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Uchuca Giglio-Tos, *Dectinomima* Caudell and their Allies (Orthoptera: Tettigoniidae: Conocephalinae)

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ABSTRACT

This paper addresses the phylogenetic relationships of the tettigoniid genera *Dectinomima* Caudell and *Uchuca* Giglio-Tos. A new species is named of *Dectinomima* and the genus redescribed. Males of this genus present the odd characteristic of a stridulatory file with extreme tooth density: > 600 teeth.

Four new species of *Uchuca* are described, all alate. In four the vestigial file of the right tegmen is well developed; the functional file in two species terminates suddenly, well short of the wing base, something not seen before in a katydid.

This paper contains a revision of the genus *Dectinomima,* with description of the male of *D. jenningsi* and of a new species: *D. sagittata*. Based on the male genitalia, *Dectinomima* differs considerably from *Uchuca*. Both genera appear to be closely related monophyletic groups, as previously thought, but they are members of a larger generic complex, incorporating the genus *Paranelytra* and several undescribed genera from the New World. A complete analysis of their calling songs accompanies detailed descriptions of two of the new *Uchuca* spp. These acoustic signals are ultrasonic and present considerable interspecific variation in quality factor (Q).

INTRODUCTION

Dectinomima is a small poorly known genus of tettigoniid conocephaloid katydids, with species distributed in Panama, Peru and Colombia (Caudell 1910, 1918, Nickle 1992, Montealegre 1996). Three species were described at the beginning of the last century (see Caudell op. cit.): *D. jenningsi, D. peruviana* and *D. pallida,* based on a few female specimens.

The genus *Dectinomima* has been considered part of a generic complex, comprised of *Uchuca* Giglio-Tos, *Sphyrometopa* Carl and *Eppia* StÂl (Caudell 1918, Rentz 1976, Naskrecki 1999: 96). Caudell (1918: 23) raised the possibility that *Dectinomima* and *Uchuca* were the same genus. He separated females generically by the length of the tegmen and anticipated finding males of *Dectinomima* in which these organs would be longer than in their females. Caudell also used tibial spines to establish relationships within both *Dectinomima* and *Uchuca*, placing these genera initially in different subfamilies: *Dectinomima* in Copiphorinae and *Uchuca* in Agraeciinae (Karny 1912ab).

One feature shared by *Dectinomima* and *Uchuca* is their predominantly brown-black, apparently cryptic, coloration, matching their natural forest-floor

litter habitat. These insects spend the day in concealment in curled leaves (Nickle and Castner 1994, Naskrecki 2000) and are rarely seen unless disturbed into a jump. They are probably omnivores, feeding on detritus on the ground, and two specimens were seen (by FM-Z) eating lepidopteran eggs.

No evidence has been offered to justify the separation of *Dectinomima* and *Uchuca*. The characters given by the original descriptors and other authors (see appendix 1) are generally ineffective for separation at the generic level. A lack of male specimens often contributes to this kind of misinformation.

In this paper we present the description of a new species of *Dectinomima* and describe, for the first time, the male of a second species. We describe four new species of *Uchuca,* redescribe *U. grisea* Giglio-Tos, and present a calling song analysis for two species of this genus. Table 1 allows separation of the genera. We attempt to clarify the phylogenetic associations of the generic complex to which *Uchuca* and *Dectinomima* belong.

METHODOLOGY

Fieldwork

Colombia: FM-Z carried out fieldwork on Colombian spp. on a trip to the Amazon drainage at the National Natural Park (PNN) Amacayacu in the Departamento de Amazonas (lat 3°50'-3°02' S, long 69°54'-70°20' W, elevation 100 m) between April-May 2000. Specimens were hunted at night along footpaths with the aid of headlamps. This park, of 293.5 ha, has an annual rainfall of ~3000 mm and a mean temperature of 27°C. We reviewed additional material collected occasionally (by FM-Z) in the Pacific coastal rainforests of Colombia between 1995-1997: Bajo Calima, San Isidro and Escalerete. These three sites are all in undisturbed tropical rainforest in the Departamento del Valle del Cauca, belonging to the municipality of Buenaventura. They are reached via the old route from Cali to Buenaventura (Simon Bolivar Road). Rainfall in the region is extreme: between 3400-6000 mm per year with peaks of precipitation between March-May and October-November.

Ecuador: Fieldwork in Ecuador was performed by GKM on several trips between 1985-1990 to the following localities: 1) Mishaualli, Prov. Napo: lowland rainforest 17 km east of Tena at the junction of the Rios Misahualli and Napo (lat 1° 2' S, long 77° 40' W; elevation 400 m). 2) Jaguar, Prov. Napo: the focal point of this locality is a hotel in mostly undisturbed lowland rainforest; it is on the north bank of the Rio Napo 2 h downriver from Misahualli by canoe (lat 0° 59' S, long 77° 30' W; 300 m). 3) Tinalandia, Prov. Pichincha: a small forest preserve southwest of Quito, at km 112 of Via Santo Domingo de los Colorados, 16 km SE of Santo Domingo (lat 0° 19' S, long 79° 3' W; elevation ~600 m). This is lowland rainforest, typical of the western slopes of the Andes, with ecological affinities reaching into Colombia.

