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Curious katydids from the Andes of Colombia and Ecuador: three new species, a new genus and acoustic baffles

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Abstract

Four katydid species are treated taxonomically and/or acoustically. Two new species of *Ecuaneduba* are described from Colombia: *E. gambitaensis* sp. nov. and *E. inzaensis* sp. nov. A closely related new species from Ecuador is placed in a new cognate genus: *Acanthoraculus milagro* gen. et sp. nov.; its call is analysed and also the calls of *Ecuaneduba aequatorialis*. Since these genera, *Ecuaneduba* and *Acanthoraculus*, comprise at present the only New World representatives of the subfamily Hexacentrinae, we include them in their own tribe Ecuanedubini. A similar situation exists for a small group of Mecopodinae, for which the tribe Tabariini is proposed. Pronotal shapes, subnotal and subtegmenal spaces — adapted for sound generation — are diverse in these four taxa; costal fields may function as acoustic baffles that reduce short-circuiting.

Key words

Ecuaneduba, acoustic, sound, Tettigoniidae, new species, baffle, stridulation

Introduction

In 1989 near Baeza on the eastern slope of the Andes in the Quijos Valley of Ecuador (Provincia del Napo) Andrew Mason and Glenn Morris recorded songs and collected specimens of an unknown flightless katydid with an unusual produced pronotum as part of its tegmenal sound generator. In 1999 a second and closely related species was discovered in the south of Ecuador (Zamora-Chinchipe) at the northern border of Podocarpus National Park by Holger Braun; calling songs were also recorded for this species.

In November 2005 the orthopterist A.V. Gorochov travelling in Ecuador, collected the Quijos Valley species. He described it in 2006 as *Ecuaneduba aequatorialis*. Undecided as to which subfamily should receive this new genus, he gave it the name *Ecuaneduba* — ‘neduba’ recalling its superficial similarity to the North American genus *Neduba* (Tettigoniinae [Decticinae], Nedubiini). [Nedubiini includes species with variously produced pronota (see Rentz & Birchim 1968) and genera from North and southern South America, as well as Australia.] The subsequent year (2007) Gorochov carefully placed this species into the Hexacentrinae, previously considered a tribe of either Conocephalinae or Listroscelidinae, with Hexacentrinae and Conocephalinae being possible sister groups (Gorochov 2007).

Recently two additional *Ecuaneduba* species from Colombia were discovered by Juliana Chamorro-Rengifo in the insect collection of the Universidad Nacional in Bogotá. The features of these species support generic separation of the smaller Ecuadorian species, which is considerably more delicate and differently colored than *E. aequatorialis*. With the systematic position now resolved, we describe

the additional species and indicate something of the bioacoustics of this remarkable group of four brachypterous tettigoniids from the northern Andes.

Methods

Collection sites (Fig. 1) and depositories are included in the species accounts below. Photographs of the holotypes of the three new species and of a specimen of *Ecuaneduba aequatorialis* are available at Orthoptera Species File Online, subsequently abbreviated OSF (Eades & Otte).

Sound analysis for *E. aequatorialis*

We obtained recordings of nine *E. aequatorialis* males. Samples of five of these singers were made in the field at relatively low (montane) temperatures, 9.6 to 12.3 °C; four other males were recorded indoors in small cylindrical Al-screen cages (mesh of 8 strands/cm, cage diam. 5 cm, height 10 cm, pinned to sound-absorptive foam). Indoors, insects sang at higher temperatures: 19.3–23.7 °C.

The insect's song/call is defined as the signal's most inclusive stereotypically repeated time-domain pattern. In acoustic Ensifera songs/calls are comprised of phonotomes: all the signal produced during one cycle of the tegmenal stridulatory apparatus (Walker & Dew 1972). Phonotome is thus a synonym of syllable. Pulses are wave trains: sound elements delimited by abrupt amplitude changes within phonotomes.

Eight singers were recorded with audio-limited equipment: a Sony Walkman WM D6C Stereo Cassette-Corder with an ECM 909 microphone. The ninth (19.3 °C) was recorded onto a Racal instrumentation tape recorder running at 30"/s: the output of a Brüel & Kjær 1/4" microphone (4135) was conveyed from a B&K Impulse Precision sound level meter (2204) set on linear response (frequency response flat through the audio to 70 kHz). Sound levels measured with this meter were made using its 'Impulse Hold' setting, the clamped microphone's tip 10 cm from and directed at the tegmenal generator, the microphone long axis normal to the plane of the insect's back.

Values for all song parameters of the nine males were averaged for the available recorded calls. For one male we had only a single call. For the male recorded with ultrasonic-capable equipment, 17 calls were available. Of the remaining 7 males, 3 contributed 10 calls, one nine calls, one eight calls, one 4 and one 3. For measure of within-phonotome parameters the penultimate train was selected.

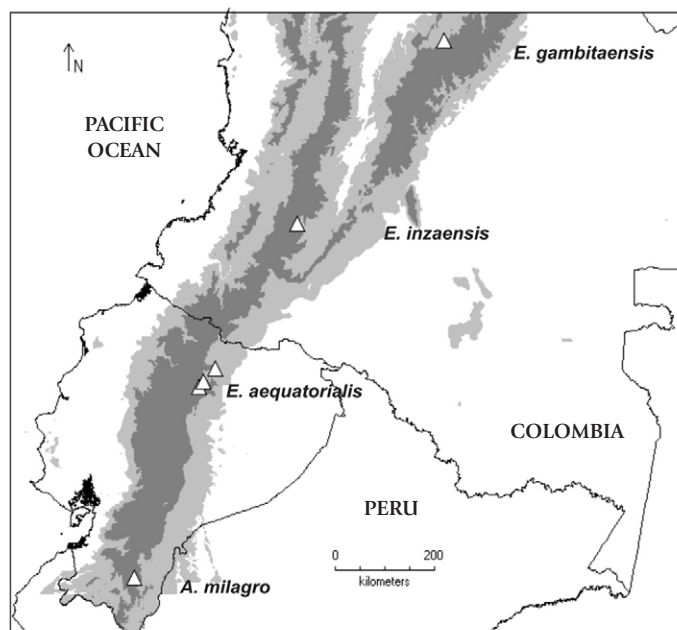


Fig. 1. Distribution map of Ecuadubini species in the Andes of Colombia and Ecuador.

Analysis of audio-limited (<20 kHz) recordings.— Output of the Sony-Walkman cassette tape recorder was digitized at 44.1 ks/s with a PC sound card (Sigma Tel), [attenuated 20 dB (Hewlett Packard 350D),] and opened in Cool Edit Pro 2.1. Each array was subjected to Cool Edit's noise reduction (NR)*¹ and then various time parameters (period and duration of pulse trains *etc.*) measured. Spectral analysis was applied to (signed integer) binary files imported to DADiSP 2002 © ver 6 (DSP Development Corp.) spreadsheet software. Each power spectrum was estimated in DADiSP using Welch periodogram averaging across a time sample of 8192 points that completely incorporated just one penultimate pulse train (spectral resolution, for averaged 8192-point FFTs calculated for each of 127

segments overlapping by 64 points, was 5.38 Hz). Spectra were then expressed in dB relative to the maximum spectral peak.

Analysis of broad-spectrum recordings (flat to 70 kHz).— slowed output (by a factor of 8) of the Racal instrumentation recorder was digitized into Cool Edit at 96000 ks/s with the Sigma Tel sound card. Noise reduction and a 21-dB digital amplification were applied. Signed-integer binary files were imported into DADiSP (sample rate thus $8 \times 96000 = 768000$ ks/s). Estimated power spectra obtained in DADiSP were based upon a time-domain sample of 65536 points that completely captured one penultimate pulse train. Welch periodogram averaging was performed to obtain the spectrum: 4096-point FFTs of 63 segments, overlapped 1024 points, gave a frequency resolution of 187.5 Hz.

