Erechthis Katydids (Tettigoniidae: Conocephalinae) in the Caribbean: New Species from the Bahamas and Hispaniola

Authors: Luca, Paul A. De, and Morris, Glenn K.

Source: Journal of Orthoptera Research, 25(2) : 49-59

Published By: Orthopterists' Society

URL: https://doi.org/10.1665/034.025.0203

Journal of Orthoptera Research 2016, 25(2): 49-59

Erechthis katydids (Tettigoniidae: Conocephalinae) in the Caribbean: new species from The Bahamas and Hispaniola

Paul A. De Luca and Glenn K. Morris

(PAD) School of Chemistry, Environmental & Life Sciences, The College of The Bahamas, Oakes Field Campus, P.O. Box N-4912, Nassau, The Bahamas. Email: paul.deluca@cob.edu.bs
(GKM) Department of Biological Sciences, University of Toronto Mississauga, 3359 Mississauga Road North, Mississauga, Ontario, Canada, L5L 1C6.

Abstract

Two new species of Caribbean conocephaline katydids (Agraeciini) are described for the previously monotypic genus *Erechthis*: one from the island of Eleuthera in the Bahamas, one from Hispaniola. The first-named species *Erechthis gundlachi* occurs on both Cuba and Hispaniola. A median projection (prong) of the subgenital plate is taken as a major generic diagnostic trait. This structure's morphology suggests a device for removal of rival sperm. The mate attraction song of males of the Eleutheran species is a steadily repeating series of chirps, each composed of 3 – 5 pulse trains. In the audio the frequency spectrum is broadband from 11 to beyond 20 kHz, with a coherent peak near 7 kHz. Inconsistency in some within-male song features may reflect this species' isolation from congenerics. The Eleutheran species bears a striking turquoise-colored face apparently absent in the other two species. We hypothesize that this coloration is a predator-avoidance adaptation. Possible Caribbean dispersal scenarios are discussed for these species.

Key words

Eleuthera, Greater Antilles, species description, Agraeciini, bio-acoustics

Introduction

While evaluating arthropod biodiversity at the Leon Levy Native Plant Preserve (Fig. 1) (Eleuthera Island, the Bahamas) in the summer of 2013, PAD collected several specimens of a large turquoise-faced katydid (Orthoptera: Tettigoniidae: Conocephalinae) from coppice forests within the park boundaries (Fig. 2). Males were singing at night with sustained chirping on various species of palm vegetation. These specimens were determined to be a new species close to *Erechthis gundlachi* Bolívar, 1888.

Erechthis gundlachi is known originally from Cuba (Bolívar 1888) and more recently the Dominican Republic of Hispaniola (Perez-Gelabert 2014). Yong (2015) gives its wider distribution on Cuba and includes effective photos of living coloration: pale straw-brownish yellow contrasting with the bay brown of a median body dorsal stripe. In studying a series of museum specimens of *Erechthis*, we then discovered a third species (grouped as *E. gundlachi*), this from the island of Hispaniola.

Erechthis is placed within the tribe Agraeciini. The unresolved taxonomy of 'agraeciine' conocephaloids was recently much improved by Chamorro-Rengifo *et al*. (2015). They reworked the polyphyletic genus *Agraecia*, creating a new subtribe Agraeciina, that consists of 3 new genera: *Iaratrox*, *Starkonsa*, *Yvelinula*, along with *Agraecia*; the latter is left with just three species: *Agraecia punctata* Saint-Fargeau & Audinet-Serville, *Agraecia dorsalis* Karny and *Agraecia agraecioides* (Rehn 1911). From these agraeciines *Erechthis* is distinguished "in the shape of the fastigium verticis which is much longer than the scapus and has a pointed apex" (Chamorro-Rengifo *et al.* 2015). Gorochov (2015) created a new tribe, Cestrophorini, involving two other possibly related agraeciine genera, *Cestrophorus* and *Acanthacara*: these species share *Erechthis*' produced and acuminate fastigium verticis, but differ in other features (open eardrums, a shallow prothorax). Currently we are unsure which if any of these taxa makes a convincing 'sister genus' to *Erechthis*.

As Tettigoniidae *Erechthis* spp., belong to a family well-known for stridulation. Male katydids broadcast a calling song to attract females and to mediate rivalry (Gwynne 2001). We present an analysis of the calling signal of the Eleutheran species based upon field recordings of four individuals. Variability among *Erechthis* species in the structure of the median prong of the male subgenital plate and of the cerci is discussed in relation to their function during copulation. We also discuss the adaptive potential of the striking turquoise head color of the Eleutheran species, and propose dispersal scenarios for these three species in the Caribbean.

Methods

Field-Site: The Bahamas.—The Leon Levy Native Plant Preserve, hereafter LLNPP, is approximately 10 ha in area, reached off Banks Road outside Governor's Harbour, Eleuthera, the Bahamas (central coordinates of LLNPP: 25.188°N, -76.212°W). It is the only national park on Eleuthera and is operated by the Bahamas National Trust in conjunction with the Leon Levy Foundation. Vegetation at the LLNPP is predominantly Dry Broadleaf Evergreen Formation-Forest/Shrubland (coppice), with the most common plants including poison wood (*Metopium toxiferum*), pigeon plum (*Coccoloba diversifolia*) and gum elemi (*Bursera simaruba*). The site is also characterized by several species of palm, such as buccaneer (*Pseudophoenix sargentii*), coconut (*Cocos nucifera*), sabal (*Sabal palmetto*), silver top (*Coccothrinax argentata*) and thatch (*Thrinax morrisii*). Man-made walking trails run throughout the coppice forests (Fig. 1) and it was from along these trails that the new 'blue-faced' *Erechthis* species was collected.

Collection and study of specimens.—Searches on Eleuthera were made over two successive years (2013 – 2014) during the summer months (June, July). We collected specimens at night (between 20:00 – 1:00 h) with temperatures ranging from 25 – 30°C. We located singing males by tracking their song by ear to the source and capturing individuals by hand or with a sweep net. Just one female was located. All the males, except one, were found on various species of palm (*i.e.*, buccaneer, coconut, sabal, silver top and thatch), at heights

Fig. 1. Map of The Leon Levy Native Plant Preserve. Asterisks on walking trails mark where *Erechthis levyi* specimens were collected. Star indicates holotype collecting location (Welcome Center). Entire park site spans 10 ha in area. Inset: Enlarged view of walking trails in the Edible History Garden. One male was collected here on a banana tree.

of 2 – 3 m above the ground. The exceptional male, still on site, was collected from a banana tree located in a fruit orchard (Fig. 1, Edible History Garden). The single female was discovered on the ground along the Tower Loop Trail. Locations where individuals were collected are indicated in Fig. 1. We euthanized specimens by placing them in a freezer for several hours, then preserved them in 70% isopropyl alcohol.

Five of the 6 specimens of *E. gundlachi* hail from the Philadelphia Academy of Sciences (ANSP), several determined to this species by M. Hebard in 1926. The remaining specimen, a female, also determined by Hebard, is from the University of Michigan Museum of Zoology (UMMZ). Male holotype and female allotype specimens of *E. levyi*, along with 4 paratypes are deposited in ANSP, with the other 4 paratypes deposited in UMMZ. All specimens of *E. ayiti* are returned to ANSP.

Specimens were studied and compared using a stereomicroscope (Nikon SMZ1000) fitted with a camera (DSFi1). Some photos were z-stacked using Helicon Focus (6.5.1 Pro). For scanning electron microscopy we employed a NeoScope (JCM 5000, Jeol).

Measurements (mm) and graphite drawings were made using a calibrated microscope (software: Nikon Elements), or in the case of body length, we used digital calipers (Fowler, Sylvac). Landmarks for measures were: **body length**: tip of fastigium verticis to tegmina extremity; **pronotum length**: disc in dorsal view midline distance cephalic margin to caudal; **mesofurcal pits separation**: distance in ventral view between furcal pit centres; **metafemur length**: distance from anterior coxotrochanteral articulation distad to femorotibial joint, excluding genicular lobes; **ovipositor length:** from ovipositor extremity to clasper sockets of female's subgenital plate, *i.e.*, where the cercal teeth of the male engage during mating.

