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Resonant sound production in *Copiphora gorgonensis* (Tettigoniidae: Copiphorini), an endemic species from Parque Nacional Natural Gorgona, Colombia

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Abstract

This article describes the acoustic characters of *Copiphora gorgonensis*, a new species endemic to Gorgona Island National Park, Colombia. It is closely related to *C. brevicauda*, a congener distributed in the Pacific rainforest of Ecuador and Colombia, and also reported in Central America and other countries of northern South America. Here we provide diagnostic characters for identification; we study the mechanics of stridulation using laser vibrometry and optical motion detectors. Distinguishing features include: the highly tonal song of males with a carrier frequency peaking at 23 kHz; pulses repeated with a high rate of nearly 50/s and wing motion exhibiting a typical subsinusoidal pattern, as has been described for other Copiphorini. The natural frequency of the right forewing is close to that of the calling song and the wing-motion patterns indicate that sound vibrations are the result of sustained tooth impacts, corresponding to the natural frequency of wing vibration, *i.e.*, the tonal characteristic of the calling song in this species is the result of resonant stridulation. This resonance, and the amplitude component of the song, are attributed to the mirror frame and its surrounding cells and veins. These results are contrasted and discussed in regard to published literature on tettigoniid stridulation.

Introduction

The Parque Nacional Natural (PNN) Gorgona in Colombia is a natural island paradise supporting many species of organisms. Best represented are the mammals, reptiles, birds and many marine invertebrates and vertebrates (*e.g.*, Alberico 1986). The insect fauna has been poorly studied, and just recently a large macrosample of the entomofauna was undertaken (by us), focusing especially on the tettigoniid fauna. New species are being discovered, providing new inputs to understanding the biogeographic history of the island and its fauna. Here we report a new species of *Copiphora*: *C. gorgonensis*, a species of copiphorine katydid endemic to PNN Gorgona. It is one of the commonest species of katydid heard at night in Gorgona. The calling song of males is highly tonal and is made by resonance.

Most Ensiferans (*e.g.*, Gryllidae, Gryllotalpidae, Tettigoniidae and Haglidae), with some exceptions, generate sounds on a tegmino-tegmina basis, rubbing together specialized regions of the forewings or tegmina (Morris 1999). Typically in tegmino-tegmina stridulation, one wing bears a row of teeth, the file, and the other bears a scraper that is swept along this file to produce a series of stimuli (impacts) with the file teeth; these are subsequently effective upon the surrounding cell membranes. Although in most species of Ensifera the fore wings are bilaterally symmetrical (or almost so), the mechanism of sound production by tegmina stridulation is inherently asymmetrical, as one wing is always on top of the other (Forrest 1987). Katydidids have developed a strong level of morphological asymmetry as a result of this behavioral asymmetry. Male katydidids stridulate usually with the left tegmen (file-bearing wing)

on top of the right one (scraper bearing wing) and sound is radiated mainly by the scraper-bearing tegmen, which possesses specialized membranes enclosed by complex venation: *e.g.*, the mirror (Bailey 1970, Broughton 1964, Morris & Pipher 1967).

This paper describes a new species of *Copiphora*, analyses its mechanism of stridulation, and discusses the findings in relation to the literature. The mechanism of stridulation is addressed using highly sensitive motion detectors, microscan laser vibrometry and ultrasonic sound-capable acoustic equipment.

Methods

Study area. — PNN Gorgona is a small Colombian island with an area of 13.3 km², situated in the southwest Pacific Ocean (lat 2° 47', 3° 6' N; long 78° 6', 78° 18' W). The island rises from sea level to an elevation of 338 m; the average temperature is 26°C and the annual rainfall 6000 mm. Ecologically it is tropical rain forest with similar terrestrial habitat to that found on the mainland. The island is separated from the continent by only 35 km, with maximum ocean depths of 85 m. The nearest point on the mainland is in Punta Reyes, where the town of Bazán is located, in the municipality of El Charco, Nariño. Additional information can be found at: www.parquesnacionales.gov.co.

Sound recordings. — Specimens were taken at night from understory vegetation in PNN Gorgona and transported to the University of Toronto, Canada, where their songs were recorded with wide-bandwidth equipment (1 to 70 kHz). These recordings were obtained using Brüel & Kjær (B&K, Nærum, Denmark) equipment: a 1/4" (Type 4135) condenser microphone was connected to a sound level meter (Type 2204). Each insect sang freely from an artificial perch also used to record wing motion (see below). The microphone signal was connected to a computer data acquisition board (National Instruments (NI) BNC-2110, Austin, TX, USA; 16 bit), sampled at 400 kilosamples per second (kss) and stored to the hard disk of a computer. Sound levels (re 20µPa) were measured with a B&K 2204 sound-level meter (Fast or Impulse/Hold as indicated), its microphone placed at a distance of 10 cm from the dorsum of the insect singer. Sound analysis was done using Matlab software (The Mathworks, Natick, MA, USA).

We recorded stridulatory wing movements and associated sound production from eight males. Sound production was monitored with a B&K 1/4" microphone type 4939. Wing movements were recorded using an optomotion detector (Hedwig 2000), highly sensitive to ultrasonic frequencies. For recording wing movements, a small piece of reflective tape (Scotchlite 7610 and 8850 retroreflective tape manufactured by 3M and distributed by Motion Lab Systems

Inc., Baton Rouge, LA, USA) was placed on the left forewing and its position monitored with the photodiode of the motion detector. Movements of the forewing evoke changes in the current of the diode, which are recorded simultaneously with sound output. Sound and wing-movement signals were recorded on separate channels of the computer data acquisition board (NI BNC-2110) and analysed using Matlab software (sampling rate of the recording was 400 kss, for each channel). The temperature in the room was $23.5 \pm 0.97^\circ\text{C}$. The reflective tape (2 mm square) was attached to the left tegmen, in a manner that allowed movements to be recorded from a dorsal view (perpendicular to the wing surface).

Forewing resonance.—A small number of specimens were collected in November 2009 and transported to Bristol, UK, for laser vibrometry experiments. Wing resonance was measured in five male specimens using laser Doppler vibrometry, in response to sympathetic vibration. Vibration velocities were measured by a microscanning laser Doppler vibrometer (Polytec PSV-300-F; Waldbronn, Germany) with an OFV-056 scanning head, fitted with a close-up attachment. The laser spot location on the tegmen membrane was monitored by live video feed to the vibrometer's controlling computer. This system allows accurate measurement of the wing surface motion, without requiring the use of a reflective medium.

For the experiments, the whole stridulatory field in both tegmina was measured using 150–180 measurement points. Tegminal vibrations were examined in the frequency domain in response to acoustic stimulation with periodic (chirp) signals in the range 1–45 kHz. The spectrum of the stimulus was corrected to be flat at 55 dB (re 20 μPa SPL). The acoustic signals were generated by the PSV 300 internal data acquisition board (National Instruments PCI-4451; Austin, TX, USA), amplified (Sony amplifier model TAFE570, Tokyo, Japan) and passed to a loudspeaker (ESS AMT-1, ESS Laboratory Inc., Sacramento, CA, USA) positioned 15 cm from the specimen. For recordings, an intact specimen was mounted on a Blu-Tack holder using metallic clamps to fix legs. The wings were laterally extended by fixing the axillary sclerites with bee's wax.

