, or their being an honest signal of male vigor. Whatever the selective forces, the wide range of PD values (×4.8) and the tightness of the relation of PD to PR suggest that the optimal PD changes in step with the evolution of

higher and lower pulse rates.

The measurements of PD made for Fig. 17D were used to calculate the pulse duty cycles for Fig. 17E: (Pdc = PD/PP) or (Pdc = PD/(1/PR)). PD measurements from the beginning to end of a pulse's wave form include a short time at the end during which the wings continue to vibrate at their own rather than a driven frequency. Because duty cycle is defined as the active or powered portion of a cyclic event, this non-powered portion should be excluded in calculating Pdc. Zero-crossing analysis (Bennet-Clark & Bailey 2002) is a method of detecting the switch from powered to non-powered vibration of the forewings, but we opted not to use it in determining Pdc. Fig. 17E shows a steady increase in duty cycle from 0.20 to *ca* 0.70 where it plateaus. Because deducting the non-powered portion of the raw PD would have slightly reduced the Pdc values that this figure displays, we assume that the actual plateau values are slightly less than shown.

When CF@25°C is displayed as a function of PR@25°C (Fig. 17F) no pattern is evident other than that members of the same species group tend to have similar carrier frequencies. This is compatible with the low value of CF as a character by which to distinguish closely related *Anaxipha* species. The one case where CF does usefully distinguish species is between *exigua* and *vernalis*, which have nearly identical pulse rates, are sympatric, and overlap seasonally. *A. exigua* has an unusually high CF for its group and pulse rate, and *vernalis* is in a tie for the lowest CF of the 13 species. These observations suggest a fresh look at Fig. 17B, C. It is *vernalis* (the triangle at 45 p/s) that is well below the general trend in 17B and above it in 17C. And it is true that evolution of a lower CF would be aided by a longer file (Fig. 17C) with lower tooth density (Fig. 17B).

Fig. 18 shows the trends in PP, PD and PI in relation to PR at 25°C on a log/log plot. The trends in PD and PI are linear and tight (with r^2 of 0.95 and 0.99, respectively) but the slope for PI is much steeper, indicating that as species evolve higher or lower pulse rates, PI changes much faster than PD. It is noteworthy that the data in Fig. 18 are for 13 species at their 25°C PR but that similar changes occur within the songs of each of these species as their pulse rates change with temperature.

Early in the development of this paper, in hope of documenting such changes in PD and PI in several species, TW searched his *Anaxipha* song data for individual males that had quality song recordings made at a wide range of tightly controlled temperatures. He soon found a number of individuals that qualified in all respects except sound quality. This was because the temperature control room that provided ambient temperatures well above and below 25° C had been quiet enough to make recordings that permitted precise measurements of PR and PP, but not of PD or PI. Much later, DF, while using his *Anaxipha* song data to complete Fig. 17E, realized that he had data that would provide useful estimates of PD and PI over wide temperature ranges for six mid-Atlantic species. These estimates and what might be concluded from them are in SMFig_PD&PIbySixSpp.

SMFig_OecanthusFiles compares features of file and song of 13 species of North American *Oecanthus* spp plotted against PR in a manner paralleling that of Fig. 17 for the 13 *Anaxipha* species recognized here. In number of file teeth and length of file the relationship to PR proved similar to that in *Anaxipha* spp. However, for file tooth density and carrier frequency, no trends similar to those in *Anaxipha* are evident.

Are there crickets smaller than North American Anaxipha *that are as loud?*—The males of certain species of *Anaxipha* are among the smallest crickets known by us to make calling songs easily heard at several meters by persons of normal hearing. Their only rivals in this respect are certain similarly tiny and easily heard mogoplistines in which the males have an elongate pronotum that covers all or most of the short forewings (Love & Walker 1979). During calling these crickets drop their abdomen to create a space that may serve as an amplifying chamber, whereas calling *Anaxipha* produce their calls with the sound producing system that we propose is prototypical for crickets.

In measuring *Anaxipha* for this study, we noticed that the males of the smaller species did not decrease in body length as much as did the females. Our convention for measuring body length is explained in Methods, but it may help to repeat here that the forewings were included when they extended at rest beyond the tip of the abdomen, and, in females, the ovipositor was excluded from the measurement. This method insured that for nearly all specimens our measurement was independent of the unpredictable changes in body length that can be caused by varying degrees of abdominal extension or contraction after death and preservation. In practice, for all *Anaxipha* we measured, except for a few females of *litarena* and *rosamacula*, our measure of body length ended with the tips of the forewings. Knowing that this body length might be a poor predictor of body mass and lacking weights of specimens of *Anaxipha*, we settled on hind femur length as the most practical attribute for estimating body mass.