We reviewed material borrowed from the following museums and institutions:

United States National Museum, Washington, D.C. (USNM)
University of Michigan Museum of Zoology (UMMZ)
Academy of Natural Sciences, Philadelphia (ANSP)
MusËe de Paris France (MUPA)

Museo de Instituto di Zoologia Sistematica dell'Universita di Torino, Italy (MIZT)
Museo de EntomologÃa Universidad del Valle, Cali Colombia (MEUV)
Instituto de Ciencias Naturales, Universidad Nacional de Colombia (ICN)

Song recordings

Calls of some Colombian specimens were recorded at a field station in the Amazon using the zero-crossing output of a U30 (Ultrasound Advice) bat detector onto a Sony Walkman Professional tape recorder. Though limited to the audio range these recordings allowed us to determine amplitude modulation patterns (pulse patterns). The Colombian specimens *(Uchuca* spp.) were later transported alive from the Amazon to Palmira (Dpto. del Valle del Cauca), and recordings made here with equipment flat in frequency response from 500 Hz to 70 kHz; the temperature in the room was 24°C. Ultimately specimens were transported to Canada alive and their songs recorded in a laboratory at the University of Toronto, also using ultrasonic-effective equipment. Live males of *Dectinomima jenningsi* were transported from Panama to Canada.

All recordings in Canada were performed in a sound-proof room. Recorded insects sang enclosed individually in small cylindrical metal screen cages atop a foam block to avoid reflections. Full-frequency recording utilized the output of a Br¸el & Kjaer 1/4" (4135) condenser microphone clamped and alligned normal to the dorsum of the singer. The microphone output was amplified with a sound level meter (B & K 2204) and conveyed to a Racal instrumentation tape recorder, running at a speed of 30"/s. Signals were later digitized using a board (Tucker Davis) at a sampling rate of 180 kHz, then analyzed with DADISP software. The temperature in the room ranged from 24.4° to 24.8°C.

Sound levels (re 20 ºPa) were measured with the 1/4" condenser microphone and 2204 sound level meter. Unless otherwise stated, readings were taken on Hold with the microphone placed 10 cm from the insect's dorsum. Scanning electron micrographs were obtained using a Hitachi S-2500 microscope belonging to the Department of Zoology, University of Toronto.

We calculated an acoustic property of the song generator apparatus of two of the species described here: the quality factor Q, which describes the damping properties of resonant systems (Bennet-Clark 1999b, and references therein). Q supplies an index of the sharpness of tuning of a simple resonant system, one that produces a symmetrical frequency power spectrum (Bennet-Clark op.cit). The quality factor can be calculated in several ways. We calculated it by measuring the logarithim of the decay (decrement) per cycle; this is given by:

$$Q = \frac{\pi}{Ln\ decrement}$$

RESULTS

Genus **DECTINOMIMA** Caudell

Dectinomima, Caudell, 1910: 96. Type species: *Dectinomima jenningsi* Caudell. Karny, 1912: 10.

Redescription

Fastigium blunt, moderately protruding, as wide as scapus or slightly wider (Fig. 1M,N). Pronotum in profile with dorsal line convexly curved, in transverse section considerably arched, rounding widely into lateral lobes. All three zones of pronotal disk moderately narrow, cephalic margin weakly rounded; caudal margin regularly strongly arcuate; principal transverse sulcus weakly impressed, almost inconspicuous; lateral lobes of pronotum longer than deep; cephalic margin of lobes moderately arcuate oblique, ventrocephalic margin oblique but sinuate dorsad, ventrocaudal angle roundly obtuse, caudal margin oblique; in general arcuate posteroventrad, with weak humeral sinus; surface of lateral lobes conspicuously punctate. Brachypterous, tegmina hidden by pronotum; pronotum produced more in males than females. Male cercus robust, bearing irregular internal swelling mesodorsally and elongate mesointernal tapered projection anteriorly or posterorly upcurved (Figs. 1A-C, G-I). Cercus has an apical projection moderately concave, acute, upcurved. Titillators prominent, sclerotized curled, divergent (Fig. 1F, L). Supranal plate of male trigonal, longitudinally excavate. Subgenital plate of male hexagonal, basally broad, with two minute styles directed laterad. Subgenital plate of female, elongate, sulcate laterally, minutely or broadly incised apically (Fig. 1E, K). Supraanal plate of female broadly triangular, longitudinally excavate. Tenth tergite of male and female truncate, medially deeply, broadly notched. Paraprocts similar in both sexes, elongate, projected posteriorad, converging medially, apically strongly arcuate lateriorad. Female cerci conical, slightly bent inwards, basally constricted, proximally conspicuously expanded laterad, with apex acute. General coloration shiny black-brown. Lateral lobes of pronotum with conspicuous black mark dorsally, continuing onto the terga dorsolaterad.

Dectinomima jenningsi Caudell

Dectinomima jenningsi Caudell 1910: 96. Holotype female, Central America, Panama, upper RÌo Peguini, USNM Washington, D.C., USA.
Dectinomima jenningsi Karny 1912: 10.
Dectinomima jenningsi Hebard 1927: 142.
Dectinomima jenningsi Naskrecki and Otte 1999: (CD ROM) Vol. 1. *Dectinomima jenningsi* Eades 2001.

Distribution.—Rainforest along the Central Cordillera in Panama.

Diagnosis.— (Figs. 1, 3, 5, Tables 2, 3). Prosternum armed. Male cercus bearing irregular internal swelling mesodorsally and elongate tapered projection curved posterodorsad (Fig. 1G-I).

Description of the male.— *Head*. Fastigium moderately produced, but conspicuously blunt; about same diameter as widest part of scapus (Fig. 1N). Scapus dilated distally mesad. No facial marks occur.

Thorax. Pronotum conspicuously convex, without lateral carinae, surface smooth. Anterior margin almost truncate, produced posteriorad rounded, covering small strongly shortened tegmina. Lateral lobes minutely punctate, ventroanterior edge moderately sinuous; ventroposterior angle acutely rounded, continuing into curved posterior edge. Thoracic spiracle hidden by swollen oval region of pronotal lobe.