The quality factor 'Q' is a dimensionless index that indicates the sharpness of the resonance: the higher the 'Q', the sharper the resonance (Bennett-Clark 1999b, 2003). 'Q' is defined as the ratio of the frequency of the peak response divided by the spectral width at the two values above and below resonant frequency with amplitudes 0.707 times the peak value (Fletcher 1992).

Results

Taxonomy.—We describe a new species, *Copiphora gorgonensis* (Tetrigonidae: Copiphorini), using sound recordings, the Orthoptera Species File (OSF) and published literature. This species is relatively abundant in PNN Gorgona. Individuals from Gorgona can be distinguished from *C. brevicauda* (with two subspecies, one in Ecuador and one in Costa Rica) mainly by distribution, acoustics and a few morphological characters. Morphologically it differs from both *C. brevicauda costaricensis* and *C. brevicauda brevicauda* in that the frons is bright orange, bearing six pale spots (Fig. 1A). The face of *C. b. costaricensis* and that of *C. b. brevicauda* exhibit similar spottings but the former is pigmented black (Naskrecki 2000) and the face of *C. b. costaricensis* is bright yellow.

The calling song of *C. b. costaricensis* lies in the audio range (near 10 kHz) with chirps (groups of syllables) given in groups of 5 to 7 and a chirp period of nearly 5 s. Every chirp contains between 8 to 13 syllables.

In *C. gorgonensis*, this chirp pattern does not occur, males stridulate

continuously for several minutes, and the frequency of the calls is nearly 23 kHz (see bioacoustics section, Figs 2–4).

C. brevicauda has also been found on the Colombian mainland adjacent to Gorgona (Montealegre-Z 1997), but when compared with *C. gorgonensis*, those individuals differ in coloration and size. Individuals identified as *C. brevicauda* from the mainland are smaller than *C. gorgonensis*; their bodies more homogeneously pale green; the frons exhibits black markings [similar to those reported by Naskrecki (2000) for *C. b. costaricensis*], but lacks the vibrant bright yellow facial coloration.

On the basis of its isolation from the mainland after the last ice age, the morphological differences shown above, and distinctive acoustic behavior, the latter presumably a reproductive isolating mechanism, we propose species status for the Gorgona population.

Copiphora gorgonensis sp. nov.

Holotype: 1 ♂ MEUV, November 2010 (Fabio A. Sarria-S).

Allotype: 1 ♀ MEUV, November 2010 (Fabio A. Sarria-S).

Paratypes: 4 ♂♂, 4 ♀♀ MEUV, October 2007 (F. Montealegre-Z).

Type locality.—COLOMBIA, Dept. del Cauca, PNN Gorgona, elevation 0–320 m.

Etymology.—The specific epithet refers to the type locality, PNN Gorgona.

Diagnosis.—Fastigium more or less flattened laterally at apex, shorter than that of *C. brevicauda brevicauda*. Frons bright orange, with four pale yellow or amber spots. Contrasting black clypeus, labrum and mandibles (Fig. 1). Lateroposterior edge of mandibles blue. Femoral spines small, but green as the body. Abdomen colorful in both sexes, with spiracle area light purple. Abdominal sternites yellowish, and laterally between segments pleura light reddish or pink (Fig. 1D).

Description

Head.—Fastigium short (Fig. 1). Frontal ocellus white, circular, as broad as 1/3 of eye diameter.

Tegmina.—Tegmina pale green, with some scattered spotting, extending well beyond terminalia. Female and male similar in coloration. Tegminal apices rounded. Mirror somewhat pentagonal, fusion of veins CuPa β +CuPb+AA1 massive (O. Béthoux, pers. com.), branch CuPa β surrounding the mirror about 3 \times thinner than the fusion (Fig. 4A); stridulatory file holding 205–220 teeth; intertooth distance gradually increasing towards basal region of the file (Fig. 1F); tooth density = 100–110 teeth/mm. Dorsal field of left tegmen as shown in Fig. 1G.

Male genitalia.—Subgenital plate basally broad, gradually narrowing, with medial round notch, bearing elongate styles (Fig. 1D). Tenth tergite bilobular, medially broadly incised.

Female genitalia.—Subgenital plate basally broad, distally narrow with a V-shaped notch, with internal margin of pseudostyli straight (Fig. 1C). Measurements given in Table 1.

General biology.—Observations made upon two different pairs maintained in captivity. Males call and alternate calls with tremulation [as observed in *C. rhinoceros*, (Morris 1980)]. When the female ap-