Making acoustic recordings.—For the Eleutheran species, we were able to make field recordings of the mate attraction songs of four males on a single night in June 2013. Two males were caught immediately after recording, the other two escaped. We used a Sony Zoom Q3 digital audio recorder (48 kHz sampling rate) with a frequency response up to 24 kHz, saving recordings as stereo MP3 files. Upon locating each singing male we directed the microphone toward the dorsal surface of its thorax from a distance of 1 – 3 m, avoiding obstructions (*e.g.*, tree branches or leaves). The gain level on the recorder was adjusted for each male to avoid overload distortion. Recordings varied in length from 6 – 48 s (mean = 20 s, N = 4 males).

Song analysis.—We analyzed temporal and spectral features using Audacity 2.0.2 (http://audacity.sourceforge.net/). Spectral measurements employed the 'Spectrum' function (FFT size = 8192 Hz, Hamming window), and we used a frequency cut-off of –20 dB relative to the highest amplitude frequency in the song, as frequencies below this threshold are unlikely to have biological relevance (Ewing 1989). For each male, we measured 10 consecutive chirps from the middle portion of a male's recording. We report descriptive statistics of song parameters as the mean ± standard error (SE).

Results

Genus *Erechthis* Bolívar, 1888

Type Species: *Erechthis gundlachi* Bolívar by original syntypy. ♂&♀ syntype specimens, MNCN, Madrid.

Bolívar I. 1888. Ėnumération des Orthoptères de l'ile de Cuba. Mémoires de la Société zoologique de France 1: 116-244.

In 1888 Ignacio Bolívar was a still a rather young professor at the University of Madrid, just 38. He named *E. gundlachi* after his much older (78) colleague in Cuba, Juan Cristobal Gundlach. An expatriate German, Juan Cristobal made Cuba his home in 1840, becoming over the next half century the authority on its natural history. His name has been applied to a great number of animal

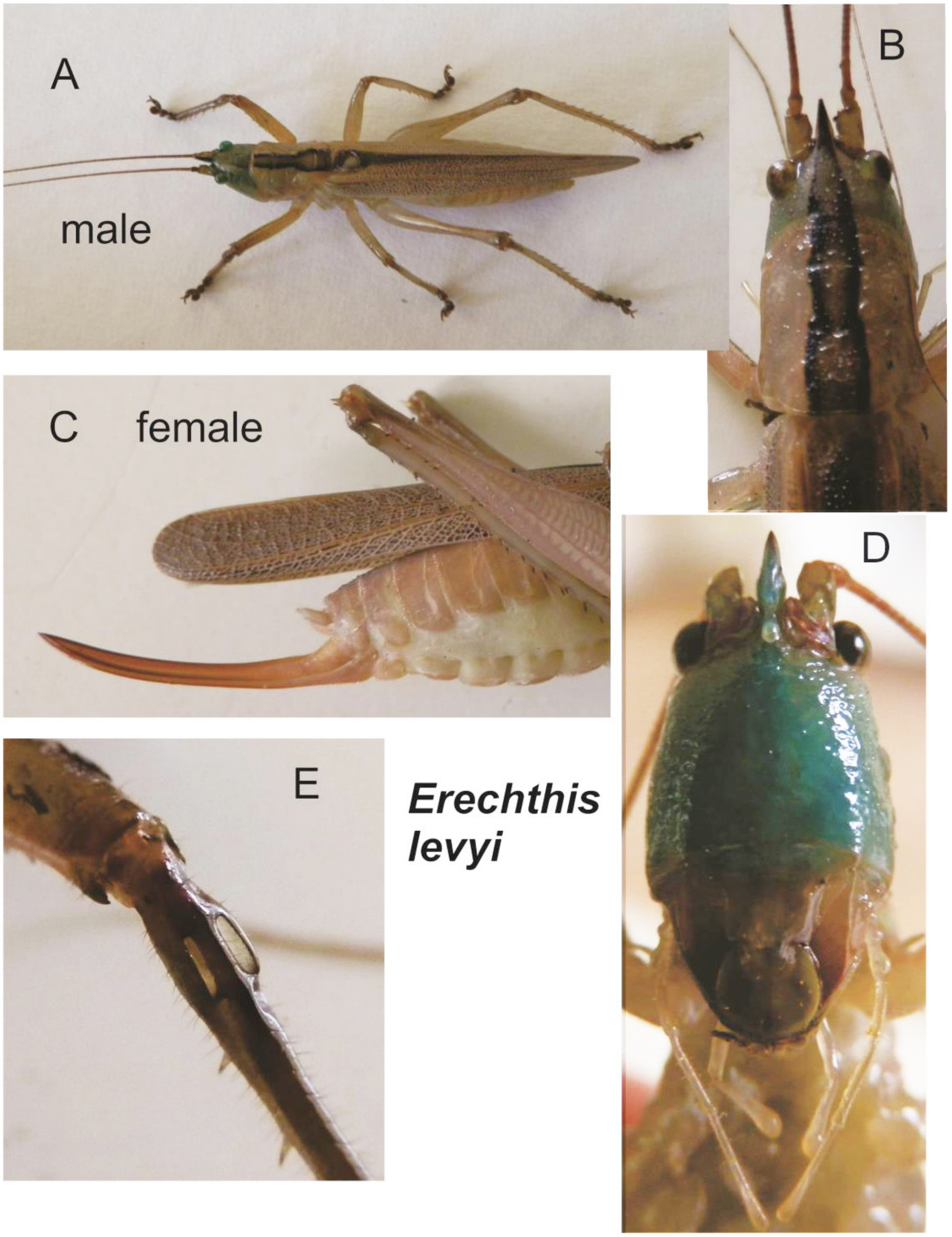

Fig. 2. A. Habitus of *Erechthis levyi* male. B. Dorsal aspect of pronotum and fastigium verticis of head showing length relative to antennal scape and bay/castaneous dorsomedian stripe. C. Female ovipositor right lateral aspect showing tegmina body overreach. D. Turquoise frons and frontal fastigium with prominent ocellus between antennal scrobes. E. Protibia tympanal slits. For color version, see Plate I.

and plant taxa. Bolívar worked with Cuban specimens of his own collecting and also others sent by his "benevolent" colleague.

The genus *Erechthis* is based upon two specimens, syntypes, one of each sex, the pair "No. 121 de la coll. Gundlach et la mienne" (Bolívar 1888). The specimen collected by Juan Cristobal is a female (see photographed label, Orthoptera Species File); the syntype male is Bolívar's specimen. In the introduction to 'Enumération' Bolívar anticipates many Cuban taxonomic "interessantes surprises". The discovery of other *Erechthis* species on "autres Antilles" of the Caribbean was indeed a surprise to us!

Genus diagnosis.—The primary diagnostic feature of the genus *Erechthis* is the remarkable median prong of the male subgenital plate. Produced rearward in the midline, tapering and decurving, its tip is coarctate, *i.e.*, swollen distad [as noted by both Bolívar (1888) and Redtenbacher (1891)]; it ends in a strong decurved spine in all 3 species (Figs 3, 4).

Fastigium verticis (fv) prominent, acuminate to downcurved pointed apex and just exceeding antennal scape. Pronotal metazonal shoulders laterally compressed, adding slightly to subnotal sound-space volume. Prosternum unarmed. Tubercle lacking (or very weakly developed) on posterior angle of mesobasisternal lobes.

Genus distribution.—Caribbean: Cuba, Hispaniola (Haiti and the Dominican Republic), the Bahamas (Eleuthera Island).

Genus etymology.—Unspecified by Bolívar, presumably per Greek mythology, Erechtheus, a king of Athens, the patronymic of Orithya his daughter (source: Epistles of Ovidius Naso online).

Genus description.—
Color: In dry pinned specimens body color is "straw-yellowish to light brown" (Perez-Gelabert 2014), fuscoflavescent or amber. A contrasting broad dorsal band, badius/castaneous (Fig. 2A, B), darker brown marginally, marks the dorsum from fastigium across the pronotal disc, well onto anal sound field and the contiguous midline tops of the flexed tegmina.

In living specimens (Fig. 2A, C herein, Fig. 1 of Yong 2015) tegmina, especially anal field, conspersed (sprinkled with minute irregular dots). In *E. levyi*, turquoise shading of the head and distal limbs; this coloring perhaps absent in the other two species.