Legs. Anterior femur short, moderately thick basally, ventrally bearing 1 to 3 spines on distal half of anterior margin; foretibia moderately longer, with 6 small spines on each margin. Midfemur shaped like anterior, with same number of spines; midtibia with 6 spines on both margins. Hind femur strongly swollen basally, abruptly narrowed over distal third, with 5 spines on anterior margin, posterior margin with 3. All genicular lobes with spines.

Wings. Subcostal vein extremely weak, parallel to R on basal half, slightly diverging on distal half. Ma strong, straight, reaching apical margin of wing; Mp curved over basal two-thirds, bifurcate on distal third, both branches conspicuously narrower than main trunk. Mirror area subquadrate, adjoined by large triangular cell. Scraper regions strongly narrowed, projected downwards. Stridulatory file very short (1.7 mm), straight, with ~370 teeth (n=1) (Fig. 3A-C), a density of 217 teeth/mm.

Abdomen. Subgenital plate, apically truncate, styles very reduced (Fig. 1J). Titillators ending acuminate strongly downcurved apically(Fig. 1L).

Female. Differs from male only in size, pronotal length and genital characters. Ovipositor conspicuously curved and acuminate. Subgenital plate elongate, basally broad, with 2 lateral and 2 medial longitudinal depressions; apically deeply, broadly incised, ending in two large triangular lobes (Fig. 1K, O).

Coloration.— General coloration dark brown. Fastigium frontalis with cream band extending from lateral ocelli to anterior part (Fig. 1N). Rest of face atropurpureus. Pronotum fulvescent. Abdominal terga amber, with medial longitudinal rhomboidal marks. Abdominal pleurites fulvid, pleuroabdominal membrane purpureal, abdominal sternites atropurpureus. Fore and middle legs brunneus; hind femur ventrally atropurpureus, dorsally brunneus. Supraanal plate, cerci and paraprocts, cream.

Specimens examined.— (n=5, 2 males, 3 females). PANAMA: Provincia Cocle: PNN Omar Torrijos: El Cope: 780 m, 2 males, 3 females, F. Vargas & F. Montealegre, V 29 - VI 4 2002 (ANSP). Upper RÌo Piguini: 1 female (holotype No. 12918), A.H. Jennings, III-1909 (USNM).

Dectinomima sagittata n. sp.

Type locality.— Colombia, Valle del Cauca, Buenaventura: Escalerete: 100-150 m, (3°42' N, 75° 50' W). Holotype male, type depository: MEUV.

Etymology.— Named in reference to the arrow-shape of the frons mark (L. sagitta = an arrow).

Distribution.— *D. sagittata* occurs in rainforest along the Pacific coast in the Departamento del Valle del Cauca in Colombia. Probably its distribution extends to other areas in the Departamentos of ChocÛ in the north and Cauca to the South.

Diagnosis.— (Figs. 1 A-F, 2, 4; Tables 2, 3). Black sagittate facial mark (Fig. 1M). Prosternum unarmed. Male cercus bearing an irregular internal swelling

mesodorsally (Fig. 1B indicated by an arrow) and elongate tapered projection curved caudodorsally (Fig. 1ABC). Apically cercus bearing laminar projection, originating in swollen region but becoming slender, moderately concave, then apically acute and curved upward. This projection is distally tripartite; one of these ending in a curved hook (Fig. 1C, arrow).

Description.— Head. Fastigium moderately produced, conspicuously blunt; about 1.2x widest part of scapus (Fig. 1M), dorsally finely punctate. Scapus dilated distally mesad.

Thorax. Pronotum conspicuously convex, without lateral carinae (Fig. 2), surface smooth; anterior disc margin weakly rounded, posteriorad produced rounded, covering small strongly shortened tegmina. Lateral lobes densely punctate, ventroanterior edge sinuous; ventroposterior angle acutely rounded, continuing into curved posterior edge, which just overlies swollen callosity covering thoracic spiracle.

Legs. Anterior femur short, moderately thick basally, bearing 3 spines on distal half of anterior margin; foretibia of similar length, with 6 small spines on each margin. Midfemur shaped as anterior, with same spination; midtibia with 6 spines on both margins. Hindfemur strongly swollen basally, abruptly narrowed over distal third, with 7 anterior-margin spines, posterior margin 4. Posterior tibia with 6 and 4 spines on anterior and posterior margin respectively.

Wings. Subcostal vein extremely weak, parallel to R, latter strongly thickened, curving apically to its termination. Ma present as wide swelling, occupying great part of postradial field; Ma shaped like R, but curving moderately toward anal field, branching there in some small veins. An inconspicuous vein, originating at initiation of stridulatory vein, runs distad toward anal margin: possibly this vein is C1. Region in which vein curves, strongly dilated. Stridulatory file very short (1.33 mm), straight, with 606 teeth, tooth density 456/mm (n=1) (Fig. 4BD). Stridulatory vein (dorsal view) 1.5 mm; mirror somewhat trapezoidal (Fig 4A).

Abdomen. Subgenital plate, apically truncate, styles very reduced (Fig. 1D). Titillators ending in two projections, one above digitate, one below twisted spatulate (Fig. 1F).

Female. Differs from male only in size, pronotal length and genital characters. Ovipositor conspicuously curved, acuminate. Subgenital plate elongate, constricted, with small incision apically, so ending in two small rounded lobes; characterized subterminally by small deep lateral depression (Fig. 1E).

Coloration.— General coloration dark brown. Fastigium frontalis atrous, continuing to black sagittate mark of frons (Fig. 1M). Rest of face, legs, abdomen fulvid. Lateral lobes of pronotum with conspicuous atrous mark dorsally, this projecting to dorsal part of terga laterad. Abdominal terga amber with some small continuous lateral dark bands. All specimens with dark contrasting spot dorsally (basal and distal) on foretibiae. In some specimens mid-and forefemora flecked with brown.