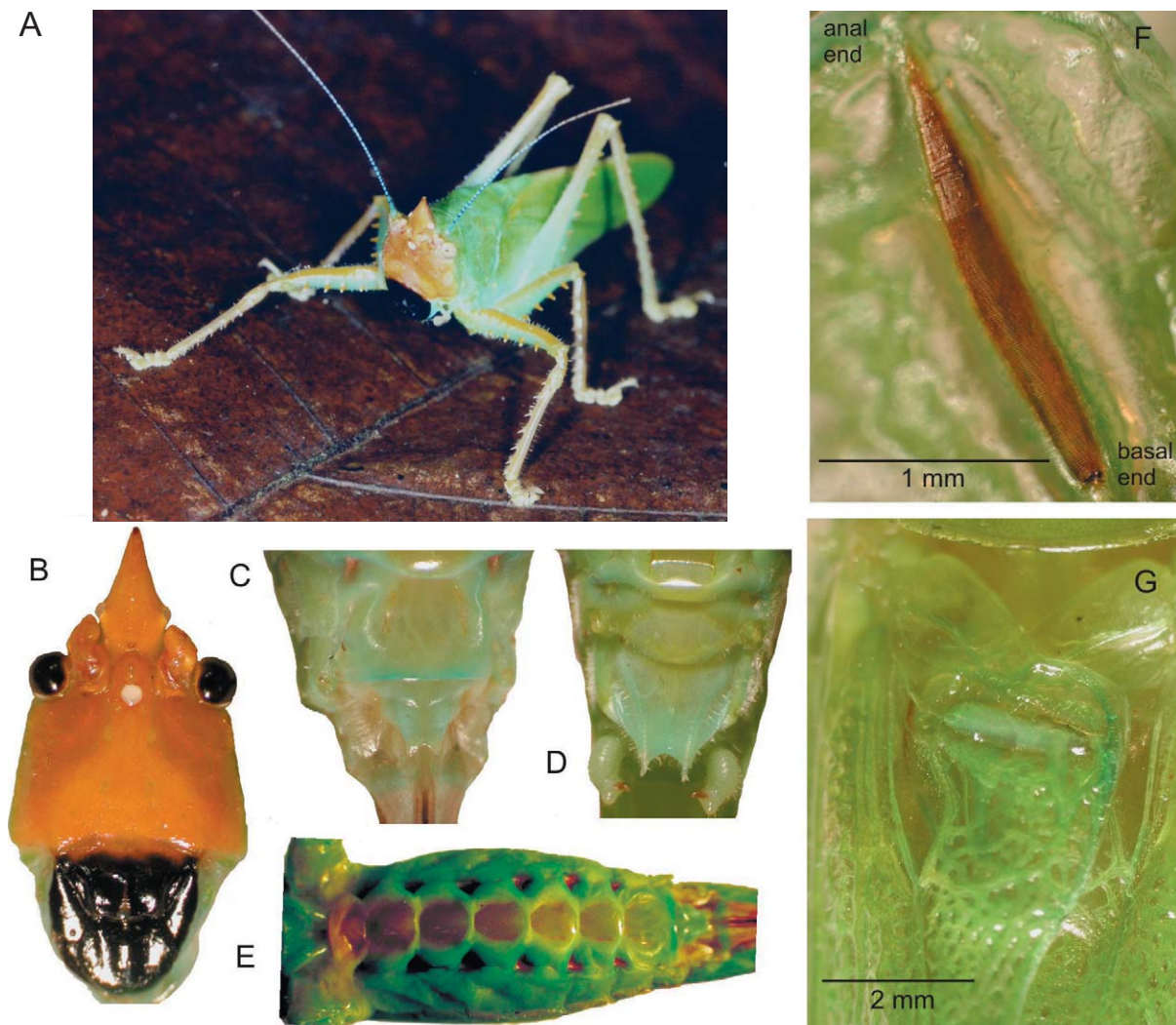


Fig. 1. Appearance of *C. gorgonensis*. A. Male standing on leaf at night. B. Rostrum showing pale facial markings. C. Female terminalia showing subgenital plate. D. Male terminalia showing subgenital plate and cerci. E. Abdomen of female showing coloration. F. Stridulatory file. G. Stridulatory field, left wing lying above right in dorsal view. For color version, see Plate XII.

proaches the male to a distance of ~ 10 cm, he stops singing, and begins to tremulate regularly with 5 to 10-s silent intervals between tremulations. The female also tremulates, usually during the male's silent intervals. The two converge and the male curves his abdomen as described by Morris (1980) for *C. rhinoceros*. In the lab males and females can be easily maintained with a diet of bee pollen, dry cat food and water. No cannibalism was observed. Females begin to lay eggs some 8 wk after adult moult. After laying, nymphs take some 12 wk to hatch and another 10-12 wk to reach adulthood. This suggests but one generation per year.

Song description.—The singing of this insect is not apparent to the human ear, even at close range. With a heterodyning device ('bat detector') it was possible to discern a trill. Further analysis is based

on recordings of 12 males; means are given.

At 23.5°C , the song of this species is a trill of pulses, each pulse a short sinusoidal wavetrain of 9.0 ± 0.4 ms duration; each pulse is produced by a single continuous closing stroke (Fig. 2A). Calls were given at a more or less steady rate of 49.4 ± 2.2 per minute (range 45-53 calls/min, $n=13$).

The mean sound intensity of the call of nine specimens was 97.70 ± 2.4 dB (SPL meter operating in fast impulse mode) as recorded at 10 cm from the microphone tip, with the microphone directed at the dorsal field of the tegmina. There is a single sustained wavetrain pulse with each cycle of wing movement. The envelope of the pulse rises gradually within the first 5-6 ms, reaches maximum amplitude and sustains this till near the end (Fig. 2B), falling over the last ~ 1 ms. The spectrum peaks very narrowly at 23.0 ± 0.7 kHz

Table 1. Morphological measurements (mm) of males and females. Fastigium measured from the ventral tooth to the apex. Body size includes wings.

	Fastigium	Pronotum	Body	Mirror	Tegmina	Forefemur	Hindfemur	File	Ovipositor
Mean for Males	3.7	8.9	58.0	2.0	44.7	8.8	19.5	1.9	NA
SD	0.2	0.1	2.3	0.2	0.9	0.4	0.6	0.2	NA
Mean for Females	3.9	8.9	61.2	NA	46.5	9.3	21.5	NA	41.4
SD	0.2	0.3	0.9	NA	2.1	0.2	1.1	NA	1.7