Sound analysis for *A. milagro* sp. nov.

(This species is described below, along with its own new genus.) A single male, the type specimen, was collected and accommodated in a dome-shaped gauze cage (edge length of base 30 cm, height 15 cm) inside a scientific station at lower elevation with slightly higher temperatures. It was kept alive for several weeks and provisioned with plant leaves and fresh pieces of cucumber. Recordings were made with a Laar Bridge Box XL (BVL von Laar, Klein-Görnau, Germany), which has an ultrasound-sensitive microphone and a digital-loop memory, from which fragments of 5.12 s (at 400 ks/s sampling rate), 10 times slowed down, were stored on DAT (digital audio tape) using a Sony Walkman (TCD-D7 and TCD-D100). Three recordings of the complex call were made at 18°C, all three very similar, and one is analyzed below. In addition to the Laar Bridge Box, a Mini-3 bat detector (Ultrasound Advice, London) was used for acoustic monitoring in the forest.

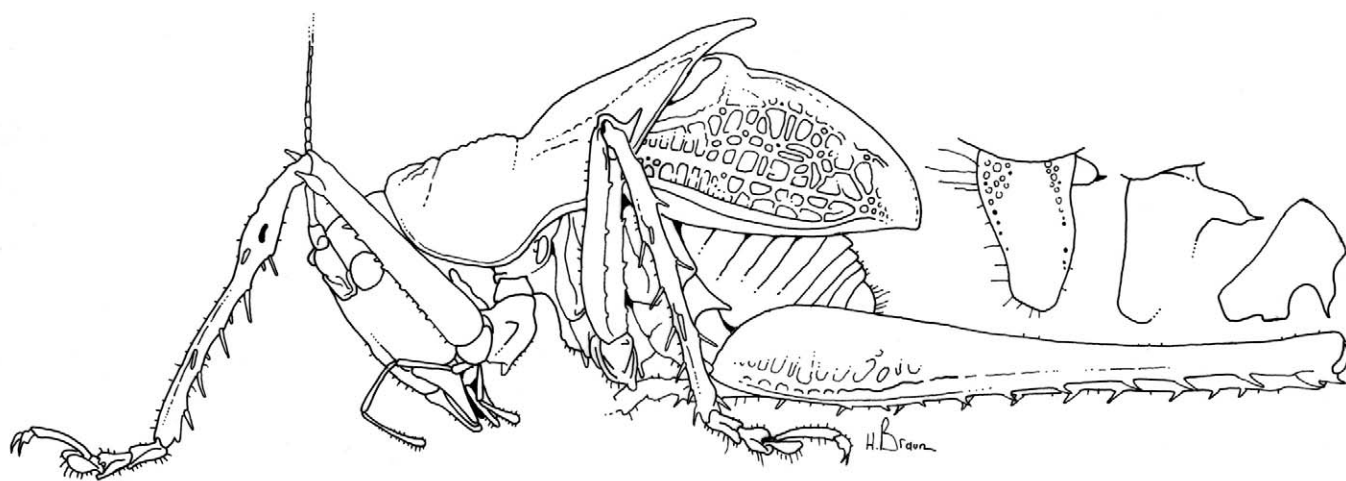


Fig. 2. *E. aequatorialis* male habitus (body length 17 mm, pronotum 11.5 mm, hind femur 17.5 mm) and left cercus in dorsal and dorso-internal view (cercus ~1.5 mm long, internal part damaged; on extreme right is left cercus in dorsal outline redrawn from Gorochoy 2006, his Fig. 3). Specimen from Río Huagra Yacu, Baeza, Ecuador, leg. G.K. Morris 23 April 1989.

¹ Cool Edit Pro 2.1, Syntrillium: the effect of the Noise Reduction (NR) function on spectral peak values was tested for these recordings, using NR vs not using it; applying this had no effect on calculated peak values.

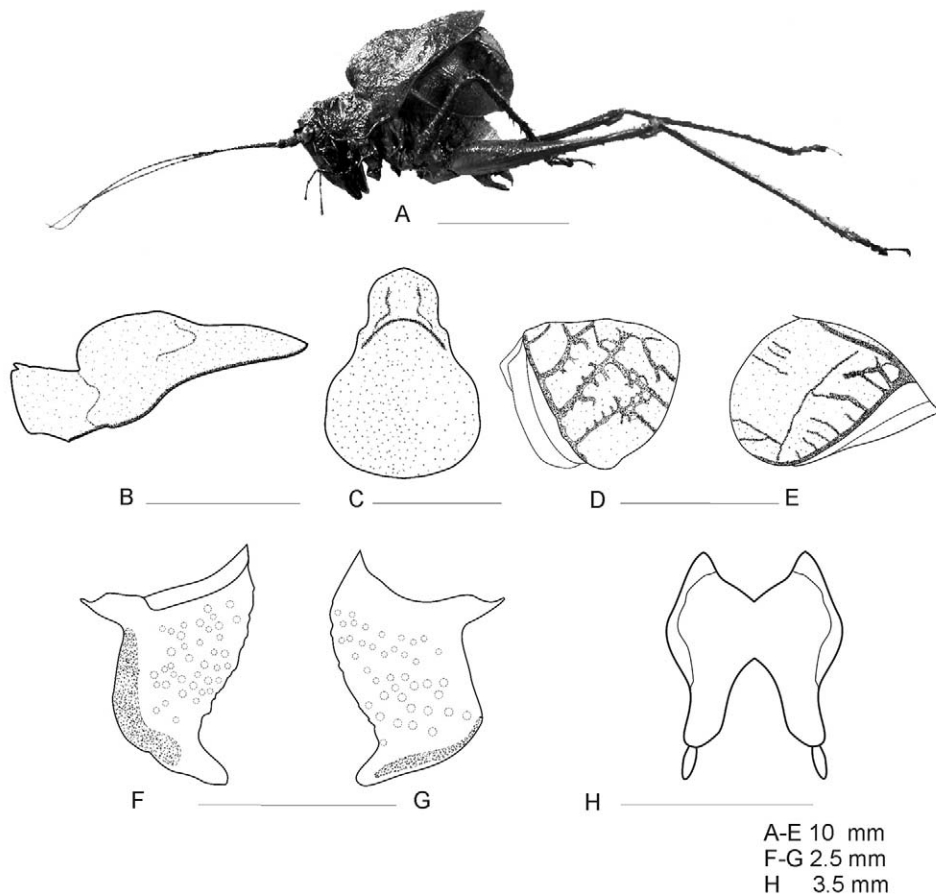


Fig. 3. *E. gambitaensis* sp. nov., male holotype. A. Habitus lateral view. B. Pronotum lateral view. C. Pronotum dorsal view. D. Left tegmen dorsal view. E. Right tegmen lateral view. F. Right cercus dorsal view. G. Right cercus ventral view. H. Subgenital plate ventral view.

A-E 10 mm
F-G 2.5 mm
H 3.5 mm

SYSTEMATIC TREATMENT

Ecuaneduba aequatorialis Gorochoy, 2006 (Fig. 2)

Gorochoy 2006: 47, *Ecuaneduba aequatorialis* (systematic position unclear); Gorochoy 2007: 209, *E. aequatorialis* (Hexacentrinae).

This species has been described in detail, with drawings of male habitus, male and female pronotum, male stridulatory apparatus, and male and female genitalia (Gorochoy 2006). We include another habitus figure of a male specimen (Fig. 2). The female has tiny vestigial tegmina that protrude only a very little from behind the hind margins of the lateral lobes of the pronotum. The overall coloration of the insect is dark reddish brown, which contrasts in males with the bright ochre reticulation of the tegmina. Eyes, tips of the palps and the small medial processes of the cerci are ochre as well. Behind the eyes is a faint ochraceous stripe, which is highlighted by blackish markings below it. The abdominal sternites are very dark, as well as the lateral pattern on the proximal third of the hind femora, the frontal aspect of the first antennal segments, and certain other body parts.