Head: Frons smooth to weakly rugose, taller than broad (Fig. 2D); broadest at mandible base, tapering slightly upward to protruding globose eyes. Prominent scrobal sclerites (ss) frame a tall triangular frontal fastigium (ff) bearing a large median ocellus. [Scrobal sclerites "the pits in which the antennae are set" (Torre-Bueno 1962) rim the pit at the antennal scape base.] Fastigium verticis (fv) viewed dorsally acuminate, conical-convex (without fovea), tip acuminate decurved, declinate, projecting beyond scape to antennal pedicel, strongly keeled ventrally; where fv keel meets apex of ff there is a deep transverse low point (fastigial notch); scapes cylindrical, without lobes or spines, attaining antennal pedicel.

Thorax: Pronotum: Margined narrowly throughout, fore, aft and sides. Anterior edge weakly arcuate, posterior edge truncate. Second transverse sulcus marks metazona as subequal in length to prozona and mesozona taken together; metazona shoulders laterally compressed at humeral angle; rear half metazona angled slightly up and projects atop sound field, adding slightly to volume of subnotal acoustic cavity. Disk unevenly glabrous to weakly rugose. Obtusely rounded humeral angle puts both lateral lobes in view dorsally. Greatest lateral-lobe depth at prothoracic coxa; acoustic spiracle recessed, not visible laterally, little evidence of bulla.

Tegmina: Radial sector branching off well beyond mid-tegmen length. Typically the left tegmen sound field (anal region modified for sound radiation) of tettigoniids shows as thicker than the right: the mirror and harp cells of the right (scraper) tegmen are far thinner than those on the left (left tegmen on top when flexed). This distinction is minimal in *Erechthis* spp: the left (file) tegmen's cell membranes are almost as transparent as those of the right (scraper tegmen). Truss and pedestal veins of the anal margin, those that support the canted tegmen during stridulation (Morris *et al.* 2016) are very heavily sclerotized and thickened.

Legs: Tibiae densely spined. Fore pro- and mesofemora spines weak on anteroventral margins, absent from the ventroposterior margins. There is usually a row of 5-8 modest spines on the anteroventral margin of the hind femur. All femorotibial joints armed with a pair of wide-based stout genicular apical spines, sclerotized brown tipped.

Terminalia: Male cerci stubby cylindrical tridentate (with 3 protuberances = cercal teeth) these weakly variably developed. Male subgenital plate with a large median produced curving coarctate projection. Subgenital plate of male with long styli. Female ovipositor an upcurving blade.

Erechthis gundlachi Bolívar, 1888

Type material.—*Erechthis gundlachi* Bolívar, 1888., per syntype photos on Orthoptera Species File (Cigliano *et al.* 2016)

Distribution.—Caribbean region: Cuba; Hispaniola (Dominican Republic).

Etymology.—Named for J.C. Gundlach, naturalist of Cuba.

Material examined.—♀ Camoa, Cuba, Havana Prov., 20 X 1920 #3, J. Cabrera, *Erechthis gundlachi* Bol., Det. Hebard, 1926, [ANSP]. ♂ Camoa, Cuba, Havana Prov., 20 X 1920, #3, J. Cabrera, *Erechthis gundlachi* Bol., Det. Hebard, 1926, [ANSP]. ♂ San Domingo, M.A. Frazer, *Erechthis gundlachi* Bol., Det. Hebard, 1926, [ANSP]. ♂ Sánchez, Dom. Rep. VII 1938, Darlington [ANSP]. ♂ Gibara, Oriente, Prov. Cuba, 29 XII 1922, J. Cabrera, *Erechthis gundlachi* Bol., Det. Hebard, 1926, HEBARD CLN [ANSP, used in Fig. 4B]. ♀ LasVillas Prov Trinidad, Cuba, 15 VII 1956, C. & P. Vaurie [UMMZ].

Erechthis levyi n. sp.

Holotype.—♂ Levy Preserve [Welcome Center Coconut Palm], Eleuthera, the Bahamas (type locality), 4VII 2014, P. De Luca, ANSP.

Distribution.— Caribbean region: the Bahamas (Eleuthera Island).

Etymology.—The specific name honours Leon Levy, a prominent Wall Street financier and philanthropist, who deeply admired the island of Eleuthera's natural beauty. The Leon Levy Foundation is a private, not-for-profit foundation created from his estate in 2004. One mission of the foundation is to encourage and support conservation of natural landscapes around the world. This was realized in the Bahamas in 2011 with the opening of The Leon Levy Native Plant Preserve on Eleuthera, wherein this species was discovered.

Material examined.—♂ holotype, Welcome Center, Levy Preserve, Eleuthera, Bahamas, 4 VII 2014, P. De Luca, coconut palm [ANSP]. ♀ allotype, Levy Preserve, Eleuthera, Bahamas, 12 VI 2013, P. De Luca, ground along Tower Loop Trail [ANSP]. ♂ paratype, Edible History Garden, Levy Preserve, Eleuthera, Bahamas, 4 VII 2014, P. De Luca, banana tree [ANSP]. ♂ paratype, Levy Preserve, Eleuthera, Bahamas, 12 VI 2013, P. De Luca, buccaneer palm [ANSP]. ♂ paratype, Levy Preserve, Eleuthera, Bahamas, 2 VII 2014, P. De Luca, silver thatch palm [ANSP]. ♂ paratype, Trail from Wetland to Edible History Garden, Levy Preserve, Eleuthera, Bahamas, 17 VII 2014, P. De Luca [ANSP]. ♂ paratype, Levy Preserve, Eleuthera, Bahamas, 2 VII 2014, P. De Luca, buccaneer palm [UMMZ]. ♂ paratype, Welcome Center, Levy Preserve, Eleuthera, Bahamas, 27 VI 2014, P. De Luca, coconut palm [UMMZ]. ♂ paratype, worker's area stuck on tape, Levy Preserve, Eleuthera, Bahamas, 8 VII 2013, S. Fernandez [UMMZ]. ♂ paratype, Levy Preserve, Eleuthera, Bahamas, 12 VI 2013, P. De Luca, buccaneer palm [UMMZ].

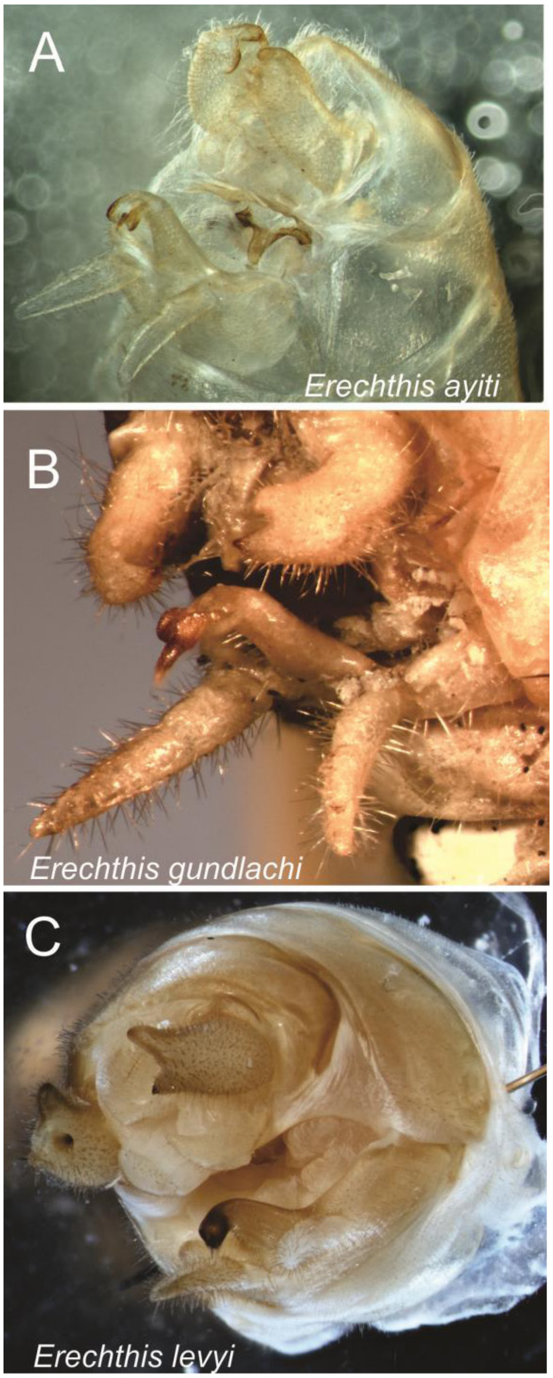

Fig. 3. Male terminalia of the three *Erechthis* species, compared from right lateroposterior aspect. Median subgenital plate prong and cerci of distinct shape. A. *E. ayiti*. B. *E.gundlachi.* C. *E. levyi.* Sclerotized titillators, an inner part of the insect's phallomeres, happen to be visible in the cleared specimen of *E. ayiti* just basad of the prong. For color version, see Plate I.