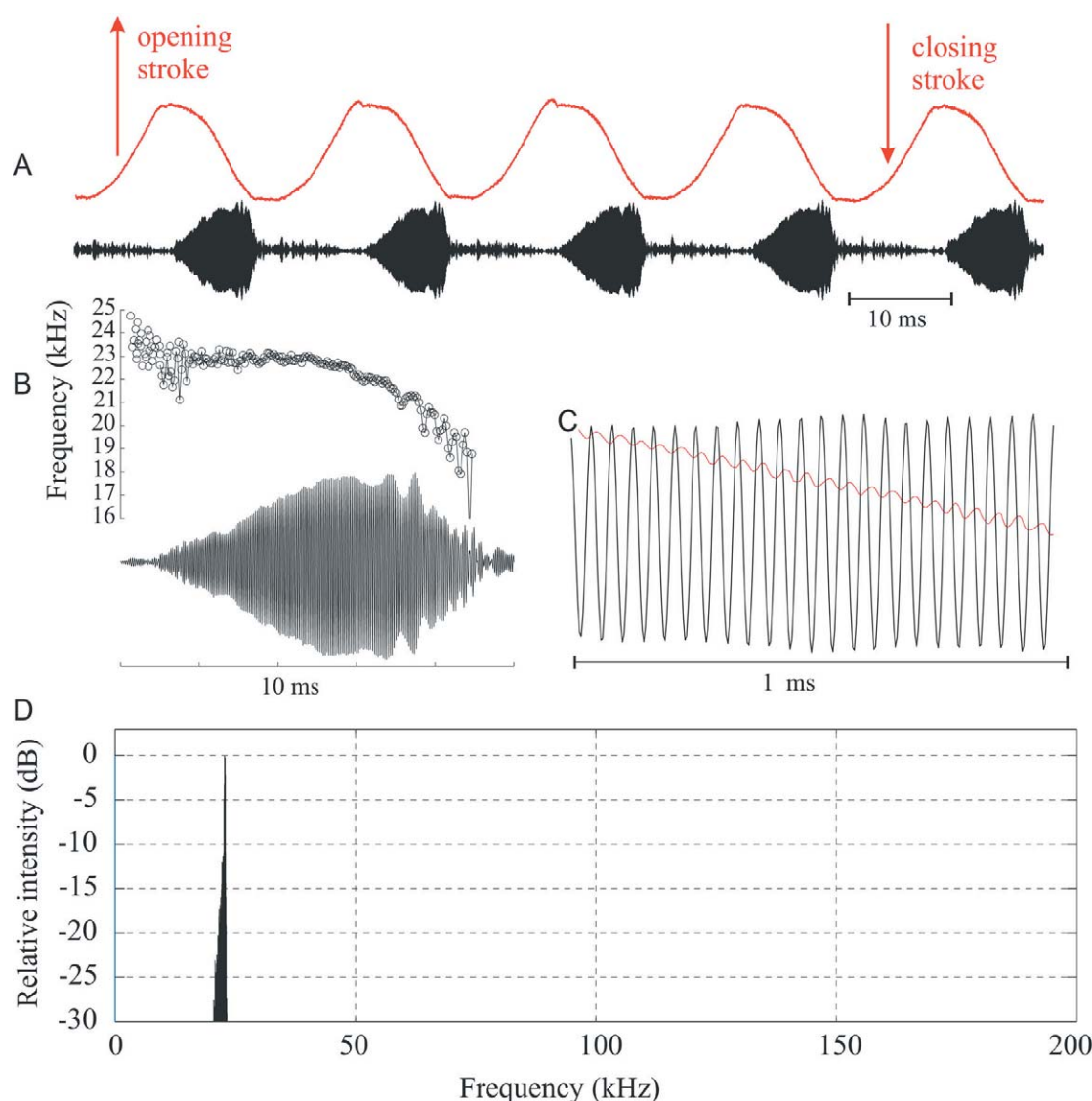


Fig. 2. Analysis of sound and stridulatory movements. A. Sequence of 5 syllables [pulses] (black) and associated wing movements (red). Each pulse is the total sound emitted per cycle of wing movement, *i.e.*, a phonatome. B. Single pulse at high resolution and above corresponding instantaneous frequency. C. Cycles of the pulse in B at high resolution (1 ms). The (red) overlaid trace represents associated closing wing motion. Note the presence of ripples on this motion, associated with an individual sound cycle. D. Spectrum of the pulse shown in B. For color version, see Plate XIII.

($n=12$, range 22.0–24.0 kHz; Fig. 2D). Zero crossing analysis shows that pulses are modulated by 5–7 kHz; modulation usually occurs between 25 kHz and 18 kHz (Fig. 2B). No harmonic components of the fundamental frequency are apparent at 30 dB below peak maximum to up to 200 kHz. The call's remarkable tonality is reflected in a very high Q value, calculated from sound pulses to be 55.3 ± 10.2 ($n=12$).

Wing resonances.—Scanning laser vibrometry indicates the right-mirror area resonates at 19.8 ± 1.7 kHz (Fig. 3). Although this resonance is close to the calling-song carrier (23 kHz), a mismatch of nearly 2.2 kHz is observed (see below).

Q for this observed wing resonance is 20.2 ± 2.3 , much lower than that calculated from the calling song: Q (mean) from song = 50.0 ± 13.7 , significantly different (t test = 4.9, $df = 4$, $p = 0.008$) from that obtained by vibrometry. The left stridulatory area does not exhibit a particularly sharp resonance, however broad-band activity was observed between 5–10 kHz (Fig. 3).

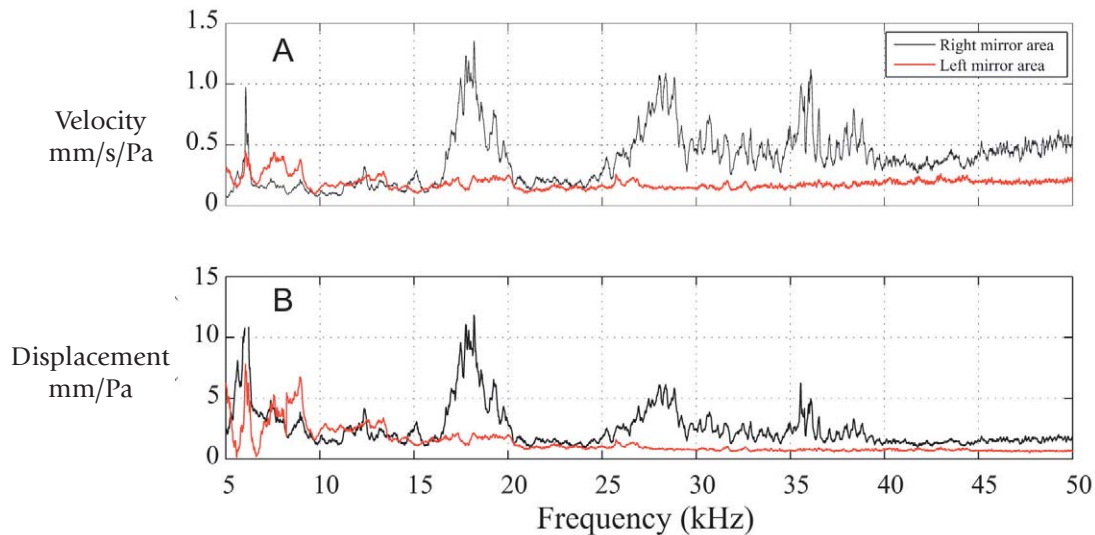
Wing oscillation/deflection at the resonant frequency is dominated by the mirror membrane (Fig. 4). The mirror frame (veins CuPa β +CuPb+AA1 and CuPa β) vibrates well at the average wing resonant frequency, but except for regions 4 and 5 (the CuPa β branch adjacent to the harp, see Figs 4A, 5AB), the thick fusion

CuPa β +CuPb+AA1 moves with lower amplitude than the rest of the frame and than the central membrane (Fig. 4D).

Fig. 5A shows the vibrational pattern of seven regions of the mirror frame in one specimen. There is indeed an obvious deflection (displacement) pattern that suggests a resonance of the mirror frame at nearly 2 kHz lower than the frequency of the call (Figs 4B–D, 5D). The maximum deflection of the mirror frame occurs in regions 4 and 5 (the CuPa β branch adjacent to the harp), and in the central membrane. The 3D reconstruction of the vibration suggests a simple mode of vibration of the whole area, with an obvious nodal region at the scraper (Figs 4E–J, 5A, 6), therefore there is a phase inversion between the vibration of the scraper and that of the mirror (at area 11 in Fig. 5A), this is demonstrated in Fig. 6.

Dominant vibration patterns of the wing are all concentrated in the mirror membrane (area 8), as indicated in the map (Fig. 5A), although the center of the mirror membrane is the only region showing high-frequency modes (~ 28 kHz and ~ 35 kHz, Fig. 5B). These modes are not observed in the carrier of the call (Fig. 2D). Curiously, resonant vibration also occurs in other regions of the stridulatory area (*e.g.*, scraper and other adjacent cells), but in these areas, there were no high-frequency components observed. Therefore, the average right wing resonance is dominated by mirror frame and surrounding cells.

Fig. 3. Scanning laser vibrometry of right and left tegminal resonances. A. Average vibrational velocity response of all points scanned (see Fig. 4B) on the stridulatory area. B. Average vibrational displacement response of all points scanned on the stridulatory area. Black trace depicts the right stridulatory area, red the left one. For color version, see Plate XII.



The observed mirror resonances and deflections show that the mirror frame vibrates at a frequency close to that of the carrier of the call (Fig. 2D) and to that of the average wing resonance (Fig. 3), and its deflection pattern is that expected in a cantilever (e.g., Morris & Pipher 1967, Bailey & Broughton 1970).