Distribution and habitat.—Ecuador, eastern slope of Andes, Provincia del Napo, Río Quijos valley from 1300 – 1900 m (GKM). In early April of 1989 over successive nights we found a large population of singers above Baeza in a forest remnant bordering a small brook: the locale was reached by walking the steep main street to beyond the hospital, and continuing uphill upon a well-travelled muddy

donkey trail. This same katydid was also located later along the banks of a tributary of the Río Quijos — the first bridged stream on the highway when travelling up-valley from Baeza in the direction of Quito. This stream was signed Río Huagra Yacu. *E. aequatorialis* sang in company with *Myopophyllum speciosum* (Morris *et al.* 1994) at both these sites. Gorochoy reported the species from near El Chaco, which is further down the Río Quijos (1500 m, forest, “near a small river”), and from near the San Rafael Falls (1300 m, primary forest), where Río Quijos undergoes a name change to Río Coca (at the boundary to Provincia Sucumbíos).

Ecuaneduba gambitaensis Chamorro-Rengifo, sp. nov. (Fig. 3)

Etymology.—The specific epithet refers to Gambita municipality of Colombia where the holotype was collected.

Type specimen.—Holotype ♂, labelled: ICN-MHNOR01133 [handwritten on white paper]. Santander, Gambita, Margen del río Luisito, 2600 m. 02/05/1983, col. Ricardo Sánchez [handwritten on white paper]/ *Ecuaneduba gambitaensis* Chamorro-Rengifo [handwritten on red paper]. Depository: Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia (ICN).

Diagnosis.—Differing from *E. aequatorialis* and *E. inzaensis* by (i) the very elongated pronotum (Fig. 3 A-C), extending almost to the seventh abdominal tergite, (ii) the shape of the pronotum, presenting

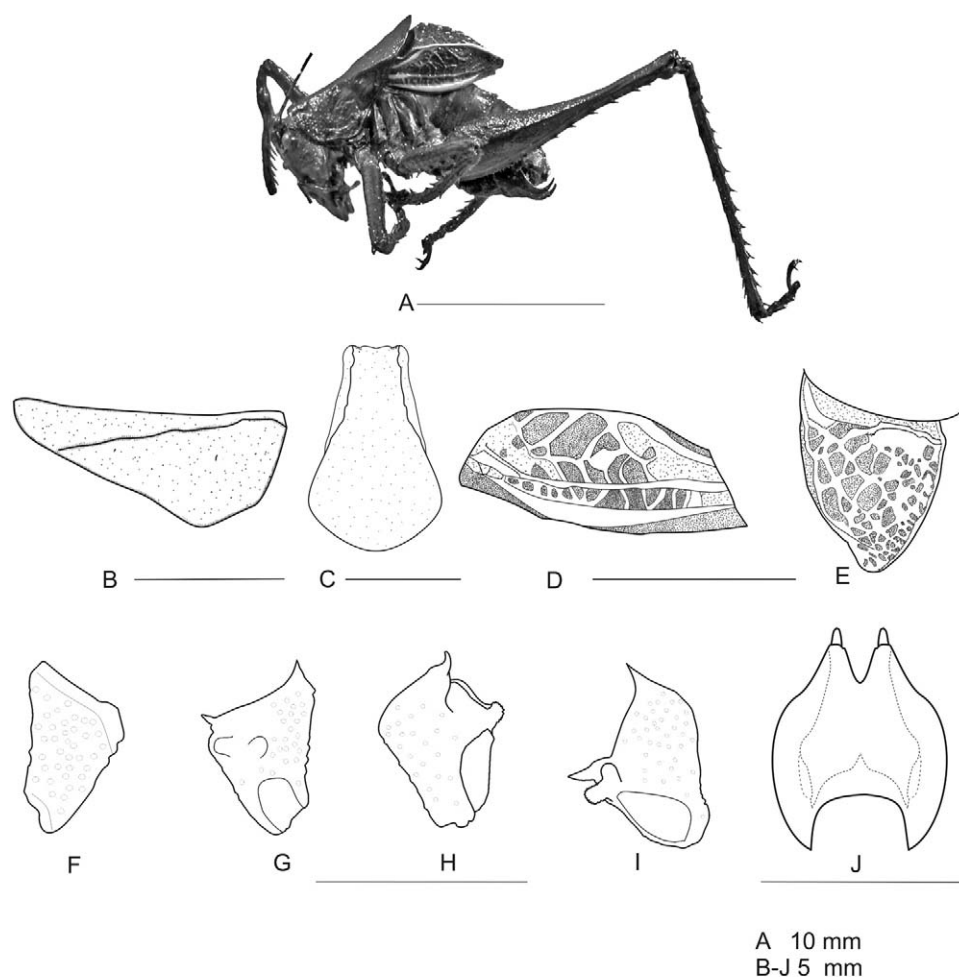


Fig. 4. *E. inzaensis* sp. nov., male holotype. A. Habitus lateral view. B. Pronotum lateral view. C. Pronotum dorsal view. D. Right tegmen lateral view. E. Left tegmen dorsal view. F–I: Right cercus. F. External (lateral) aspect. G. Internal aspect. H. Dorsal side. I. Posteriodorsal view. J. Subgenital plate ventral view.

a distinctive hump very conspicuous in lateral view, (iii) the shape of the cerci (Fig. 3 E,G), which are dorsoventrally flattened, with the apical portion projecting externally into a rounded tip, (iv) a deep internal lateral invagination of the cerci, extending from the internal lateral spine all along the inward-facing portion.

Description.— Male (holotype). General coloration reddish brown, with some parts lighter, almost dark yellow including the dorsal part of the tegmina, dorsal part of the abdomen and proximal part of the hind femur. Generally cuticle surface irregular, not smooth. Head. Narrow in lateral view, about half as long as body; fastigium prominent heart-shaped, evident in frontal view; antennomeres reddish brown. Thorax. Pronotum (Fig. 3 A–C) very produced, covering stridulatory area of tegmina and extending beyond it (in dorsal view of the specimen only a minute portion of the tegmina is visible), in lateral view reaching almost same distance as seventh abdominal tergite; with a large hump at base of metazona; no distinct lateral edges, this enhancing pronotum's rounded appearance, its hind margin rounded. Tegmina (Fig. 3 A,D,E) partially covered by posterior part of pronotum, very inflated, with semicircular lateral appearance; veins very broad with indistinct, short, incomplete ramification. All veins reddish brown and on lateral portions only a little protruding (in contrast to *E. inzaensis*); lateral portions of the tegmina reddish brown; dorsal portion of left tegmen yellowish with protruding reddish-brown veins. Middle femur with four ventral spines on its external edge; middle tibiae with mobile spines of approximately the same size: on the dorsal side with 4 internal

and 2 external spines, ventrally with 6 internal and 5 external ones. Hind femur with 9 internal and 10 external ventral spines, internal and external genicular lobes with one spine, hind tibia with 9 spines on each dorsal edge. Abdomen. Cerci (Fig. 3 E,G) broad and very pubescent, surface with rounded tubercles of varying size; pointed cercal tips curved outward; with an internal basal process bearing a spinule, from which extends a longitudinal furrow along inner face of the cercus. Subgenital plate (Fig. 3 H) with a deep v-shaped incision.

Measurements.— Length of body 17.5 mm, pronotum 15 mm, hind femur 17 mm.