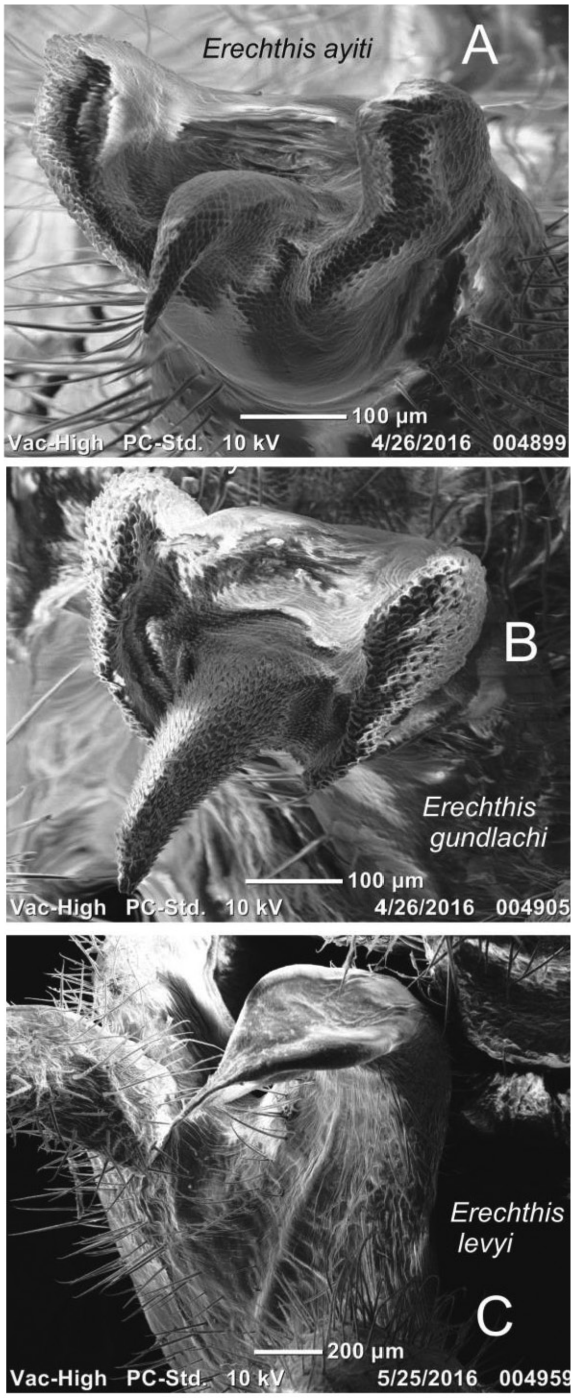

Fig. 4. Scanning electron micrographs compare highly diagnostic prong tips. A. *Erechthis ayiti*. B. *Erechthis gundlachi.* C. *Erechthis levyi*.

Erechthis ayiti n. sp.

Holotype.—♂ holotype, Coffee Exp. Sta., Fond des Negres, Haiti [Hispaniola], III-IV 1980, C.H. Arndt

Distribution.—Caribbean region: Hispaniola (Haiti and the Dominican Republic).

Etymology.—Name used for the island of Hispaniola by the Taino people. Translates as "land of high mountains" (Ayiti 2016).

Material examined.—♂ holotype, Coffee Exp. Sta., Fond des Negres, Haiti [Hispaniola] C.H. Arndt, III, IV 1930, [someone re-attached abdomen inverted, ANSP]. ♀allotype, Coffee Exp. Sta., Fond des Negres, Haiti [Hispaniola] C.H. Arndt, III, IV 1930, [ANSP]. ♂ paratype, Coffee Exp. Sta., Fond des Negres, Haiti [Hispaniola], C.H. Arndt, [ANSP]. ♂ paratype, Coffee Exp. Sta., Fond des Negres, Haiti [Hispaniola], C.H. Arndt, [ANSP]. ♂ paratype, 12 km SE San

Table 1. Species diagnosis (males).

Species	Subgenital plate prong	cerci
E. ayiti	Decurved terminal spine smooth scaly, emerging from cavity of bracketing flanges (Fig. 4A)	3 protuberances present: weakly developed, delimiting depression on inner distal aspect (Fig. 5A)
E. gundlachi	Decurved terminal spine emerges from between flanges; spine surface aculeate, invested with fine retorse teeth (Fig. 4B)	Protuberances only 2: dorsal and mesal tooth; mesal tooth with terminal sclerotized spine (Fig. 5B)
E. levyi	Decurved terminal spine enclosed dorsally, no flanges (Fig. 4C)	3 protuberances well developed, mesal tooth with sclerotized terminal spine (Fig. 5C)

Table 2. Average measurements (mm) for various body structures for each *Erechthis* species. Numbers in parentheses indicate the sample size contributing to each average.

Species	Body length	Pronotum length	Mesofurcal pit interval	Metafemur length	Ovipositor length
E. ayiti ♀	50.6 (2)	6.9 (2)	0.81 (2)	21.6 (2)	16.6 (2)
E. ayiti ♂	51.3 (4)	6.9 (7)	0.78 (7)	19.7 (5)	
E. gundlachi ♀	48.6 (2)	6.7 (2)	0.79 (2)	18.3 (2)	14.5 (2)
E. gundlachi ♂	39.3 (4)	6.1(4)	0.64 (4)	16.4 (4)	
E. levyi ♀	51.2 (1)	9.2 (1)	1.4 (1)	20.5 (1)	22.5 (1)
E. levyi ♂	46.9 (9)	8.5 (9)	1.17 (7)	18.3 (8)	

Francisco de Macoris, Duarte, R. Dominicana [Hispaniola], 21 II 1978, H.R. Roberts, cacao [ANSP]. ♂ paratype, Mt. Brouette, Haiti, 23 III 1926, G.E. Folis [ANSP]. ♂ paratype, 1500 meters, Morne Malanga, Massif de la Selle [highest peak in Haiti], Haiti, 2nd week, I 1928, James Bond [ANSP]. ♀ paratype, Coffee Exp. Sta., Fond des Negres, Haiti [Hispaniola], C.H. Arndt, III, IV 1930 [ANSP]. ♂ paratype, Furcy, Hayti, Mann Coll. [ANSP, used in Fig. 3A].

Three-species diagnosis and measurements (Table 1, Table 2).—Table 1 summarizes male diagnostic features separating the three species of *Erechthis*. In males of all three species subgenital plate prongs arise broadly, becoming narrowed and decurved as they project rearward. The dilated tip of the prong of *E. levyi* is obtect (covered) (Fig. 4C), but not so in *E. ayiti* and *E. gundlachi* where it has lateral flaring flanges that cup the central downturning spine (Figs 4A, B). For *E. levyi* the whole structure, styli and prong, recalls the curved neck and head of a goose (Fig. 3C); the long styli of the subgenital plate give wings to this illusion. The prong of *E. gundlachi* is unique in showing a relatively abrupt change in curvature about halfway along its length (Fig. 3B). The prong spine tip curves downward in all three species. Under a light microscope the prong flanges look similar in *E. gundlachi* and *E. ayiti*, but their surfaces show clear differences with the SEM: the terminal spine in *E. gundlachi* (Fig. 4B) is aculeate, densely covered with microteeth all oriented at the same angle pointing basad; in *E. ayiti* (Fig. 4A) the terminal spine is relatively smooth and covered with apparent 'scales'. There was some incidence of mechanical damage to the prong as seen in our specimens, *i.e.*, it is likely subject to wear and tear during mating.