Stridulatory motor pattern.—Wing movements are relatively simple, as is typical for other Copiphorini [e.g., *P. pallicornis* (Montealegre-Z 2005, Montealegre-Z & Mason 2005)]. The pattern of stridulation involves a single opening and closing stroke without pause, and a single type of phonatome (Fig. 2A). Males open the wings to a maximum, quickly position the plectrum and file, and gradually close them. The total opening and closing of the forewings (phonatome period) lasts ~18–20 ms ($N=12$). Recordings using the opto-electric position sensor show that high-frequency ‘ripples’ in the position signal are detectable when sound and wing movements are shown at full resolution, corresponding to the sound-radiating oscillations of wing membranes likely generated by tooth impacts (Fig. 2C). This is consistent with previous observations in other katydid and cricket species using pure tones, where tooth contacts occur at a frequency matching that of the calling song frequency and at the resonant frequency of the right tegmen (Bailey 1970, Bennet-Clark 1999a, Elliott & Koch 1985, Koch *et al.* 1988, Montealegre-Z & Mason 2005, Suga 1966).

Discussion

Taxonomic status.—*C. brevicauda* is a neotropical species with an apparently broad distribution, from the northwest region of South America to Central America, as well as Venezuela (Naskrecki 2000). It is possible that a few of the forms currently placed within this taxon are different species, but their recognition is not achievable without reliable song recordings. Because we only have recordings of the Gorgona species, it is difficult to evaluate to what extent our species differs from the population of the type locality of *C. brevicauda*. The only acoustic data available for *C. b. costaricensis* are provided by Naskrecki (2000). Unfortunately, these recordings were obtained with audio-limited equipment, and only the temporal pattern can be used to infer differences. The sound files provided by Naskrecki (2000) in his book’s supplementary CD ROM, appear

tonal to the human ear, and suggest that the calling frequency is indeed in the audio range. The population on the mainland identified by Montealegre-Z (1997) as *C. brevicauda* is also morphologically quite different from the Gorgona species. Although we don’t have sound recordings of specimens from the mainland in Ecuador (the type locality), and mainland Colombia, we consider these differences significant and here give the Gorgona populations a species status. In addition, *C. brevicauda* has been reported in other island ecosystems near Ecuador, e.g., Galapagos (a volcanic island group), as an introduced species (Peck 1996). The Gorgona population, however, might not have been introduced anthropogenically: the presence of other katydid species in Gorgona and the piece of land in Ecuador that was connected with Gorgona during the last glacier (see below) suggest allopatric divergence of the two populations (FM-Z in prep.).

Isolation of the Gorgona population dates from the end of the last ice age. Most geological and biogeographic studies of the zone suggest that Gorgona is, from all points of view, a continental ‘small island’ (Gansser 1950), and that some 17,000 years before the present, this island was connected to the continent as part of a chain of mountains skirting the Pacific coasts of Colombia and Ecuador (Alberico 1986, Pregill & Olson 1981). During the Pleistocene, large glaciers formed that covered a large portion of the polar regions, as well as the peaks of high mountains in the tropics. During the last glaciation, 17,000 years ago, sea level decreased by some 120 m (Pregill & Olson 1981). This was enough to connect Gorgona with the rest of the continent by a land bridge. Several species of vertebrates and invertebrates are shared between the region of Esmeraldas in Ecuador and PNN Gorgona in Colombia, although some species are endemic to Gorgona (Alberico 1986). This suggests that the mainland populations and those from Gorgona were separated by vicariance at the end of the last glaciation, some 11,000 yBP.

Acoustic behavior.—The use of pure-tone signals for specific communication seems to be synapomorphic to the genus *Copiphora* (Montealegre-Z & Morris 2004, Naskrecki 2000). The range of carrier frequencies employed across species is quite diverse, from the audio range (e.g., 8 kHz) to the moderately high ultrasonic (~32 kHz) (Montealegre-Z 2009, Morris 1980, Morris *et al.* 1994).