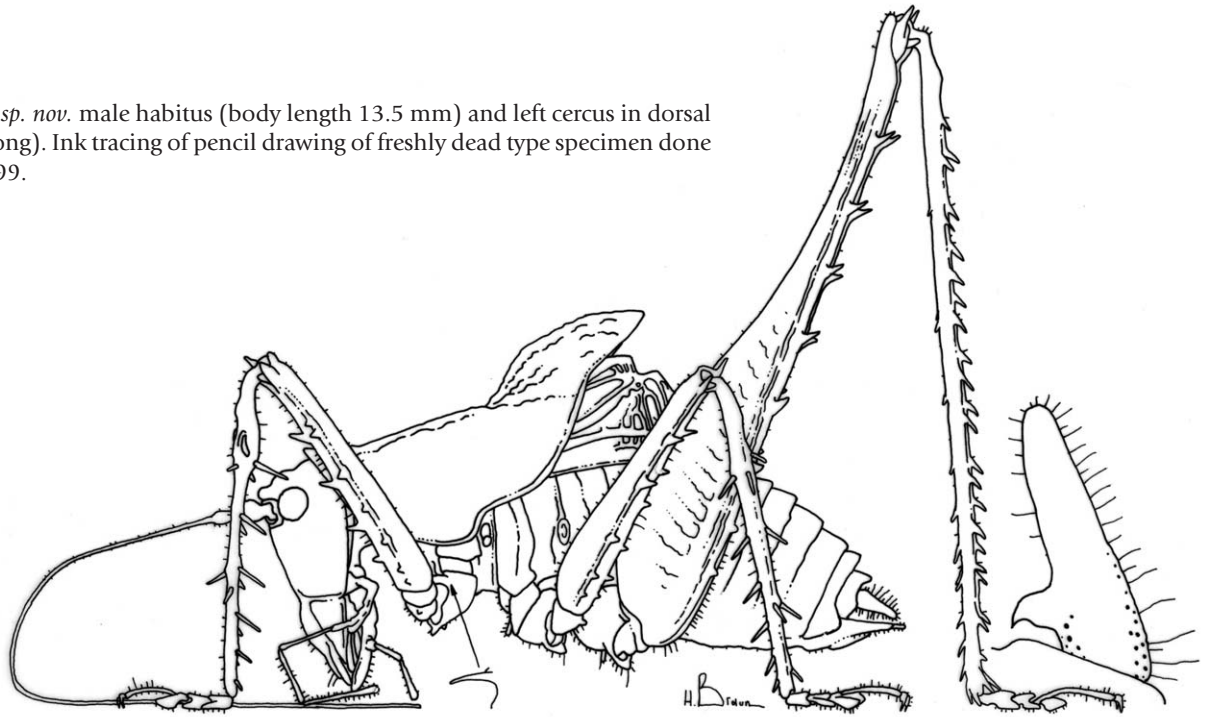
Notes.— The specimen lacks forelegs and the antennae are incomplete.

Ecuaneduba inzaensis Chamorro-Rengifo sp. nov.
(Fig. 4)

Etymology.—The specific epithet refers to Inzá municipality of Colombia where this holotype was collected.

Type specimen.— Holotype ♂, labelled: ICN-MHNOR01132 [handwritten on white paper]. Cauca, Inzá, tierras blancas, 2200 m, 26/03/1982, col. Grupo I [handwritten on white paper]/*Ecuaneduba inzaensis* Chamorro-Rengifo [handwritten on red paper]. Depository:

Fig. 5. *A. milagro* sp. nov. male habitus (body length 13.5 mm) and left cercus in dorsal view (~1.5 mm long). Ink tracing of pencil drawing of freshly dead type specimen done 13-22 August 1999.



Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia (ICN).

Diagnosis.— Differs from *E. aequatorialis* and *E. gambitaensis* by (i) the shape of the pronotum (Fig. 4 A,B,C), with flat dorsal surface and well-developed lateral ridges; (ii) the much shorter tegmina (Fig. 4A), reaching only the fourth abdominal tergite; (iii) cerci (Fig. 4 E,G,H,I) robust and cylindrical, with a deep invagination on the internal side, extending from the second half to the apical margin, (iv) and with two tubercles almost in the middle of the internal side of the cercus (Fig. 4 G,I) and (v) the cercus having a tiny internal spinule on its base (Fig. 4 G,H,I).

Description.— Male (holotype). General coloration dark brown with some lighter areas, with the veins of the tegmina mostly yellow. The cuticle surface is irregular, not smooth. Head. Maximum vertical length of head, around $0.4 \times$ the length of the body; fastigium verticis semitriangular; antennomeres 6, 10 and 18 light yellow. Thorax. Pronotum (Fig. 4 A,B,C) with flat dorsal surface (Fig. 4C), with hind margin rounded and almost reaching first abdominal segment. Tegmina (Fig. 4 A,D,E) reaching fourth abdominal tergite, subcostal vein notably inflated, base of R and the stem of M and Cu also widened and prominent due to yellow coloration. Tibia of the foreleg with six pairs of articulated spines on ventral side: six on inner and six on outer margins. Two articulated spines on dorsal side, only on outer margin, not in pairs. Hind femur with 7 spines on inner and 9 on outer ventral margin; external genicular lobe with 2 spines. Abdomen. Cerci (Fig. 4 F-I) with little rounded tubercles and hairs on entire surface, similar to *E. gambitaensis*; cylindrical, decreasing in diameter from base to tip (the base four times as wide as tip); externally without any protruding structures (Fig. 4F), internally at the first third with two rounded tubercles which point in opposite directions (Fig. 4 G-I), with a spine near these tubercles which is directed anteriorly (Fig. 4 G-H). Subgenital plate with a v-shaped incision, its depth almost a quarter the total

length of the plate, with the lateral margins widened behind the base and then narrowed in the apical third.

Measurements.—Length of body: 14 mm, pronotum 9 mm, hind femur 15 mm.

Notes.— The specimen lacks its left hind leg and the antennae are incomplete.

Acanthoraculus Braun & Morris gen. nov.

Type species.— *Acanthoraculus milagro* sp. nov., described below.

Before JCR discovered the Colombian specimens in the collection in Bogotá (and still unaware of Gorochoff's 2006 paper), we considered describing the two species from Ecuador as members of a single genus. However, the three species of *Ecuaneduba* are too similar to include this tiny katydid, found in the very south of Ecuador, among them.

Diagnosis.— This genus is similar to *Ecuaneduba*, but its (so far) only member is smaller and much more gracile. The coloration, while also mostly dark, reddish brown and ochreous, includes contrasting light-green body parts. The perpendicular lateral processes on all three sternites are more delicate and digitiform (in contrast to the spiniform processes of *Ecuaneduba*). The auditory spiracle is very small and oval, its smaller diameter only about the same as the base of the terminal segment of the maxillary palps (a little smaller than depicted in Fig. 5). In males the tegmina overlap only in the stridulatory area under the pronotum, the short tips are neatly aligned and adpressed at the anal margins along the body midline (Fig. 10).