Material examined.— (n=8, 2 males, 6 females). COLOMBIA: Valle del Cauca: Buenaventura: Escalerete: 180 m, 1 male (holotype), F. Montealegre, XI 18 1995 (MEUV). Bajo Anchicaya: 270 m, 1 female, F. Montealegre, X 20 1995 (MEUV). Bajo Calima: 70 m, 1 female, F. Montealegre, VI 17 1995 (MEUV); 1 female, F. Montealegre XII 1996 (ANSP); 2 females (MEUV), 1 male (ANSP),F. G. K. Morris, F. Montealegre and F. Vargas, V 13-16 1996. San Isidro: 60 m, 1 female, F. Montealegre, XII 1996 (ICN).

Remarks.— Montealegre (1996) indicated this species as possibly belonging to a new genus, basing this conclusion on the absence of prosternal spines. But this is not a reliable trait: in some cases the incidence of prosternal spines varies between species of the same genus (e.g., *Panacanthus* spp. Montealegre-Z and Morris 2004). After reviewing Caudell's type material, we have included this species in *Dectinomima* mainly for its overall similarity to *D. jenningsi*, terminalia of the female and the traits that differ in general pattern from *Uchuca,* such as size and coloration (see discussion). It is possible to find some homologous parts in the male genitalia (cerci and titillators), however the structure of these genital traits is different in both species.

Genus **UCHUCA** Giglio-Tos

Uchuca Giglio-Tos 1898: 89. Type species: *Uchuca grisea* Giglio-Tos, designated by monotypy; Karny, 1912: 23.
Uchucha Kirby, 1906: 263, mispelling of *Uchuca*.

Redescription.— Fastigium convex dorsad, apex blunt, truncate, about as broad as first antennal segment, this segment broadly expanded distally interiorad; surface of fastigium smooth. Pronotum in profile with dorsal line slightly arched, in transverse section moderately convex. Disk of pronotum somewhat narrow in all zones, cephalic margin truncate, caudal margin of disk usually arcuate; principal transverse sulcus weakly impressed, lateral lobes of pronotum moderately longer than deep; cephalic margin of lobes straight oblique, ventrocephalic angle straight, ventrocaudal angle roundly obtuse, caudal margin rounded, with weak, almost inconspicuous, humeral sinus; surface of lateral lobes moderately punctate. Prosternum armed. Tenth tergite varies from minutely incised to conspicuously projecting (Fig. 5P-T). Male cercus bearing elongate acuminate compressed projection, varying in size interspecifically. Cercus basally with another sclerotized appendage, also varying interspecifically in size from moderately developed to noticeably lengthened (Fig. 5F-J). Titillators curved rod-shaped, projecting dorsolaterally, converging ventrally, apically acuminate and either smooth or dentate on ventral edge (Fig. 5V-Y). Female subgenital plate emarginate posteriorad; lateral margins terminating distad in a lobe, directed dorsomesad, between a mesodistal emargination. Dorsal and lateral aspects of plate parted by carina. Lateral margins bear deep sulcus, elongate or reduced (Fig. 5A-D).

Remarks.— When describing this genus, Giglio-Tos (1898) considered the relationship between *Uchuca* and *Anthracites* from Indo-Malaysia and pointed out a resemblance of both genera to Decticinae. We think these genera are unrelated (see discussion), and that other genera, including some from the Old World, may be more properly linked to *Uchuca* and *Dectinomima*.

Uchuca grisea Giglio-Tos

Uchuca grisea Giglio-Tos, 1898: 89. Holotype male and lectotype female (dry-preserved) South America: Ecuador: Valle de Santiago; Museo de Instituto di Zoologia Sistematica dell'Universita di Torino, Italy.
Uchuca grisea Kirby, 1906: 263.
Uchuca grisea Karny, 1912: 23.

Distribution.— Known only from the type locality: Valle del Santiago, Ecuador.

Diagnosis.— (Figs. 5AFKPV, 6A, Table 4). Terminal projection of male cercus narrower than in other species, extremely elongate, acuminate. Basal sclerotized appendage strongly pollicate (Fig. 5F). Cercus with two distal lobes ventral and dorsal, between which longest portion formed. Dorsal lobe usually touches basal pollicate appendix; ventral lobe narrower, terminally acuminate. The two arched untoothed sclerites of titillators apically acuminate, not bifurcate (Fig. 5V). Upper membranous part of titillators with thin chitin layer.

Redescription.— *Thorax*. Pronotum in male produced caudad in rounded extension reaching beyond stridulatory area of tegmina; cephalic margin of disk truncate.

Legs. Genicular lobes of forelegs with vestigial spine externally, internally unarmed, genicular lobes of midlegs externally unarmed; other genicular lobes unarmed. Front femur with two, middle femur with three, widely spaced short spines on ventroanterior carina; hind femur with 6-7 spines on ventroanterior margin, 4 on ventroposterior.

Wings. Tegmina and wings attain second tergite, never extend to abdomen; apex of tegmen rounded. Sc and R of tegmina parallel to wing extremity, curved slightly upward terminad; Ma, Mp diverging from half total length of tegmen. Male tegmina not approximating mirror-image symmetry.

Abdomen. Tenth tergite in midline strongly triangularly incised posteriorly (Fig. 5P). Male subgenital plate moderately retuse; styli distinct, curved laterad (Fig. 5K). Female subgenital plate broadly incised quadrangular, truncate in middle; lateral sulci short, only reaching lateral portion of each lobe (Fig. 5A).

Color description.— Lightest colored regions of body honey-yellow. Post ocular region and dorsal region of pronotal lobes fuscotestaceous; occiput and pronotal disk irrotare fulginous; apex of fastigium fuliginous. All femora and abdominal pleurites fulvescent; dorsally moderately covered with minute fuliginous spots; subtympanal and distal regions of fore- and mid tibiae fulvid. Basal appendix of cercus hypographous distally. Ovipositor glassy, ochraceous.