The short cylindrical cerci have 2 – 3 tapering cercal prominences/teeth distally: termed here dorsal (dt), ventral (vt) and mesal (mt). Dorsal and ventral are directed posteriorly; between them the mesal projection curves toward the midline. These prominences are developed variably and diagnostically for the three species (Fig. 5). They are most prominent tooth-like and tapered in *E. levyi* (Fig. 5C). In the other two species they are rounded, mitten-like. In *E. gundlachi* the distal half of the inner-facing region is deeply excavated and there is apparently no ventral tooth; both the dorsal and mesal teeth are greatly reduced and the region between excavated (Fig. 5B). A similar excavation is visible in the distomesal face of the cercus of *E. ayiti* (Fig. 5A).

Measurements are given in Table 2. *E. gundlachi* is a smaller, more finely structured species than either *E. ayiti* or *E. levyi*. The species from Eleuthera is apparently the broadest, based upon mesofurcal pit distance.

Acoustic signal of E. levyi.—In the time domain, the mate attraction song of *E. levyi* appears as a steadily repeated sequence of short chirps, each composed of a series of 3 – 5 pulse trains. The interval between chirps averages 187 ± 23 ms (Fig. 6A). Within each chirp, pulse trains resolve as 4 – 5 sustained, poorly delimited pulses (Fig. 6B, C), the first always of lower amplitude. Time-resolved further, these *Erechthis* pulses, unlike the stereotyped pulses of *Conocephalus* spp., (*e.g.*, Morris *et al.* 1978), last longer and vary widely in amplitude. Whereas *Conocephalus* pulses have a stereotyped brevity

Table 3. Descriptive statistics of *E. levyi* song parameters. Male #2 had 5 pulse trains in some of its chirps. For each male, pulse train (PT) and interval (I) values represent the mean measured from 10 consecutive chirps. Also provided is the mean ± standard error (SE) for all four males. Units are in milliseconds.

Male	PT1	I1	PT2	I2	PT3	I3	PT4	I4	PT5
1	4.8	12.8	15.3	11.6	19.8	10.8	17.8	-	-
2	14.4	4.3	17.3	10.6	17.6	11.4	20.0	11.8	21.8
3	13.3	5.3	20.0	10.7	20.9	12.3	20.5	-	-
4	15.6	7.2	21.4	11.4	23.9	12.3	23.3	-	-
Mean	12.0	7.4	18.5	11.1	20.6	11.7	20.4	11.8	21.8
SE	2.5	1.9	1.4	0.2	1.3	0.4	1.1	-	-

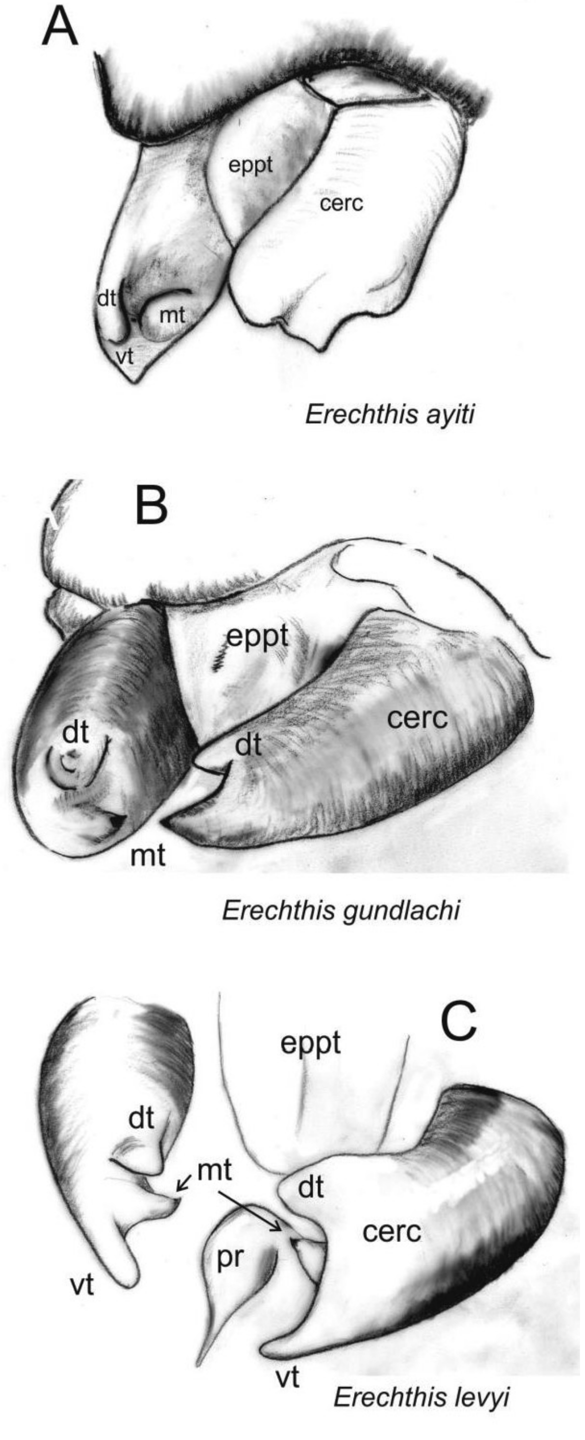

Fig. 5. Cercal protuberances ('teeth') compared for the three *Erechthis* species. A. *E. ayiti*. B. *E. gundlachi*. C. *E. levyi*. Teeth prominent in *levyi*, reduced in *ayiti*; ventral tooth absent in *E. gundlachi* (mt, mesad-directed tooth; dt, dorsal tooth; vt, ventral tooth; eppt, epiproct; cerc, cercus; pr, prong).

— a rapid onset to peak amplitude always followed immediately by exponential decay to silence — *Erechthis* 'pulses' are sustained, with a varying amplitude envelope (Fig. 6B, C), one that also varies among successive pulse trains. Table 3 provides descriptive statistics for pulse trains and intervals for the songs of four males.

In the frequency domain, the spectrum combines an isolated lower audio peak that averages 7.1 ± 0.49 kHz (range: 6.5 – 8.5 kHz) with a more extensive band from 11 kHz to perhaps beyond 24 kHz (the frequency range limit of our equipment) (Fig. 6D). The low frequency peak is lower in amplitude by an average 12 ± 2.6 dB (range: 8 – 19 dB).

Discussion

For the Bahamas *E. levyi* represents the first record of a new katydid species discovered in these islands. The Bahamian entomofauna is in general poorly known (Elliot 2003); the taxonomy of only a few groups has been studied in detail [*e.g.*, ants (Morrison 1998); beetles (Browne *et al.* 1993, Turnbow & Thomas 2008); butterflies (Miller *et al.* 1992); cicadas (Sandborn 2001); grasshoppers (Smith *et al.* 2003) and termites (Scheffrahn *et al.* 2006)]. Bahamian katydids have been completely overlooked, and as Perez-Gelabert (2014) first noted for the katydids of Hispaniola, this is surprising, since most katydids are large and conspicuous in their habitat, especially per their audible acoustic behavior. Although *E. levyi* has so far been described from specimens collected only on Eleuthera, we expect it to have a wider distribution in the Bahamas, particularly on islands with the same coppice forest habitat as that found at the LLNPP.

The form of terminalia among males readily distinguishes the three *Erechthis* species. Such structural specificity in genitalic structures is commonplace in insects and usually explained in terms of sexual selection. For example, a recent comparative study of phallus diversity among katydids suggests certain specific structures (*e.g.*, titillators and other modified ventral sclerites) may function to ensure female mating via cryptic choice (Chamorro-Rengifo & Lopes-Andrade 2014, Vahed 2015, Wulff *et al.* 2015). Many katydid genitalic structures must also be under natural selection, *e.g.*, for correctly positioning the spermatophore for transfer (Heller & Liu 2015). In some katydids, modified cerci are used to grip females tightly during copulation (Wulff & Lehmann 2016).