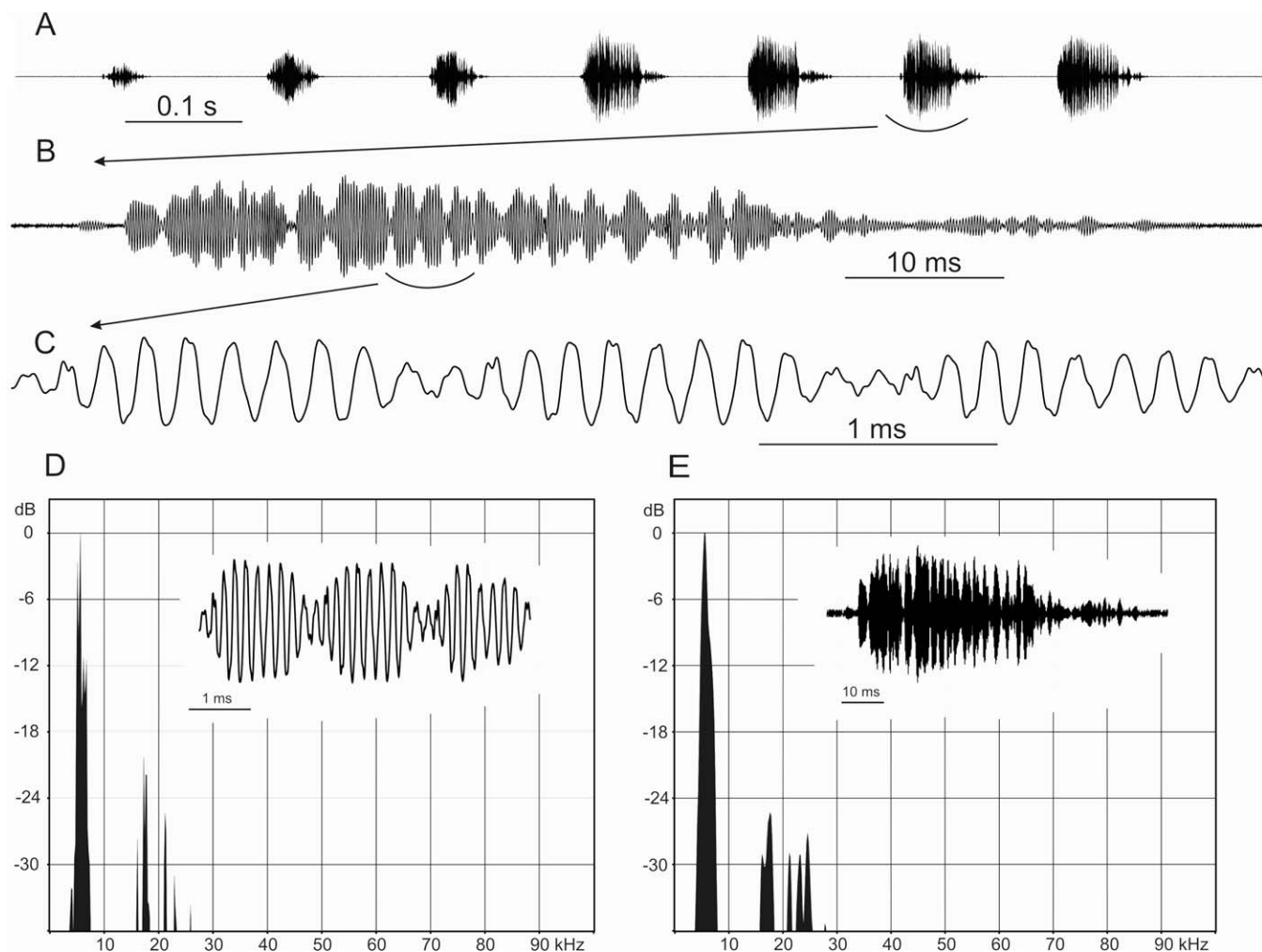


Fig. 6. *E. aequatorialis* calling song analysis. A. Call sequence of 7 phonatomes of incrementing amplitude. B. Penultimate phonatome at higher resolution. C. Three poorly separated pulses from the mid-region of the phonatome in B. D. Power spectrum of the three inset pulses showing high-Q peak at about 5 kHz. E. Welch-smoothed spectrum of the inset phonatome.

Acanthoraculus milagro Braun & Morris *sp. nov.*
(Fig. 5)

Braun 2002: 79 "Milagro-Zwergschrecke"; Braun 2008: 218 *gen. nov.* "Milagro-Zwergschrecke" (Conocephalinae: Agraeciini).

Specimen.— Holotype male (cbt041s01, originally specimen no. 250), Ecuador, Provincia Zamora-Chinipe, northern edge of Parque Nacional Podocarpus, near Estación Científica San Francisco (which is about midway on the road from Loja to Zamora), Quebrada El Milagro, 2200 m, 20 July 1999, leg. H. Braun, depository: Museum Alexander Koenig, Bonn, Germany; sound files cbt041s01r01-r03 (original recordings 6/77-79).

Description.— Coloration: this tiny tettigoniid is beautifully colored in lucent green and light brown, with contrasting dark and reddish brown patterns. The most conspicuous part is the pronotum: the light red-brown pro- and mesozona are clearly separated from the green metazona, which is divided by a reddish midline and bordered by a reddish margin that continues to the ventral margin of the pronotum. The edges of the darker brown side lobes are highlighted by a light-colored line that fades toward the metazona.

The rest of the body is mostly greenish brown with more delicate structures like mouthparts, antennae and cerci light green. The legs are mostly green as well. The tips of all the coxal and sternal processes are light green and contrast with the darkness of the belly. After death the colors become less vivid. Head: all surfaces are smooth. As in *Ecuaneduba* the mandibles are apically strongly pointed and curved inward, but concealed behind the labrum. In dorsal view the eyes are distinctly laterally protruding. The fastigium verticis is very narrow, its tip in dorsal view at best of the same diameter as the first segments of the flagellum, but ventrally much more narrowed, its lateral dorsal outline rounded angular. Thorax: except for some slight wrinkles the pronotum is mostly smooth. Only the abruptly rising metazona has a conspicuously wrinkled surface, like a blurred reticulation. The narrow pro- and mesozona are flat and descend fairly steeply into the sidelobes. The extraordinarily widened metazona is four times as broad as the narrowest point of the mesozona. In the male the tegmina are mostly reduced to the stridulatory apparatus, which is covered by the elongated pronotum. The remaining tegmen surface is laterally almost perpendicular to the stridulatory area, and the costal margin makes a delicate fold, fitting the tegmina snugly to the animal's back and so probably sealing a subtegmenal air chamber (see below). There is also consider-