Remarks.— This species presents the simplest (when compared with other species of the genus) titillator character state (smooth and not bifurcate apically) , but also the most complex and elaborated male cerci. On the basis of cerci, 10th tergite and male subgenital plate, *U. grisea* may be related to *U. similis* and *U. macroptera* (here described). When other traits are analyzed (e.g., 10th tergite, stridulatory file, female subgenital plate), this species appears to shows a large number of derived conditions, more than any other species.

Material examined.— ECUADOR: Provincia Napo: Valle del Santiago: East of Amazon Cuenca 1 male, 2 females (Giglio-Tos types), Coll. Dr. E. Festa (Nel Darien e Nel Ecuador) , 1985-1896.

Uchuca similis n. sp.

Type locality.— Peru: Provincia Loreto: Iquitos: Quistococha. Type depository: MusËe de Paris, France (holotype male, pinned).

Etymology.— The epithet similis refers to this species' resemblance to *U. grisea*.

Distribution.— Known only from the type locality.

Diagnosis.— (Figs. 5EJOTY, 5B, Table 5). Tenth tergite in middle strongly retuse, curvate dorsad (Fig. 5T). Longest portion of male cercus flat, elongate, ending acuminate; basal sclerotized appendage moderately pollicate; cercus has one distal lobe ventrally (Fig.5J). Callosity or vestigial lobe dorsally, almost touching basal pollicate appendix. Titillators strongly sclerotized curving transversely ending semi-bifurcate, with conspicuous deflected acicular spine, dentate below (Fig.5Y). Region dorsad of titillators sclerotized (Fig. 5Y, arrow).

Description.— *Thorax*. Pronotum in male produced caudad over stridulatory area and part of tegmina; caudal section of disk produced in semirounded extension; cephalic margin of disk truncate.

Legs. Genicular lobes of femora unarmed on fore and external middle legs, the rest armed. Front femur with two, middle femur with three, widely spaced short spines on ventroanterior carina; hind femur with 9 spines on ventroanterior margin, 3 on ventroposterior.

Wings. Tegmina and wings brachypterous~, just reaching 1st tergite; apex of tegmen quite rounded. Sc and R parallel until tegmen extremity, curved slightly upward at the end. Ma and Mp diverging from origin. Male tegmina imperfectly approximate mirror-image symmetry.

Abdomen. Male subgenital plate deeply emarginate, semitriangular posteriorly; styli distinct, curved ventrolaterad (Fig. 5O).

Color description.— Lightest colored region of body honey yellow. Postocular and dorsal regions of pronotal lobes fuscotestaceous; occiput and apex of fastigium fuliginous, pronotal disk immaculate, whitish grey. Darkest regions of foretibia and abdominal pleurites atropurpureus; mid femur, tibia, hind femur with darkest areas fulvescent.

Remarks.— Overall similarity suggests a close relation between this species and *U. grisea*. This is consistent with the similar shape of the cercus and tenth tergite.

Material examined.— Peru: Provincia Loreto: Iquitos: Quistococha: 1 male (holotype), L. Desutter, 22 VIII 1985 (MUPA).

Uchuca amacayaca n. sp.

Type locality.— Colombia, Amazonas, PNN Amacayacu, 100 m, (3°50'-3°02 S, 69°54'-70°20'W). Type depository: ICN, Colombia (holotype male, in alcohol).

Etymology.— This species is named after the type locality, PNN Amacayacu of Colombia.

Distribution.— Amazon rainforests of Colombia, extending to the borders with Peru and Brazil.

Diagnosis.— (Figs. 5BGLQU, 7A, Table 5). Elongate portion of male cercus flexible, ending acuminate. Basal sclerotized appendage dark brown, pollicate

(Fig. 5G). Titillators apically forked, bearing two teeth on the ventral edge (Fig. 5U). Upper membrane above titillators with a semi-quadrangular thin layer of sclerotized cuticle (Fig. 5U, arrow).

Description.— *Thorax*. Pronotum in male produced caudad over tegmina; caudal section of disk produced posterior in subacute extension, covering almost entire stridulatory field of tegmina; cephalic margin of disk truncate. Lateral lobes with greatest depth 1.2x greatest length (Fig. 7A); ventral margin oblique truncate, caudal margin rounded, humeral sinus hardly evident. Prosternum with two minute spines.

Legs. Armature genicular lobes of femora: external and internal of fore, external of both mid and hind, unarmed. Internally mid and hind with a vestigial spine. Front femur with two, middle femur with three, widely spaced short spines on ventroanterior carina; hind femur with 6-8 spines on ventroanterior margin and 3 on ventroposterior.

Wings. Tegmina and wings never reach tenth tergite (Fig. 7A); incapable of flight; apex lanceolate. Sc and R of tegmina parallel to extremity; Rs forked on distal part; Ma and Mp diverging over first 1/5 of total tegmen length. Stridulatory vein (dorsal aspect) conspicuously broad, short. Reticulation of tegmina in costal field matching in complexity that of postradial field. Male tegmina approach mirror-image symmetry (Fig. 9AC). Both tegmina have stridulatory file (Fig. 9BD); file on left tegmen has about 109 teeth, that on the right 74 (n=1).

Abdomen. Tenth tergite posteromedially moderately triangularly incised (Fig. 5Q). Male subgenital plate somewhat retuse; styli distinct, rather short, directed laterad (Fig. 5L). Female subgenital plate terminally incised trapezoidal, truncate but weakly sinuous between the lobes; lateral sulci deep (Fig. 5B).