We have shown here that *C. gorgonensis* uses highly tonal signals

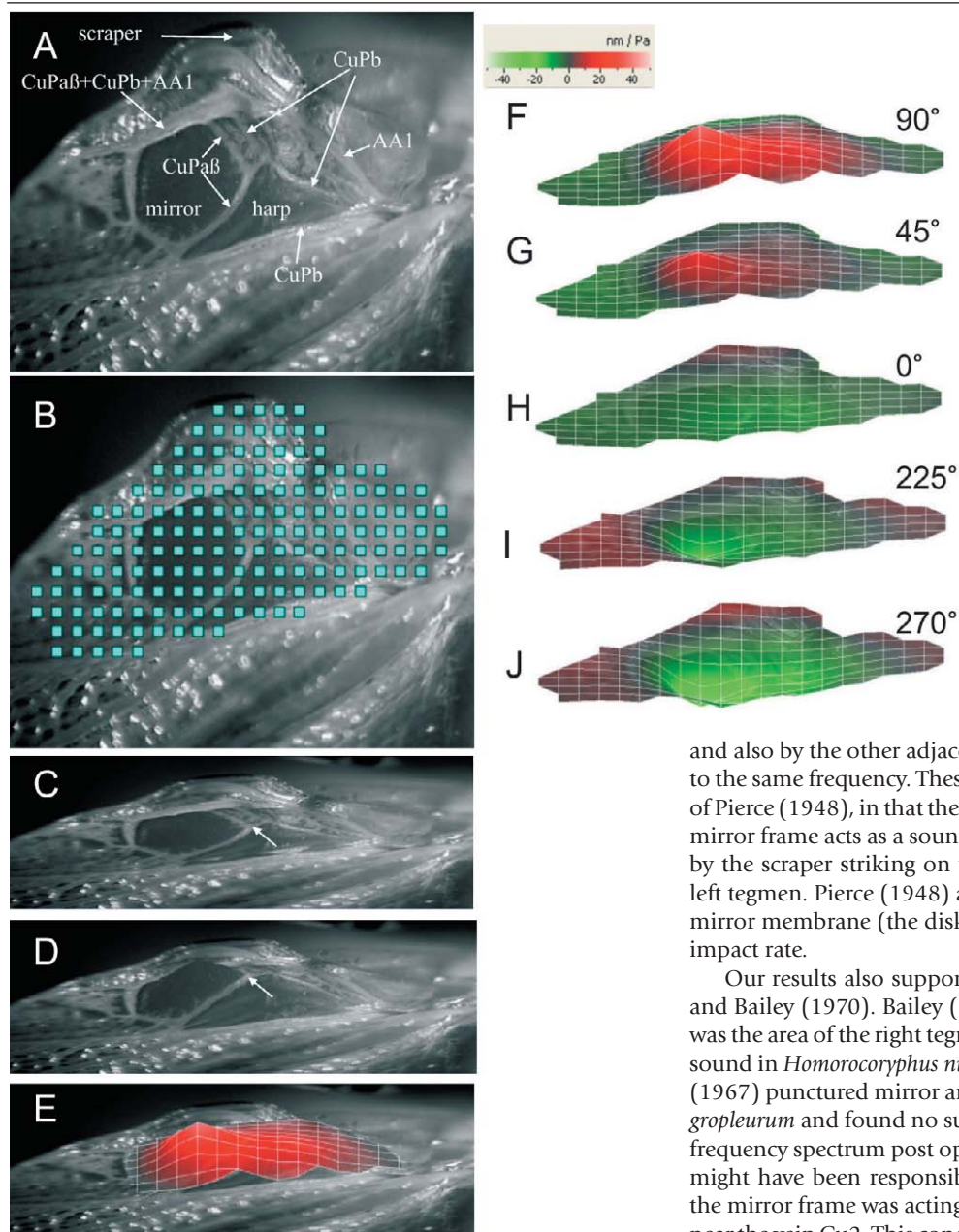


Fig. 4. Scanned area and deflection shapes of the right tegmen dorsal surface. (A-E) Orientation image relating tegmen topography to the position of the scanning lattice. Scanning points are shown in B. (F-J) Area scans of tegmen-membrane deflections at best response (18.8 kHz). Deflections shown each time for five different phases along the oscillation cycle. Red indicates positive displacements (or outward membrane deflections) and green indicates negative displacements (or inward membrane deflections). Arrow in C and D depicts the area of maximum deflection observed in the mirror frame (areas 4 and 5, see Fig. 5). For color version, see Plate XIII.

for intraspecific communication and that the mechanism involved in stridulation is resonance. Resonance, maximum deflection and probably acoustic output, are dominated by the right mirror and its surrounding cells and veins, including the harp and cells formed by the veins CuPa, CuPb and AA1 (Figs 1, 3, 4A).

The mirror membrane of the right wing resonates at a frequency some 2 kHz lower than that of the calling song, and also exhibits two more modes at 28 and 35 kHz, modes which are not evident in the calling song (Figs 3, 5D). This suggests that the mirror (vibrating freely) is a nonlinear system, but when both wings are engaged and stimulated at the right tooth-impact rate, its response is linear with the stimulus, as the association of tooth impacts and oscillations suggests (Fig. 2C).

The mirror frame, on the other hand, exhibits a particular resonance frequency, and the maximum deflection of the frame was observed in the narrower vein CuPaβ, adjacent to the harp (Fig. 4C,D). In the same way, other adjacent cells and veins exhibit resonance similar to that of the mirror frame (Fig. 5C,D). This clearly shows that wing resonance is dictated by the mirror frame

and also by the other adjacent veins and cells, mechanically tuned to the same frequency. These findings support the pioneering work of Pierce (1948), in that the area of thin membrane bounded by the mirror frame acts as a sound-producing disk, forced into vibration by the scraper striking on the teeth of the stridulatory file of the left tegmen. Pierce (1948) also suggested that in some species, the mirror membrane (the disk) vibrated in resonance with the tooth impact rate.

Our results also support the work of Morris & Pipher (1967), and Bailey (1970). Bailey (1970) concluded that the mirror frame was the area of the right tegmen responsible for the radiation of the sound in *Homorocoryphus nitidulus* (now *Ruspolia*). Morris & Pipher (1967) punctured mirror and harp membranes of *Conocephalus nigropleurum* and found no substantial frequency change in the total frequency spectrum post operation; therefore some other structure might have been responsible for the carrier. They suggested that the mirror frame was acting as a cantilever with its rotational basis near the vein Cu2. This conclusion was drawn after determining the predominant frequency, and mirror frame length, of two species: *C. nigropleurum* and *Orchelimum gladiator*.

They adopted a simplified equation taken from Rayleigh (1894):

$$f_o = \frac{k}{ML^2} \quad (1)$$

(where K is a constant [which Morris & Pipher (1967) gave a value of 1] and ML is mirror length). They found a strong relationship between the two parameters, subsequently used by other authors, incorporating more frequency and mirror-dimension values from other species into the equation (e.g., Bailey 1970, Sales & Pye 1974).

The mirror frame of *C. gorgonensis* can indeed be modelled as a cantilever, but the lever is not anchored on the basal regions of the cubital and anal veins, as previous authors believed (Morris & Pipher 1967, Bailey 1970). Instead, the mirror surface seems to pivot at the scraper area (Fig. 6) with maximum deflection of mirror veins observed in between the thin branch of CuPaβ and the harp (Figs 4, 5).