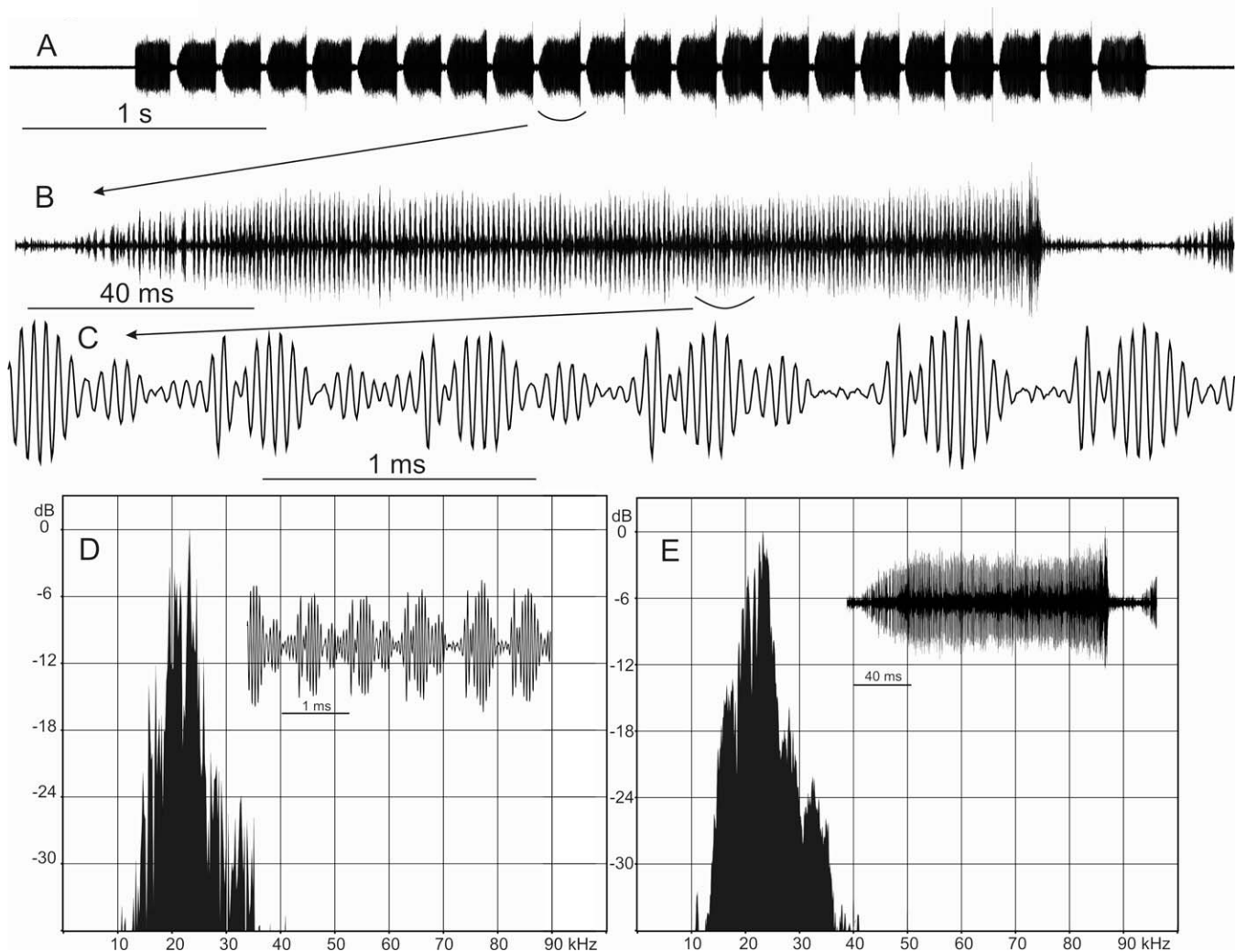


Fig. 7. *A. milagro* sp. nov. calling song analysis. A. Call sequence of 22 phonotomes. B. Mid-region phonatome at higher time resolution. C. A series of mid-region sinusoidal pulses. D. Power spectrum showing peak near 22 kHz with a somewhat lower Q than that of *E. aequatorialis*; FFT calculated upon the inset time sample of resolved pulses. E. Power spectrum of inset phonatome time sample.

able clearance between the stridulatory area and the dome-shaped metazona. The auditory spiracle is very small (reminiscent of that of *Pseudophyllinae*), directed rearward, and accompanied above by a respiratory spiracle. All three sternites have on each side a delicate digitiform process, 1.5 to 2 times as long as the tips of the palps are wide. Legs: all coxae are ventrobasally produced into a toothlet, and ventro-apically elongated into drop-shaped tips, so that the ventral contours look two-tipped, particularly in middle and hind coxae. Fore- and middle tibiae with “movably inserted” spines (reminiscent of *Listroselidinae*), including a few on the dorsal side (cf. Fig. 5). Tympana concealed, only visible in oblique frontal view, through the mostly frontally directed narrow ear openings. Hind legs relatively long. All genicular lobes armed with a spine. Abdomen: the tergites present a dorsolateral row of bulges, comprised of a little bulge on each tergite, and a coarser, more irregular and indistinct lateral row, plus small tubercles more irregularly distributed. The slender and cone-shaped male cerci are each equipped with a basal process that ends in a minuscule spinule. The male subgenital plate has a u-shaped terminal incision and fairly short styli (about as long as the processes of the mesosternum).

Measurements of holotype.— Body length 13.5 mm, antenna 18 mm, pronotum 8 mm (maximum width of metazona ~ 4 mm), hind femur 13 mm and hind tibia 14 mm.

Distribution and habitat.— Only an adult male and a female nymph were found, by HB, he walking at night along Quebrada El Milagro. The specimens sat low on the vegetation close to the creek. The fairly conspicuous calling song was heard five times with the Mini-3 bat detector on a few subsequent nocturnal excursions to that area. All seven records are from between 2120 and 2230 m. The site is on the eastern slope of the eastern cordillera of the Andes, in the transition zone of lower montane rainforest and cloud forest and was undisturbed. Possibly the species prefers a habitat type associated with small creeks, since it was not found in much more extensively investigated forest on or near ridges in that area.

Although a predatory mode of life is assumed for these katydids with their long tibial spines (Gorochoy 2007), and also indicated by the saber-shaped mandibles, the collected male was held for three weeks in captivity, living on vegetation parts and fresh pieces of cucumber.

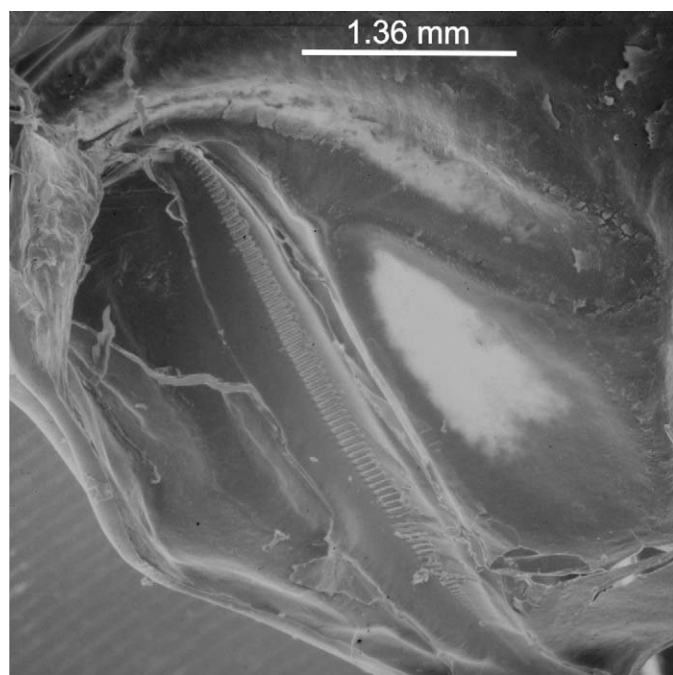


Fig. 8. Scanning electron micrograph of file of *E. aequatorialis*.

SOUND ANALYSIS

Song structure of *E. aequatorialis*

Values throughout this section are averages unless indicated otherwise. The song of this insect (Fig. 6A) is a series of 7 (2 to 18) pulse trains, each train heard by human ears as a 'zip': a call having a perceptible (to the human ear) noisy, rather than musical, infrastructure (Morris *et al.* 1989). The singing of these insects is perceived very differently by the human ear at low *vs* high temperatures. In the field at temperatures of 10 to 12 °C the call period (n =

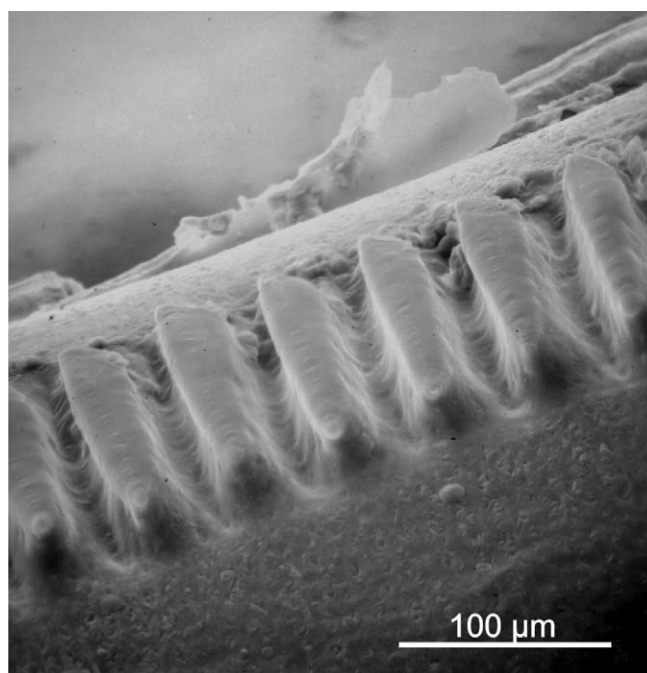


Fig. 9. Scanning electron micrograph of seven file teeth of *E. aequatorialis*.