Competition between the stored sperm of rivals can arise by cryptic intrasexual selection (Gwynne 2001). Could the evolutionary basis of the prong of *Erechthis* be as an adaptation to promote removal of a rival's sperm? This structure with its downcurving terminal spine is positioned to penetrate the female's genital chamber during coupling. Another tettigoniid offers an example where a midline subgenital plate appendage serves in sperm removal. In males of the phaneropterine *Metaplastes ornatus* there is a subgenital plate median projection involving downcurving terminal spurs (von Helversen & von Helversen 1991). When a male mounts a female, prior to transferring his sperm, he inserts his subgenital plate projection into the female's genital chamber. As the projection is withdrawn, the spurs catch upon the chamber walls turning it "practically inside out". There is also evidence that this inserted structure can stimulate (rival) sperm release by simulating the presence of an egg (von Helversen & von Helversen 1991). This intriguing hypothesis about prong function is well worth exploring with *Erechthis*; future studies examining live specimens in copula should shed light on the evolution and functional significance of these specialized reproductive structures.

Mate attraction songs in katydids are used to facilitate pair formation. The temporal pattern of the song of *E. levyi*, in comparison to that of many other tettigoniids, has a high duty cycle and lacks stereotypy: the number of pulses per train and their amplitude varies within and among males (although with only four males we acknowledge the need to increase our sample size to better characterize variability in signal parameters). Greater inconsistency in song features could be the result of isolation from congenerics

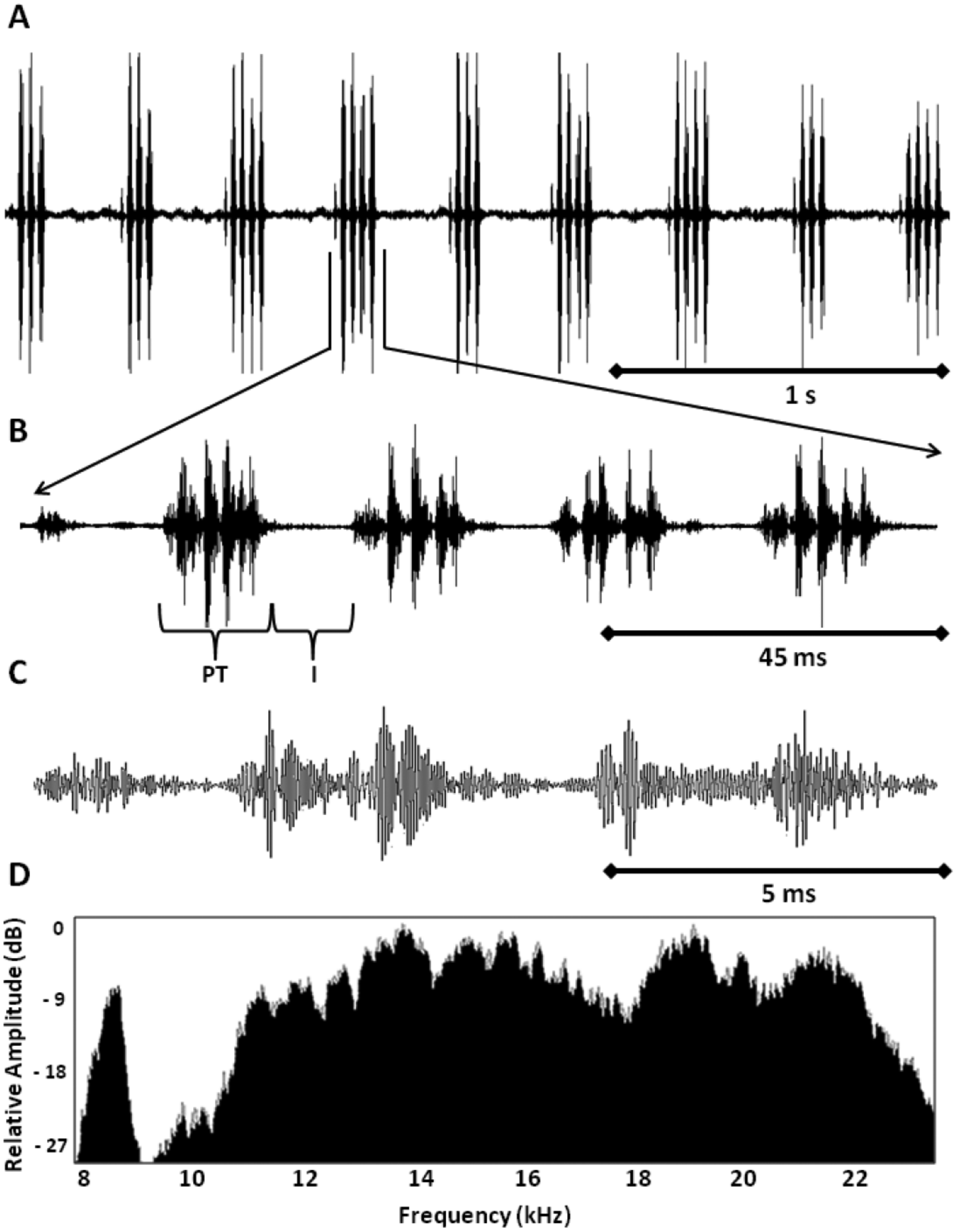

Fig. 6. Mate attraction signal of a male *E. levyi*. A. Waveform showing pattern of 9 chirps. B. Expanded view of the fourth chirp, showing finer structure of five pulse trains. Each pulse train is composed of a series of 4 – 5 pulses produced in rapid succession. PT – Pulse train, I – Interval. C. Expanded view of the fourth pulse train from panel B, showing finer structure of 5 pulses. (D) Frequency spectrum. The signal has two frequency bands, a lower peak that ranges between 6.5 – 8.5 kHz, and a higher band from 11 – 24 kHz.

on Eleuthera: here males are experiencing less selection for stereotyped signal cues functioning in discrimination of related species (Gerhardt & Huber 2002). It will be worthwhile to obtain song recordings for *E. gundlachi* and *E. ayiti* for comparison with *E. levyi*, in order to determine similarities and differences in song structure, and whether males of sympatric species are exhibiting divergence in song features compared with conspecific males from isolated (allopatric) populations.

In contrast to the flexible escapement files of crickets (Montealegre-Z *et al.* 2009), many katydid files, as here with *E. levyi*, are thickened to resist longitudinal bending under scraper shear forces. The file of *E. levyi* (Fig. 7) has ~80 broad file teeth, buttressed atop a stiffened transverse vein. *Pulse* is used here to describe song elements as continuous wave trains: the number of such trains (pulses) in a chirp (~20) seems wildly inconsistent with the number of teeth in *E. levyi*'s file. But given that each pulse/wave train of *E. levyi* varies greatly in amplitude, often becoming more intense later in the pulse (see Fig. 6C), multiple tooth contacts likely contribute to each pulse. Multiple tooth contribution to a sustained wave train is shown to be the case with another conocephaline katydid, *Panacanthus pallicornis*

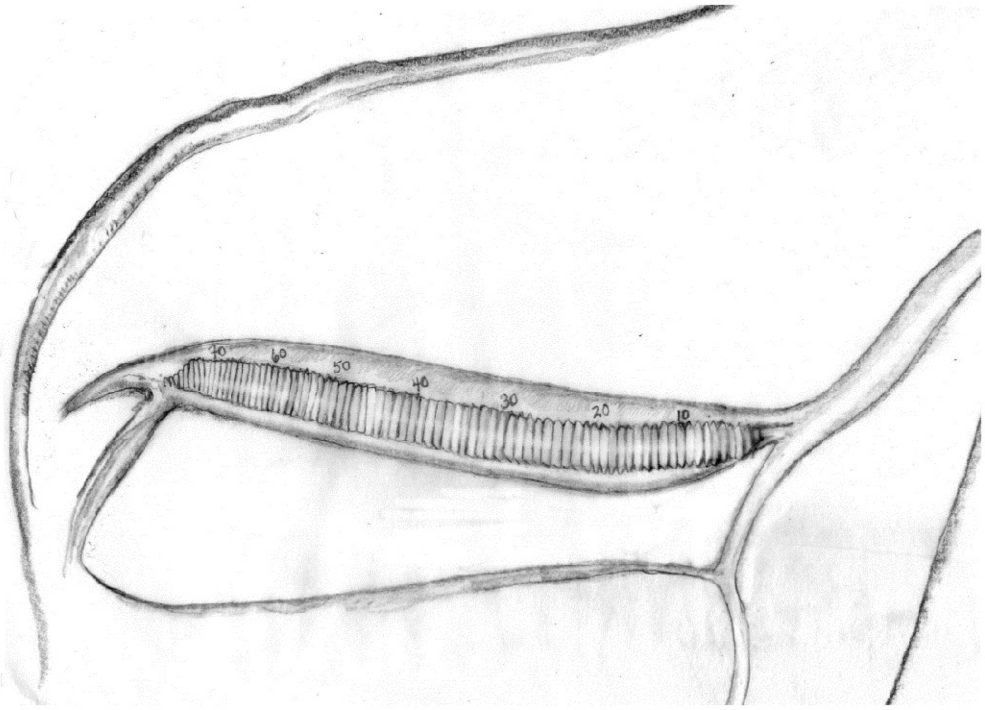

Fig. 7. Drawing of the stridulatory file of *E. levyi*. The file is located on the ventral surface of the left forewing and is composed of approximately 80 teeth. Numbers are included to better facilitate tooth count.