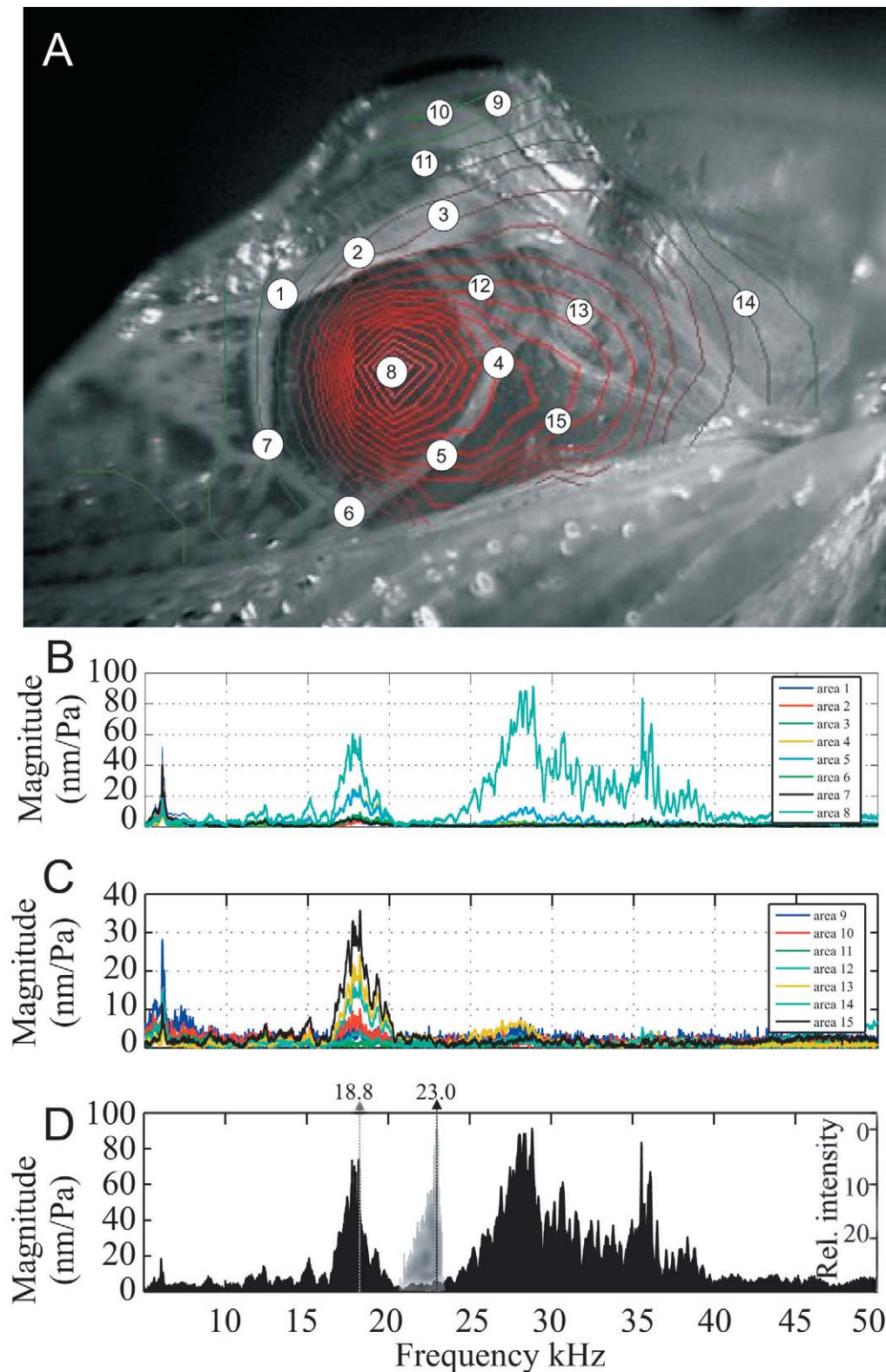


Fig. 5. The vibration of the mirror membrane, frame, and surrounding cells and veins. **A.** Vibration map of the right wing stridulatory region, showing the region (area 8) of maximum displacement at resonance (18 kHz for this specimen). Numbers indicate the different regions of the mirror frame for which local vibrations are shown in B and C. **B.** Displacement and resonances of the mirror frame areas (1-8). **C.** Deflections and resonances of other acoustically active wing cells and areas (areas 9-15) of the right tegmen. **D.** Resonance of the mirror membrane measured from the center of the mirror at area 8 (black shadow); spectrum of the calling song is shown shaded in grey with scale on the right. For color version, see Plate XIV.

This same pattern has been observed in other species of katydids where wing resonance has been studied with laser vibrometry (FM-Z unpub. data). Bailey (1970) reported phase differences between the mirror and scraper of *B. nitidula*, but did not elaborate on the mechanics of this problem. This fact was pointed out by Bennet-Clark (2003), while discussing the phase differences between scraper and harp in field crickets. Montealegre-Z *et al.* (2009) showed mechanical evidence of this phase shifter in crickets.

In crickets a scraper phase shifter is functional only if the scraper-bearing wing is stimulated at its resonant frequency. This suggests antiphase motion between scraper and harp might control the catch and release of the scraper from successive file teeth [the operational clockwork cricket (Koch *et al.* 1988)]. But crickets, having two acoustically functional forewings, need this phase shifter to bilaterally synchronize their (right-left) tegminal oscillations. In katydids the morphological asymmetry of the tegmina is associated

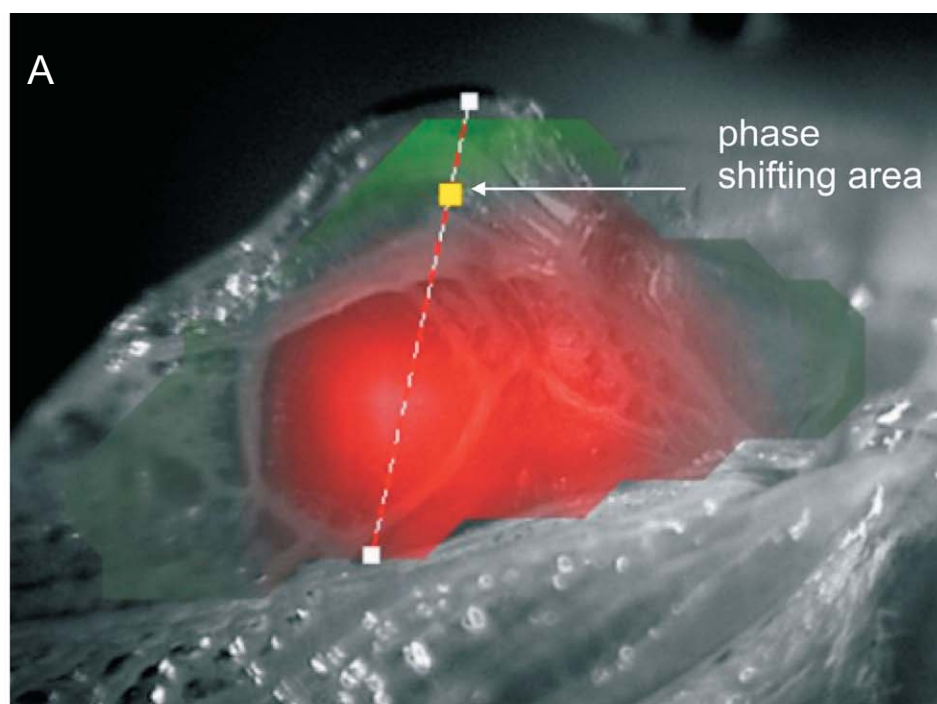
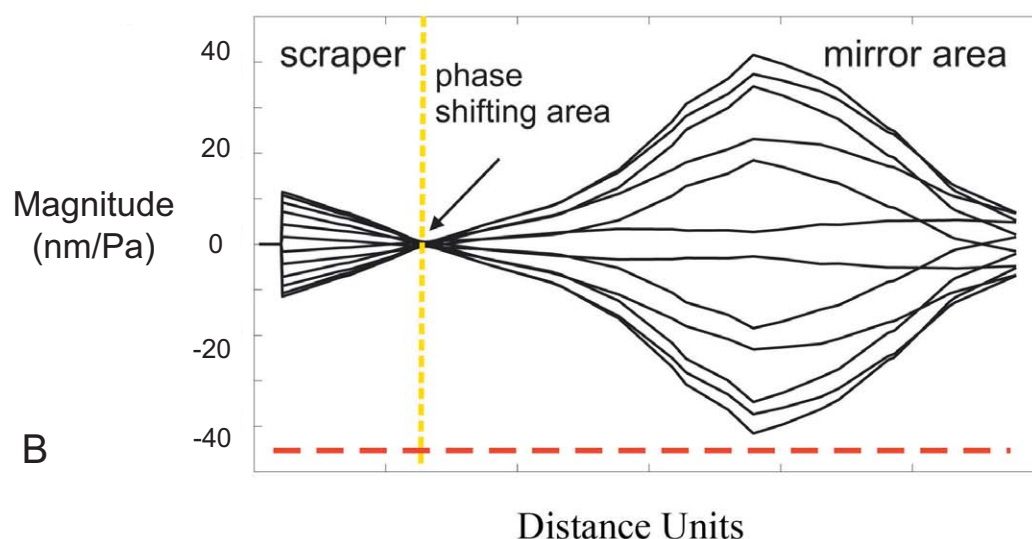


Fig. 6. Envelopes of mechanical deflections across plectrum and harp membranes in a specimen of *C. gorgonensis* along indicated transect (broken red line). The whole wing was stimulated with periodic chirps 5-50 kHz. A. The position along the transect line is given with a calibrated scale (red broken line, 4 mm). This scale corresponds to the x-axis in B. B. Deflection envelope constructed by displaying the instantaneous deflection along the transect for a series of phases (in 30-deg. increments), for a full oscillation; the laser displacement relates to sound pressure. For color version, see Plate XIV.



with dampening of the left wing (Fig. 3). What then is the purpose of having a phase shifter in the right forewing given that the left forewing does not generate significant sound or exhibit large deflections? Is this a condition preserved from the ancestors of Ensifera? Does this phase shifter provide a better and smoother drive of the system during stridulation? This question requires further attention.