5 males) was 24 s (range 10 to 33 s); call duration was 2.3 s (range 1.3 to 5.7 s). With caged males, analysed indoors at temperatures of 19 to 24 °C, the call period (n = 4 males) was 17.0 s (range 13.6 to 19.2); call duration was 1.3 s (range 0.5 to 2.1). The first few trains in the song characteristically increment in peak amplitude. (Fig. 6A).

The number of trains per call varied widely. At low temperatures each call had 7.3 pulse trains (range 2.9 to 18), with a train period (based upon the penultimate train) of 314 ms (278-357 ms). At high temperatures there were 9.2 trains per call (range 3.5 to 13.2) with a train period of 141 ms. Train rate is 3.2 per s (low temperature) and 7.3 per s (high temperature). Respective ranges are 2.6 to 4.0 and 6.8 to 8.5.

A low-level sound prolongation made determination of train's end difficult and we tried to measure to the disappearance of robust amplitude. Duration of the penultimate train (low temperature) was 153.3 ms (range 119.5 to 199.5). Penultimate train duration (high temperature) was 76.6 ms (range 68.7 to 82.1).

The pulses that make up each train are not cleanly separated, but set apart by severe amplitude envelope reductions (three such are shown in Fig. 6 C). Roughly the number of such fluctuations (pulses) per train is 30 (28 to 36) at low temperatures, 29 (22 to 37) at higher temperatures.

A single relatively narrow band of sound is emitted (Fig. 6 D,E). Ignoring the temperature differences of the recordings, we found an overall grand mean peak carrier frequency (Welch-smoothed) of 5.38 kHz (range 5.13 to 5.83). Based upon the one male recorded with ultrasonic-capable equipment, there is no significant sound energy above 20 kHz in the song of this Insect. Based upon all the males sampled, there is no appreciable energy above 10 kHz.

Sound levels were obtained for 25 songs of one male using the B&K sound level meter (2204) set on Hold Impulse, the meter needle being reset between calls. The average call duration of about 1 s is well beyond the rise time (35 ms) of this meter. For this one male, sound level averaged 106.2 dB; the B&K microphone was clamped

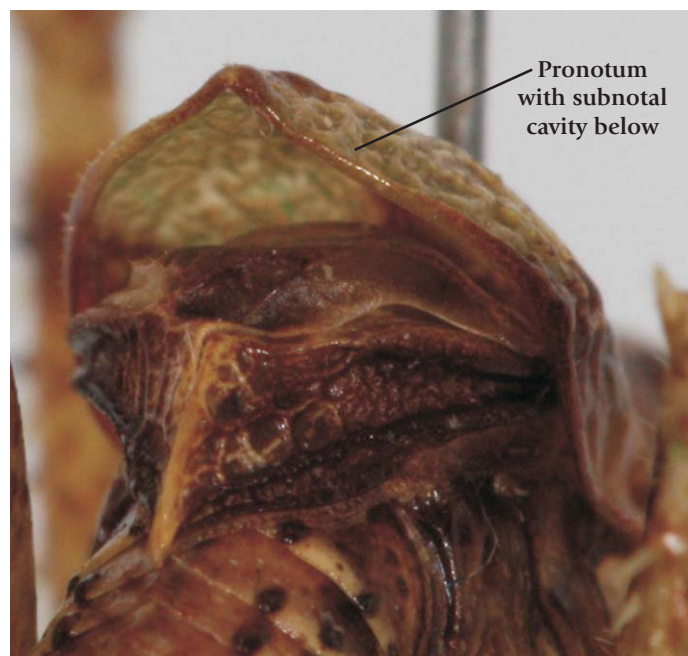


Fig. 10. *Acanthoraculus milagro* male tegmina in posterior view showing overlapping folds that isolate the subtegmina acoustically. See Plates.

with its long axis normal to the plane of the back at 10 cm.

Song structure of *A. milagro*

For the single caged male at 18 °C, each song lasted over 4 s and they were repeated at a call rate of up to about one call per minute. In the natural habitat calls were much more sporadic. In the record shown (Fig. 7 A) there are 22 phonatomes produced at a rate of ~ 4/s. Each phonatome (Fig. 7 B) lasts about 165 ms, a relatively long duration among tettigoniids, and incorporates >175 noisy pulses. The amplitude envelope of the phonatome begins gradually and drops near the phonatome end before increasing to a maximum (giving a shape like a bell on its side). Each pulse (Fig. 7 C) has an unusual form: a short, abruptly higher-amplitude wave train, is followed by a train of 7 or 8 waves, attaining lower peak amplitude and rising and falling more gradually and symmetrically.

The carrier frequency is a single rather narrow peak (narrow for what is apparently a nonresonant band stridulator) located at 23.3 kHz (Fig. 7 D) (power spectra calculated over 16,384 samples, the most part of one phonatome [insert], broken into 127 segments, overlapped by half the segment length). The sinusoids of the individual pulses are simple enough to estimate the carrier in the time domain and the insect has a surprisingly high-Q signal.

Discussion

Taxonomy.—We agree with Gorochov's (2007) inclusion of *Ecuaneduba* in the Hexacentrinae for the following reasons: in addition to the similar pronotum shape, *Ecuaneduba* and *Acanthoraculus* share several diagnostic characters with this subfamily: all three sternites have a pair of spines or digitiform processes, fore- and middle tibiae sport long spines, and the male paraprocts are equipped with finger-like processes. However, all nine other genera (a total of 40 species) of Hexacentrinae are distributed in Africa, tropical Asia and Australia. A similar situation exists for some South American Mecopodinae, another mostly Old World subfamily of Tettigoniidae. New-World mecopodines comprise three species, each in its own genus, from western South America: *Encentra longipes*, *Rhammatopoda opilionoides* and *Tabaria opilioides* (Chamorro 2009).

These two small groupings of Hexacentrinae and Mecopodinae, morphologically similar within their group, are in each case the only New World representatives of their respective subfamilies. As such, each almost certainly evolved from a single common ancestor. It seems therefore useful for practical purposes and also because it is systematically well-founded, to unite these taxa into two tribes: *Ecuaneduba* and *Acanthoraculus* into Ecuanedubini, *Encentra*, *Rhammatopoda* and *Tabaria* into Tabariini.

Ecuanedubini trib. nov. (under Hexacentrinae Karny, 1925)

Diagnosis.—Tiny or fairly small flightless tettigoniids with a widened pronotal metazona that entirely conceals in males the stridulatory areas (specula) of the greatly reduced tegmina. All three sternites on each side with a perpendicular spine or digitiform process, and all three coxae, basally spine-like elongated, so that the ventral contour looks two-tipped. The foretibia has 2-3 dorsal spines, one directly below the ear region and 1-2 spines one-third of the way from the end of the tibia. The auditory spiracle is fairly small and completely exposed below the ventral margin of the pronotum (at least in slightly posterior view).

Distribution.—Andes of Colombia, Ecuador and possibly northern Peru.

Included genera.—*Ecuaneduba* Gorochov, 2006, and *Acanthoraculus* gen. nov.

Tabariini trib. nov. (under Mecopodinae Walker, 1871)

Diagnosis.—Medium-sized and apterous tettigoniids with exceedingly long legs, giving them a somewhat spider-like appearance. The pronotum sports conspicuous lateral tubercles or spines, and the pleura also can have coniform or bilobate structures. Meso- and metasternum produced into one or two spines on each side. The hind femora often with fairly strong dorsal spines.