(Montealegre-Z & Mason 2005). The basis of this in *P. pallicornis* is a changing scraper velocity: in the file's mid-region velocity becomes appropriate for producing "successive tooth impacts...at an interval that matches the natural vibration frequency of the tegmina". Scraper velocity can be altered by thoracic muscle activity, but can also occur through elastic resonant stridulation (Morris 2008, Patek *et al.* 2011) when the springiness of scraper-associated cuticle enables very high velocity tooth contacts leading to ultrasonics.

The frequency response limitation of our recording system leaves open the possibility of ultrasonic carrier frequencies beyond 24 kHz in the spectrum of *E. levyi*. The roll-off in energy beyond 23 kHz (Fig. 6D) may be due to equipment rather than the insect. The song carrier is nevertheless a band spectrum rather than harmonically related peaks; it is the kind of spectrum made by a non-resonant generator mechanism, *i.e.*, rates of scraper-file-tooth contact fall far below carrier frequencies (Elsner & Popov 1978). The spectral frequencies of *E. levyi*, with energy at 7 kHz and from 11 to 24 kHz, are likely the result of exciting radiating tegminal speculae into action, these then vibrating at their inherent resonance frequencies (Montealegre-Z *et al.* 2006, Morris *et al.* 2016).

The turquoise face and vertex coloration of *E. levyi* (Fig. 2D) is a striking feature set against its tan-brown body (Fig. 2A). *Erechthis gundlachi* and (presumably) *E. ayiti* lack this feature, but share the same tan-brown body coloration (see live specimen photos in both Perez-Gelabert 2014, Yong 2015). Head color is unlikely to play a role in mating behaviour since both sexes share the feature (Andersson 1994). Rather, it suggests an anti-predator adaptation. Many neotropical katydid species utilize a wide assortment of strategies to protect themselves from predators, including various types of contrasting coloration and patterns that act to camouflage the body against background vegetation (see review: Nickle & Castner 1995). We have yet to encounter *E. levyi* during the day, despite our intensive searches for it on the various palm trees where males are typically found singing at night. Because of the insect's robust size, predators are most likely to be birds, snakes, lizards, tree frogs and larger spiders (*e.g.*, huntsman and tarantulas), with birds, snakes and lizards being the most commonly observed diurnally-active predators (PAD, pers. obs.). As with most nocturnal katydids, individuals normally retreat to refugia during the day, but where this might be for *E. levyi* remains a mystery. One location could be bromeliad plants, which are extremely abundant throughout the forests at this site. Bromeliads are home to a wide assortment of insects that use them as daytime refugia (Frank & Lounibos 2009). The blue-green coloration of bromeliad leaves is similar to the turquoise face of *E. levyi*, and therefore one scenario could be that individuals hide "face up" within the tight rosette of leaves which cluster at the base of the plant, thus concealing the body within one of the many deep cups that form at the base of the rosette, while leaving the head exposed to blend in with the surrounding vegetation. Similar hiding behaviours occur in other katydid species (*e.g.*, *Cocconotus*, *Teleutias*, and *Vestria*) which use the curled leaves of *Heliconia* (family: Heliconiaceae) plants to conceal themselves during the day (Nickle & Castner 1995). Searches of bromeliads are planned to determine where *E. levyi* might be hiding during the day, which may offer some clues as to the adaptive basis of its turquoise colored face.

Vicariance and dispersal are both implicated as the two major forces shaping Caribbean biogeography (Page & Lydeard 1994). The Bahamas, as part of The Greater Antilles (which includes the major islands of Cuba, Hispaniola, Jamaica and Puerto Rico), has experienced vicariant events through repeated cycles of submergence and emergence over the past 3 million years. During the Pleistocene when sea levels were up to 200 m lower, the Great Bahama Bank, made up of present-day Bimini, Andros, New Providence, Eleuthera, the Exumas, Long and Cat Island, was within 15 km of Cuba at its closest point, which likely resulted in the natural movement of many species between these two landmasses (Holzapfel & Harrell 1968, Pregill & Olson 1981, Carew & Mylroie 1997). Cycles of rising sea levels would have resulted in range fragmentation for many species as landmasses became smaller and more separated from one another by ocean, with some populations going extinct while others experienced divergence (Gillespie & Roderick 2002, Glor *et al.* 2005, Oneal *et al.* 2010). In addition to vicariance, dispersal, whether from over-water means or rafting, has also been important in moving organisms around the Caribbean, and thus promoting divergence of populations between islands (Holzapfel & Harrell 1968, Censky *et al.* 1998, Glor *et al.* 2005, Scharer & Epler 2007). Cuba represents a centre of origin for many taxa distributed throughout The Greater Antilles, including ants (Morrison 1998), crickets (Oneal *et al.* 2010), lizards (Glor *et al.* 2005) and termites (Scheffrahn *et al.* 2006). Recent extensive sampling for *E. gundlachi* on Cuba (Yong 2015), and Hispaniola (Perez-Gelabert 2014), did not uncover specimens of *E. levyi*, which suggests the latter species may be confined to the Bahamas, making it the first endemic katydid known from these islands. If Cuba indeed represents the ancestral source location, then perhaps dispersal of populations during the Pleistocene when landmasses were closer, followed by vicariance as sea levels rose, isolated populations throughout the region, with *E. gundlachi* eventually arising in Cuba and Hispaniola, *E. ayiti* in Hispaniola, and *E. levyi* in the Bahamas. Continued sampling of these islands, coupled with phylogeographic analysis of all three species, will be crucial to help us better understand the evolutionary history of this genus and determine its present day distribution throughout The Greater Antilles.

Acknowledgements

We thank Falon Cartwright, Mark Daniels and Dr. Ethan Freid from The Leon Levy Native Plant Preserve for allowing us access to this site, and for their help in collecting specimens. We are especially grateful to Chris Szczesniak for lending us his recording equipment and for his help in making the field recordings. Thanks to Dr. Robert Reisz and Diane Scott for use of their scanning electron microscope. Specimens on loan from the Academy of Natural Sciences Philadelphia and the Michigan Museum of Comparative Zoology were used in the taxonomic work reported here. This manuscript was improved by comments provided by Kristen Brochu and three anonymous reviewers. This study was funded in part by The Leon Levy Foundation and the Bahamas National Trust. We dedicate this work to the memory of Leon Levy, whose love and appreciation for the natural beauty of Eleuthera lives on in the wonderful plant preserve that bears his name.

References

Andersson M. 1994. Sexual Selection. Princeton University Press, Princeton, N.J.

Ayiti. 2016. Wiktionary, The Free Dictionary. (Last retrieved October 2015). <https://en.wiktionary.org/w/index.php?title=Ayiti&oldid=41137531>.

Bolívar I. 1888. Ènumération des Orthoptères de l'ile de Cuba. Mémoires de la Société zoologique de France 1: 116-244.

Browne D.J., Peck S.B., Ivie M.A. 1993. The Longhorn beetles (Coleoptera Cerambycidae) of the Bahama Islands with an analysis of species-area relationships, distribution patterns, origin of the fauna and an annotated species list. Tropical Zoology 6: 27-53.

Carew J.L., Mylroie J.E. 1997. Geology of the Bahamas. In: Vacher H.L., Quinn T.M. (Eds) Geology and hydrogeology of carbonate islands. Elsevier Science Publishers, Amsterdam, pp. 91-139.

Censky E.J., Hodge K., Dudley J. 1998. Over-water dispersal of lizards due to hurricanes. Nature 395: 556.