The resonant frequency, f_o , of a typical resonant system in which a mass and a spring interact, is given by Bennett-Clark (2003):

$$f_o = \frac{1}{2\pi} \sqrt{\frac{\text{stiffness}}{\text{mass}}} \quad (2)$$

How are we to explain that the observed resonance of the stridulatory area of the right tegmen of *C. gorgonensis* was 2.2 kHz lower than that region's output as the calling-song carrier? During stridulation,

as opposed to when beaming sound at an isolated tegmen, both wings engage and interact, which engagement might be expected to affect the vibration patterns of both wings. The resonance of the left wing, mirror frame, mirror membrane and adjacent cells apparently increases to an optimal value for a single frequency (near 23 kHz). Equation 2 would seem to suggest that this gain could occur by an increment of the stiffness (of the right wing) when both wings engage.

There should be considerable variation in the movement pattern of the mirror, harp and delimiting veins across species. The mirror frame can vary from delicate, as that of *Orchelimum* and *Conocephalus* (Morris & Pipher 1967), to strongly thick, as that of *Panacanthus* spp (Montealegre-Z & Morris 2004). The cantilever model assumes the mirror moves as a bar of length L , but of course this disregards the complexity of the structure. Many of the parameters included in Rayleigh's original equation must surely differ as vibrating structures have different shapes (ring, square, rectangle). More work on

the variation of the mechanical properties of the sound generator (mirror, file, *etc.*) is needed to understand these problems.

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References

- Alberico M. 1986. Biogeografía terrestre, pp. 223-244. In: von Prah H., Alberico M., (Eds) Isla de Gorgona. Bogotá: Biblioteca Banco Popular.
- Bailey W.J. 1970. The mechanics of stridulation in bush crickets (Tettigoniidae, Orthoptera) I. Tegminal generator. *Journal of Experimental Biology* 52: 495-505.
- Bailey W.J., Broughton W.B. 1970. The mechanics of stridulation in bush crickets (Tettigoniidae, Orthoptera) II. Conditions for resonance in tegminal generator. *Journal of Experimental Biology* 52: 507-517.
- Bennet-Clark H.C. 1999a. Resonators in insect sound production: how insects produce loud pure-tone songs. *Journal of Experimental Biology* 202: 3347-3357.
- Bennet-Clark H.C. 1999b. Which Qs to choose: questions of quality in bioacoustics? *Bioacoustics* 9: 351-359.
- Bennet-Clark H.C. 2003. Wing resonances in the Australian field cricket *Teleogryllus oceanicus*. *Journal of Experimental Biology* 206: 1479-1496.
- Broughton W.B. 1964. Function of the mirror in Tettigoniidae Orthoptera. *Nature* 201: 949-950.
- Elliott C.J.H., Koch U.T. 1985. The clockwork cricket. *Naturwissenschaften* 72: 150-153.
- Fletcher N.H. 1992. *Acoustic Systems in Biology*. Oxford, Oxford University Press.
- Forrest T.G. 1987. Sinistrality in the southern and tawny mole crickets (*Gryllotalpidae*, *Scapteriscus*). *Florida Entomologist* 70: 284-286.
- Gansser A. 1950. Geological and petrological notes on Gorgona island in relation to northwestern South America. *Swiss Bulletin of Mineralogy and Petrology* 30: 219-237.
- Hedwig B. 2000. A highly sensitive opto-electronic system for the measurement of movements. *Journal of Neuroscience Methods* 100: 165-171.
- Koch U.T., Elliott C.J.H., Schaffner K.H., Kleindienst H.U. 1988. The mechanics of stridulation of the cricket *Gryllus campestris*. *Journal of Comparative Physiology A* 162: 213-223.
- Montealegre-Z F. 1997. Estudio de la fauna de Tettigoniidae (Orthoptera: Ensifera) del Valle del Cauca [Diploma Thesis]. Cali - Colombia: Universidad del Valle.
- Montealegre-Z F. 2005. Biomechanics of Musical Stridulation in Katydid (Orthoptera: Ensifera: Tettigoniidae): an Evolutionary Approach [PhD. Dissertation]. University of Toronto, Toronto.
- Montealegre-Z F. 2009. Scale effects and constraints for sound production in katydids (Orthoptera: Tettigoniidae): generator morphology constrains signal parameters. *Journal of Evolutionary Biology* 22: 355-366.
- Montealegre-Z F., Mason A.C. 2005. The mechanics of sound production in *Panacanthus pallicornis* (Orthoptera: Tettigoniidae: Conocephalinae): the stridulatory motor patterns. *Journal of Experimental Biology* 208: 1219-1237.
- Montealegre-Z F., Morris G.K. 2004. The spiny devil katydids, *Panacanthus Walker* (Orthoptera: Tettigoniidae): an evolutionary study of acoustic behaviour and morphological traits. *Systematic Entomology* 29: 21-57.
- 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. 1980. Calling display and mating behaviour of *Copiphora rhinoceros* Pictet (Orthoptera, Tettigoniidae). *Animal Behaviour* 28: 42-51.
- Morris G.K. 1999. Song in arthropods, pp. 508-517. In: Davey K.G. (Ed.) *Encyclopedia of Reproduction*. Academic Press, San Diego.
- Morris G.K., Mason A.C., Wall P., Belwood J.J. 1994. High ultrasonic and tremulation signals in neotropical katydids (Orthoptera, Tettigoniidae). *Journal of Zoology (London)* 233: 129-163.
- Morris G.K., Piper R.E. 1967. Tegminal amplifiers and spectrum consistencies in *Conocephalus nigropleurum* (Bruner), Tettigoniidae. *Journal of Insect Physiology* 13: 1075-1085.
- Naskrecki P. 2000. Katydids of Costa Rica. Vol. 1. Systematics and Bioacoustics of the Cone-head Katydids. The Orthopterists' Society at the Academy of Natural Sciences of Philadelphia, Philadelphia.
- Peck S.B. 1996. Diversity and distribution of the orthopteroid insects of the Galapagos Islands, Ecuador. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 74: 1497-1510.
- Pierce G.W. 1948. *The Songs of Insects*. Harvard University Press, Cambridge, Massachusetts.
- 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.
- Rayleigh L. 1894. *Theory of Sound* 1. Macmillan, London.
- Sales G.D., Pye J.D. 1974. *Ultrasonic Communication in Animals*. Chapman and Hall, London.
- Suga N. 1966. Ultrasonic production and its reception in some neotropical Tettigoniidae. *Journal of Insect Physiology* 12: 1039-1050.