Distribution.—Andes of Colombia, Ecuador, and Peru.

Included genera.—*Tabaria* Walker, 1870, *Encentra* Redtenbacher 1892, and *Rhammatopoda* Redtenbacher, 1892.

Both tribes share a similar distribution in the northern Andes. In each case they must be the descendants of Old World populations of an ancestral species that became isolated by the separation of South America from Africa 90 to 100 mya. In the case of the Ecuanedubini the closest living relatives are probably in the diverse and widely distributed genus *Hexacentrus*, which includes three species from West Africa (Eades & Otte). There is another recently described genus in the Hexacentrinae, *Aerotegmina*, with two species discovered on East African mountains (Hemp 2001, 2006). Interestingly, like the Ecuanedubini, they have considerably reduced and modified tegmina. Wing reduction might be related to constant conditions in tropical forest ecosystems and to the montane habitat (Hemp 2001, Braun 2002), with other modifications being an adaptation for efficient sound production: in *Aerotegmina* the tegmina of males are laterally expanded, enhancing the volume of a subtegmenal air space (see below), as in *Ecuaneduba*. Such modifications are apparently a general tendency in the Hexacentrinae (Hemp 2001).

Bioacoustics

Most male tettigoniids stridulate (make sound by rubbing cuticular surfaces) with tegmina; they draw a scraper on one forewing along a file of teeth (Fig. 9) on the other and so send thinned transparent cuticular wing cells – specula (singular speculum) — into oscillation (Ewing 1989). During stridulation the tegmina are flexed over the dorsum; they are roof and sides of a subtegmenal space formed against the meso- and metanota of the thorax, and to varying degrees, depending on forewing length, formed against the terga of the abdomen. Where the pronotum becomes elaborated rearward, as in these Ecuanedubini spp., a second space is created between the upper surface of the tegmina and the underside of the pronotum: a subnotal cavity (Fig. 10). Such cavities recur among Tettigoniidae (e.g., Morris *et al.* 1975, Morris & Mason 1995).

Beyond these general outlines, there is great structural diversity among tegmenal generators of different katydid taxa. Most species are macropterous, with their tegmina used in flight as well as sound generation — but in many brachypterous species, tegmina are shortened and function solely in sound generation. Tegmina are flat or inflated to various degrees, altering the shape and volume of the subtegmenal cavity: pronota are produced flared or downturned distally, altering the shape and volume of the subnotal cavity.

Tegmina are typically bilaterally asymmetrical in accordance with file and scraper function, but sometimes approach mirror-image symmetry. Veins and specula are variously thickened and shaped. Specula can be sunken relative to their delimiting veins and overhung by shelf-like projections, *etc.* The function of this varied generator morphology is largely unexplained. Features such as those seen here in *Ecuaneubini* — elaboration of the pronotum, dilated costal fields, enlarged subtegmina and subnotal spaces — are unexplained acoustic adaptations.

Of itself, a tettigoniid speculum is a small, thus very inefficient, dipole (Fletcher 1992, p.238), meaning that, as a tiny oscillating disc with a high proportion of edge to area, its design encourages significant 'short-circuiting' about disc edges. The compression of air particles on one side is partially cancelled by the rarefaction created simultaneously on the other, and sound intensity consequently reduced. Fletcher indicates that the efficiency of such a dipole may be greatly increased by evolving its morphology toward that of a monopole. By isolating the lower surfaces of the specula from their upper surfaces, by making the subtegmina cavity into a closed box, the generator comes to radiate only from its upper surface: it becomes more of a monopole and less subject to short-circuiting.

The likely function of the costal field in these species is as an acoustic baffle that helps close off the subtegmina cavity. An acoustic baffle is an obstacle which impedes sound in its course, *i.e.*, which impedes the propagation of sound. The costal region in all the species herein is soft and flexible in life, in contrast to the relative stiffness of the rest of the tegmen, and it drapes upon the tergites of the abdomen all along the sides of the subtegmina cavity during stridulation. Its pliability makes it a good baffle because it remains undisplaced by mechanical forces. To complete the baffling of the subtegmina cavity, the rear extremities of the tegmina in *A. milagro* (Fig. 10) are adpressed and bent.

The subtegmina and subnotal spaces 'load the drivers' (specula) differently, depending upon shape, volume and isolation. The contained air of a closed small space against a vibrating membrane can provide an acoustic compliance (elasticity) (Morris *et al.* 1975), showing high resistivity rather than reactance. Compliance is frequency dependent (Speaks 1992, p. 82). Perhaps these spaces are adaptive in providing best compliances for the radiated carrier frequency?

The male pronota of the *Ecuaneuba* spp. dealt with here are rather diverse for species in the same genus. In *E. inzaensis* the posteriorly produced pronotum is low and flat (Fig. 4), perhaps the least modified from a more typical tettigoniid pronotum. It lies immediately above the two specula. In *E. gambitaensis* the pronotum is produced posteriorly above the specula, but not so tightly adjacent; it is also inflated anteriorly (hump/hunch, see above), adding to the volume of the subnotal cavity (Fig. 3). The tegmina of this species also contrast with those of its congeners by being strongly foreshortened and distended convexly. *E. aequatorialis*' pronotum is somewhat intermediate in form, lacking the forward elevation and being produced rearward with a downturned posterior margin (Fig. 2); its brachypterous tegmina are only modestly convexly swollen.

The spaces above and below the drivers in these four species are quite different, suggesting inequality of acoustic function. And it is peculiar that the specula, surely important drivers of the generated sound, are placed so oddly in regard to free-field radiation. In all four species the specula are severely occluded by the produced pronotum during stridulation. Or to say it otherwise: the subnotal

space is quite small (*E. gambitaensis* may be an exception in regard to its hump which adds volume to the subnotal space.) In *E. inzaensis* especially, the flat metazona of the projecting pronotum lies hard above the two specula. Either the specula can still radiate effectively under these shielded conditions — the pronota and swollen nonspecular tegmina being viewed as baffles, or they bring about effective secondary radiation by the pronotal projections and the nonspecular regions of the tegmina. We should consider the possibility that nonspecular tegmina regions and produced pronota may be — not baffles — but adapted as sound radiators. The robust appearance and thickness of these cuticular structures may not be an accurate indicator of their function.

Stridulation in Ensifera is either resonant or nonresonant (Morris 2008): indicated by high-Q or low-Q (band) spectra (Q is the central tendency of spectral peaks and see Ewing 1989, p.8). The high-Q peak (Fig. 6 D) produced by *E. aequatorialis* indicates a resonant mechanism, *i.e.*, that the predominant peak (carrier) of 5.4 kHz will coincide with a tooth contact rate by the scraper of 5400 teeth per s. Each pulse is markedly sinusoidal (Fig. 6 C). The carrier of *E. aequatorialis* is very close to the wavelength used by many cricket species (Otte 1992) and is markedly more narrow (higher Q) than the near-band spectrum of *A. milagro*. But unlike the situation in typical crickets, the overall amplitude envelope of the phonotome is fluctuating fairly regularly, dropping off, building, tailing off again (three such fluctuations are shown in Fig. 6 C).

The two species studied here exhibit the expected relationship of lower frequency with larger size (Morris 2008) common among singing insects. The larger species calls at 5.4 kHz (Fig. 6 D,E); the smaller species calls at about 24 kHz (Fig. 7 D,E). The ratio of the carriers (smaller to larger) is 4.3. But the size ratio (smaller to larger) based upon the body length of the two holotype males, is only ~ 0.7. Hence, in this study, body size difference predicts the carrier difference in the right direction — but rather badly.²

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²Surface area is proportional to length squared, and both volume and mass are proportional to length cubed (Whitman 2008). Thus, area, volume and mass may be better predictors of carrier differences in singing insects than length.

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