Color description.— Lightest regions of body cream. Post ocular region, apex of fastigium and dorsal region of pronotal lobe melanochroic; occiput and pronotal disk guttate fulvescent. All femora and tibiae (in part) dorsally covered with minute fulginous spots; subtympanal and distal regions of fore and mid tibiae fuscopiceous; laterally those appendices bear sometimes a fumeus coloration. Tegmina with dark spots mainly on distal part of anal margin. Basal appendix of cercus hypographous distally. Ovipositor glassy, brownish orange.

Remarks.— Some female specimens with the subgenital plate medially V-emarginate. This species has a close relationship to *U. haltikos* (here designated), see below.

Material examined.— (n=5, 2 males, 3 females). COLOMBIA: Departamento de Amazonas: PNN Amacayacu (3°50'-3°02 S, 69°54'-70°20'W), 100 m, 1 male (holotype), F. Vargas & F. Montealegre, IV 28 2000; 3 females, 1 male (paratypes), same data and collectors.

Uchuca halticos n. sp.

Type locality.—Provincia Napo, Jaguar. Type depository: UMMZ, holotype male.

Etymology.— The epithet haltikos, from Greek, means 'good leaper'.

Distribution.— Ecuadorean Amazonia.

Diagnosis.— (Figs. 5D, I, N, S, X, 7B, 10, Table 6). Longest portion of male cercus basally broad, aduncate, ending acicular. Small sclerotized, finger-like mediobasal protrusion of cercus, moderately curved caudad; a very small lobe

occurs mesodistad (Fig. 5I). Titillators diverging from (and shorter than) grooved medial sclerite, apically bifurcate, smooth not dentate on ventral edge (Fig. 5X).

Description.— Thorax. Caudal section of pronotal disk produced caudad in an acutely rounded projection covering stridulatory area completely; anterior margin of disk truncate. Lateral lobes with greatest depth < 1.2X greatest length; humeral sinus scarcely evident; ventral margin oblique truncate, caudal margin rounded (Fig. 7B). Prosternum with two minute spines.

Legs. Genicular lobes of femora armature: external and internal of fore, external of both mid and hind, unarmed. Internally mid and hind armed with small spine. Anterior femur with two, middle femur with three, widely spaced short spines on ventroanterior margin; hind femur with 7-8 spines on ventroanterior margin and 3-4 on ventroposterior.

Wings.— Tegmina and wings do not exceed abdomen apex ; incapable of flight; in both sexes tegmina hardly reach 7th tergite; apex of tegmen lanceolate. Sc and R of tegminal parallel to end; Rs forks close to middle; Ma and Mp diverging over first 1/8 of tegmen length. Stridulatory vein (dorsal aspect) very reduced; both tegmina slightly approach mirror image (Fig. 10AC). Stridulatory vein on left tegmen clearly curved laterad, with 119 teeth, vestigial file with 73 teeth (Fig. 10BD).

Abdomen. Tenth tergite medioposteriorly broadly incised V-shaped, ending in two semiacute lobes (Fig. 5S). Male subgenital plate broad basally, distally moderately retuse; styli conspicuous and normally curved ventrad (Fig. 5N). Females with distal part of subgenital plate projected semiacute and broadly incised; a very inconspicuous sulcus occurs laterodistally (Fig. 5D).

Color description.— Lightest regions of body honey-yellow. Postocular region, apex of fastigium and dorsal region of pronotal lobes brunneus; occiput and pronotal disk guttate fuliginous. All femora and tibiae (in part) dorsally freckled with fulginous spots; tympanal region of foretibia, distal regions of fore and midtibiae fuscopiceous. Basal appendix of the cercus brunneus-hypographous distally. Ovipositor moderately glassy, brown-orange.

Remarks.— Overall similarity suggests a close relationship of this species to *U. amacayaca*. The derived trait that links both species is the sclerotized digitate basodorsal appendix of the cercus and truncate stridulatory file.

Material examined.— ECUADOR: Provincia Napo: Jaguar: 1 male (holotype), G.K. Morris, IV 13 1989; 1 male, 3 females (paratypes), G.K. Morris, IV 13 1989. 1 male, 2 females (paratypes), G.K. Morris, XII 12-13 1986; 2 males, 2 females (paratypes), G.K. Morris, II 13 1988; 2 males, 3 females (paratypes), G.K. Morris, IV 20 1990. Misahualli: 1 male, 1 female (paratypes), G.K. Morris, VII 13 1985.

Uchuca macroptera n. sp.

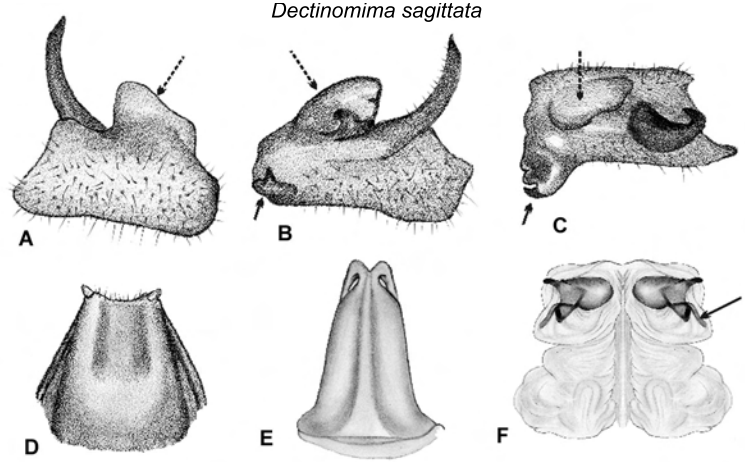
Type locality.— Colombia, Departamento del Putumayo, Route del Paujil Orito, 300 m. Type depository: MUPA, holotype male.