Fig. 19 summarizes the sexual differences in body length and femur length of 13 *Anaxipha* species arranged from left-to-right largely by descending estimated body mass (all data are in SMTbls_HFandBLmeasurements). The two bars for each species show the amount by which the male mean values for femoral and body lengths are exceeded by the female values. Because cricket females generally average larger than their males, the expectation would be that all differences would be positive—*i.e.*, that females would exceed males in both measures. This is not true for *calusa* (the heaviest species) but is true for the next five in Fig. 19, which are the five most closely related species of the *exigua* group. In the remaining seven species, males exceed females in body length, and in three of these, including the two smallest, males exceed females in femoral length as well. These results suggest that our smallest *Anaxipha* are near the size limit for producing an effective air-borne calling song. (It also reinforces our conclusion that *calusa* is a distant relative of our other *Anaxipha*.)

Supporting the notion that trigs smaller than *fultoni* are unlikely to be able to produce long-range calling songs is *Falcicula hebardi*, a North American trig that is smaller than any *Anaxipha* (Rehn 1905, Blatchley 1920). *F. hebardi* males stridulate weakly during courtship but make no calling song (Spooner 1972). TW, in the 1960's, examined series of about 40 of each sex of *F. hebardi* at UMMZ and noted that males averaged substantially smaller than females. When he measured the body lengths of the smallest and largest of each sex, he recorded that body lengths of males were 3.2 to 3.7mm, and of females 3.3 to 4.2mm. As reported in SM_Falcicula, DF's examination of the male genitalia, hind tarsi, and setation of the hind tibial spines of *F. hebardi* suggested that this species is more closely related to the clade that includes the *fultoni*, *delicatula*, *litarena* and *exigua* groups than either *calusa* or *imitator* — which brings into question the current generic status of *F. hebardi*.

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Supplementary Material

Workbooks:

SMTBls_Specimens Specimen records for North American *Anaxipha* (13 sheets).
SMTbls_Songs Song recording records of N. American *Anaxipha* (13 sheets).
SMTbls_MapData Data for distribution points on maps of Fig. 1. (13 sheets).
SMTbls_PRtrendlines All trendlines considered for Fig. 4 (3 sheets).
SMTbls_COIdata Lab and Specimen data for DNA barcoding re Fig. 14 (2 sheets).
SMTbls_PDbyRegress Regression-based pulse durations used in Fig.17 (14 sheets).
SMTbls_HF&BLdata HF&BL measurements used in Fig. 19 (4 sheets).
SMTbls_PTPilotStudy Data tables for TW's study of pulse train phrasing (5 sheets).

Spreadsheets:

SMTbl_StridFiles File characters of North American *Anaxipha*.
SMTbl_PRcalculator App that calculates PRvs °C line from a single PR-°C pair.
SMTbl_MatingTests DF's 2010 mating tests among inland spp. of *exigua* group.

SMTbl_CFTempCoefs CF temperature coefficients (literature & this manuscript).
SMTbl_PDdataByDM PD data obtained by Direct-Method and used in Fig. 17.

PDF files
SMFig_Portraits DF's portrait photos of North American *Anaxipha*.
SMFig_Genitalia 71 images of male genitalia of N. Amer. *Anaxipha*.
SM_AcalusaRelatives DF's summary of *calusa* relatives.
SMFig_PRvsTempAll PRvs°C recordings of all records in SMTbls_Songs.
SM_PTpilotStudy TW's attempt to quantify pulse train phrasing.
SMFig_PD&PIbySixSpp DF's log/log plots of PP, PD, PI of six Mid-Atlantic trillers.
SMFig_MaxLikliTree Tree based on COI sequences of N. Amer. *Anaxipha*.
SMFig_VideoAnalysis Measurements and graphs of wing movements in video.
SM_WMCsparsalsus WMC of *Allonembius sparsalsus* via ultra highspeed movie.
SM_PDbyRegression Estimating PD @ 25°C by linear regression (Fig. 17).
SM_Oecanthus files Plots of 13 spp of N. A. *Oecanthus* as in Fig. 17A,B,C,E.
SM_Falcicula DF's findings of relation of *F. hebardi* to N. Am. *Anaxipha*.
SM_PhyllopalpusMating DF's account of mating behavior in *P. pulchellus*.

Videos:
SMvideo1_calusa Video of *calusa* male courting (mov).
SMvideo2_calusaSlo Slowed video of *calusa* male courting (mov).