Chamorro-Rengifo J., Braun H., Lopes-Andrade C. 2015. Reassessment and division of the genus *Agraecia* Audinet-Serville (Orthoptera: Tettigoniidae: Conocephalinae: Agraeciini) Zootaxa 3993: 1-176.

Chamorro-Rengifo J., Lopes-Andrade C. 2014. The phallus in Tettigoniidae (Insecta: Orthoptera: Ensifera): revision of morphology and terminology, and discussion on its taxonomic importance and evolution. Zootaxa 3815: 151-199.

Cigliano M.M., Braun H., Eades D.C., Otte D. 2016. Orthoptera Species File. Version 5.0/5/0. (Last retrieved October 2015). <http://Orthoptera.SpeciesFile.org>.

Elliot N.B. 2003. History of entomological studies in the Bahamas. Gerace Research Center, San Salvador, Bahamas. 106-115.

Elsner N., Popov A.V. 1978. Neuroethology of acoustic communication. Advances in Insect Physiology 13: 229-355.

Ewing A.W. 1989. Arthropod Bioacoustics: Neurobiology and Behaviour. Cornell University Press, Ithaca.

Frank J.H., Lounibos L.P. 2009. Insects and allies associated with bromeliads: a review. Terrestrial Arthropod Reviews 1: 125-153.

Gerhardt H.C., Huber F. 2002. Acoustic Communication in Insects and Anurans: Common Problems and Diverse Solutions. University of Chicago Press, Chicago.

Gillespie R.G., Roderick G.K. 2002. Arthropods on islands: colonization, speciation and conservation. Annual Review of Entomology 47: 595-632.

Glor R.E., Losos J.B., Larson A. 2005. Out of Cuba: overwater dispersal and speciation among lizards in the *Anolis carolinensis* subgroup. Molecular Ecology 14: 2419-2432.

Gorochov A.V. 2015. Systematics of the American katydids (Orthoptera: Tettigoniidae). Communication 5. Proceedings of the Zoological Institute RAS 319: 480-503.

Gwynne D.T. 2001. Katydids and Bush-crickets: Reproductive Behavior and evolution of the Tettigoniidae. Cornell University Press, Ithaca.

Heller K., Liu C. 2015. Mating behavior of *Letana inflata*, a duetting phaneropterine bush-cricket species with unusual male genitalic organs (Orthoptera: Tettigonioidea: Phaneropteridae). Journal of Insect Behavior 28: 513-524.

Holzapfel E.P., Harrell J.C. 1968. Transoceanic dispersal studies of insects. Pacific Insects 10: 115-153.

Miller L.D., Simon M.J., Harvey D.J. 1992. The butterflies (Insecta: Lepidoptera) of Crooked, Acklins and Mayaguana Islands, Bahamas, with a discussion of the biogeographical affinities of the Southern Bahamas and description of a new subspecies by HK Clench. Annals of the Carnegie Museum 61: 1-31.

Montealegre-Z F., Mason A.C. 2005. The mechanics of sound production in *Panacathus pallicornis* (Orthoptera: Tettigoniidae: Conocephalinae): the stridulatory motor patterns. Journal of Experimental Biology 208: 1219-1237.

Montealegre-Z F., Morris G.K., Mason A.C. 2006. Generation of extreme ultrasonics in rainforest katydids. Journal of Experimental Biology 209: 4923-4937.

Montealegre-Z F., Windmill J.F.C., Morris G.K., Robert D. 2009. Mechanical phase shifters for coherent acoustic radiation in the stridulating wings of crickets: the plectrum mechanism. Journal of Experimental Biology 212: 257-269.

Morris G.K. 2008. Size and carrier in the bog katydid, *Metrioptera sphagnorum* (Orthoptera: Ensifera, Tettigoniidae). Journal of Orthoptera Research 17: 333-342.

Morris G.K., Braun H., Wirkner C.S. 2016. Stridulation of the clear-wing meadow katydid *Xiphelimum amplipennis*, adaptive bandwidth. Bioacoustics 25: 225-251.

Morris G.K., Kerr G.E., Fullard J.H. 1978. Phonotactic preferences of female meadow katydids (Orthoptera: Tettigoniidae: *Conocephalus nigropleurum*). Canadian Journal of Zoology 56: 1479-1487.

Morrison L.W. 1998. A review of Bahamian ant (Hymenoptera: Formicidae) biogeography. Journal of Biogeography 25: 561-571.

Nickle D.A., Castner J.L. 1995. Strategies utilized by katydids (Orthoptera: Tettigoniidae) against diurnal predators in rainforests of northeastern Peru. Journal of Orthoptera Research 4: 75-88.

Oneal E., Otte D., Knowles L.L. 2010. Testing for biogeographic mechanisms promoting divergence in Caribbean crickets (genus *Amphiacusta*). Journal of Biogeography 37: 530-540.

Page R.D.M., Lydeard C. 1994. Towards a cladistic biogeography of the Caribbean. Cladistics 10: 21-41.

Patek S.N., Dudek D.M., Rosario M.V. 2011. From bouncy legs to poisoned arrows: elastic movements in invertebrates. Journal of Experimental Biology 214: 1973-1980.

Perez-Gelabert D. 2014. Two new records of katydids (Orthoptera: Tettigoniidae: Conocephalinae) from the Dominican Republic, Hispaniola. Novitates Caribaea 7: 37-43.

Pregill G.K., Olson S.L. 1981. Zoogeography of West Indian vertebrates in relation to Pleistocene climatic cycles. Annual Review of Ecology and Systematics 12: 75-98.

Redtenbacher J. 1891. Monographie der Conocephaliden: Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien. 41: 315-562.

Rehn J.A.G. 1911. Notes on Paraguayan Orthoptera, with descriptions of a new genus and four new species. Entomological News 22: 247-258.

Sandborn A.F. 2001. Distribution of the cicadas (Homoptera: Cicadidae) of the Bahamas. Florida Entomologist 84: 733-734.

Scharer M.T., Epler J.H. 2007. Long-range dispersal possibilities via sea turtle - a case for *Clunio* and *Pontomyia* (Diptera: Chironomidae) in Puerto Rico. Entomological News 118: 273-277.

Scheffrahn R.H., Krecek J., Chase J.A., Maharajh B., Mangold J.R. 2006. Taxonomy, biogeography, and notes on termites (Isoptera: Kalotermitidae, Rhinotermitidae, Termitidae) of the Bahamas and Turks and Caicos Islands. Annals of the Entomological Society of America 99: 463-486.

Smith S.G.F., Smith D.L., Elliot N.B. 2003. A first look at acridid grasshoppers (Orthoptera) of the Bahamas. Gerace Research Center, San Salvador, Bahamas. 121-125.

Torre-Bueno J. de la. 1962. A Glossary of Entomology. Brooklyn Entomological Society, Brooklyn.

Turnbow Jr. R.H., Thomas M.C. 2008. An annotated checklist of the Coleoptera (Insecta) of the Bahamas. Insecta Mundi 0034: 1-64.

Vahed K. 2015. Cryptic female choice in crickets and relatives (Orthoptera: Ensifera). In: Peretti A.V., Aisenberg A. (Eds) Cryptic Female Choice in Arthropods. Springer International Publishing, Berlin, pp. 285-324.

von Helversen D., von Helversen O. 1991. Pre-mating sperm removal in the bushcricket *Metaplastes ornatus* Ramme 1931 (Orthoptera, Tettigonoidea, Phaneropteridae). Behavioral Ecology and Sociobiology 28: 391-396.

Wulff N.C., Lehmann A.W., Hipsley C.A., Lehmann G.U.C. 2015. Copulatory courtship by bushcricket genital titillators revealed by functional morphology, mCT scanning for 3D reconstruction and female sense structures. Arthropod Structure & Development 44: 388-397.

Wulff N.C., Lehmann G.U.C. 2016. Function of male genital titillators in mating and spermatophore transfer in the tettigoniid bushcricket *Metrioptera roeselii*. Biological Journal of the Linnean Society 117: 206-216.

Yong S. 2015. Distribución de *Erechthis gundlachi* Bolívar, 1888 (Orthoptera: Tettigoniidae) en Cuba. Boletín de la Sociedad Entomológica Aragonesa 56: 358-360.