Etymology.— The epithet macroptera refers to the developed wings of this species, a feature contrasting with the remainder of known species.

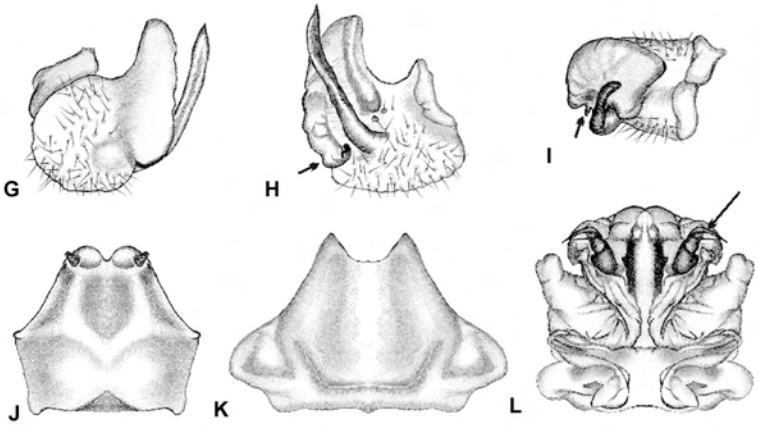
Distribution.— Amazonia from Ecuador, Peru, Colombia to French Guyana.

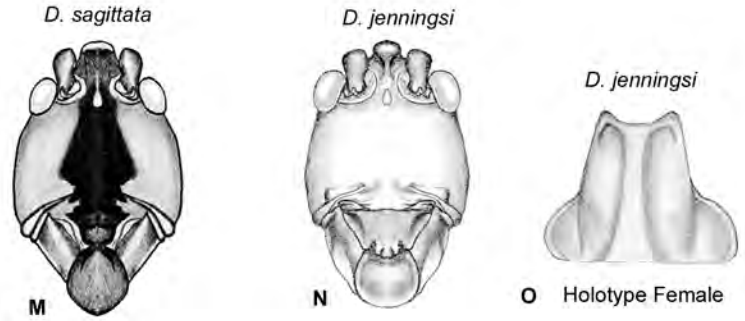
Diagnosis.— (Figs. 5CHMRW, 8, Table 7). Longest portion of male cercus basally broad, somewhat flattened, aduncate, ending acicular. Basal appendage

Dectinomima sagittata



Dectinomima jenningsi





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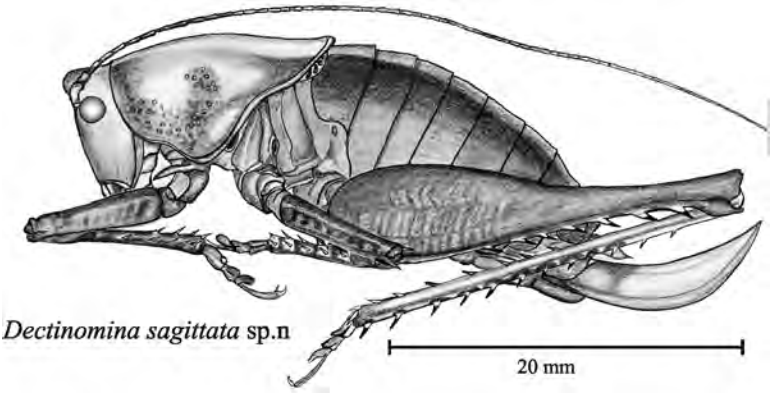

Fig. 2. *Dectinomima sagittata,* habitus of female.

curved caudad at straight angle, an additional small lobe occurs ventrodistad (Fig. 5H). Titillators apically bifurcate, smooth, not dentate on ventral edge (Fig. 5W). Females have digitate lateral appendix at base of subgenital plate, one at each side.

Description.— Thorax. Caudal section of pronotal disk produced strongly arcuate posteriorly, as projection covering almost complete stridulatory area; anterior margin of disk truncate. Lateral lobes with greatest depth > 1.1X greatest length; humeral sinus hardly present; ventral margin oblique truncate, caudal margin rounded (Fig. 8A). Prosternum with two spines.

Leg. Armature of femoral genicular lobes: unarmed, external and internal of fore, external of both mid and hind; internally mid and hind with vestigial spine, in some specimens, externally, fore genicular lobe has blunt base of vestigial spine. Anterior and middle femora each with two, widely spaced short spines on ventroanterior margin; hind femur with 5-6 spines on ventroanterior margin, 3 on ventroposterior.

Wings. Tegmina and wings markedly exceeding apex of abdomen; capable of flight; in females the tegmina exceed in most cases ovipositor apex; apex of tegmen orbicular. Sc and R of tegminal parallel to end; Rs forks close to middle; Ma and Mp diverging from first 1/8 of total length of tegmen. Stridulatory vein

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Fig. 1. Morphological features that separate *Dectinomima* spp. A-F. Genital structures of *Dectinomima sagittata* (relaxed specimen, by "relaxed" we mean that the structure has been softened with warm water, as specimens were dry-preserved). A-C. Male left cercus. D. Male subgenital plate. E. Female subgenital plate. F. Titillators. G-L. Genital structures of *Dectinomima jenningsi* (from specimens preserved in alcohol). G-I male left cercus from different views. J. male subgenital plate. K. female subgenital plate. L. Titillators. M, N. Frontal aspect of the head, of both species. O. Female subgenital plate of *D. jenningsi* (drawn from the holotype without relaxing the structure). Dashed arrows in A-C and arrows of G-I show the internal swelling, continuous arrows in same figures show the laminar and concave projection). Arrows in F, L show the deflected sclerotized appendages of the titillators.

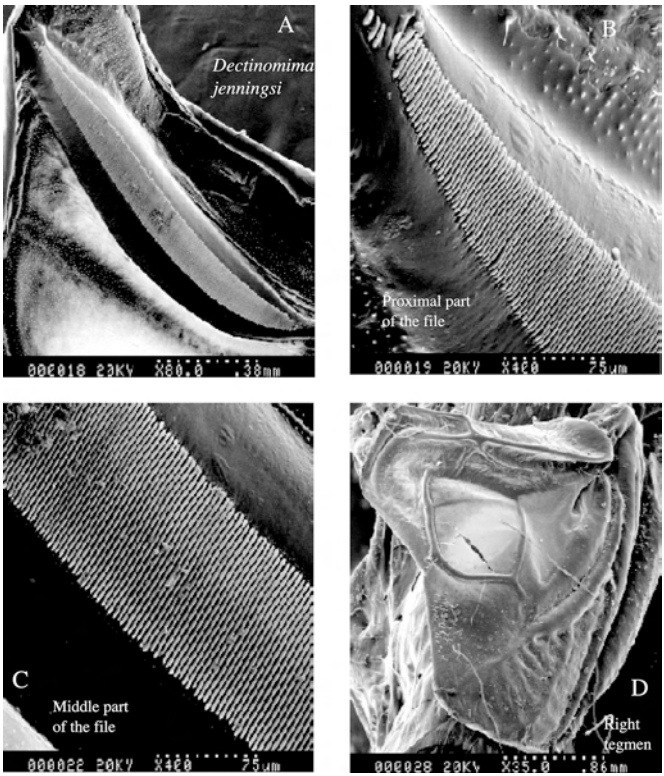

Fig. 3. *Dectinomima jenningsi:* A. Stridulatory file. B. Detail of teeth in the proximal third of the file. C. Detail of teeth in the mid region of the file. D. Right tegmen dorsal view.

(dorsal aspect) rather elongate. Both tegmina have stridulatory file, but nonfunctional right tegmen file is not very developed in dorsal aspect.

Abdomen.— Tenth tergite in middle moderately sinuate, ending in two poorly defined lobes (Fig. 5R). Male subgenital plate retuse; styli usually distinctly recurved laterad (Fig. 5M). Female subgenital plate broadly incised orbicular; lobes of plate, acuminate, retroarcuate, lateral sulci inconspicuous (Fig. 5C).

Color description.— Lightest region of body honey-yellow. Postocular and upper regions of pronotal lobes fuscotestaceous; occiput and pronotal disk irrotare fulginous; apex of fastigium and anterior face of scapus fuliginous. All femora fulvescent, dorsally moderately irrotare brunneus; subtympanal and distal regions of fore and basal and distal regions of midtibia fuscopiceous. Ovipositor glassy, ochraceous.

Remarks.— The basal lateral appendix that females bear close to the subgenital plate is an autapomorphic trait very, useful to distinguish this species and also to separate females from other species of *Uchuca* that sometimes present elongate tegmina (e.g., *U. amacayaca*).

Material examined.— (n=18, 3 males, 12 females): COLOMBIA: Departamento del Putumayo: unknown location, 300 m, 1 male (holotype), M.

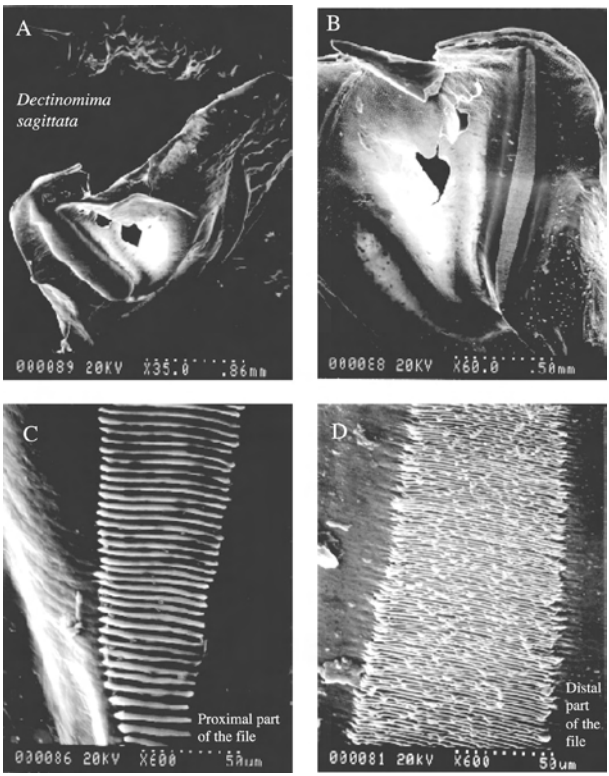

Fig. 4. *Dectinomima sagittata:* A. Left tegmen, dorsal view. B. Stridulatory file. C. Detail of teeth proximal on the file. D. detail of teeth distad.

Descamps, XI 11 1968 (MUPA). Departamento de Amazonas: RÌo Igara Parana: 30 km down river La Chorrera: 1 male (paratype), M. Descamps, VI 2 1974. PERU: Departamento Loreto: Pacaya Samiria Nat. Res: RÌo Samiria, Flooded Forest, 150 m, 3 females (paratypes), G.S. Glenn, VIII 1985 (ANSP) . Cocha Cashu: Parque Nacional del Manu: 1 female (paratype), P. Stern, IX 29-X 21 1982 (ANSP). RÌo Ampiyacu: 1 male, 4 females (paratypes), C. Amedegnato & S. Poulain, XII 1983 (MUPA). FRENCH GUYANE: Arataye, Affl. Approuagues, 8 km from Salto Parare: 2 females (paratypes), L. Desutter & P. Grandcolas, VI 13 1988 (MUPA). ECUADOR: Provincia Napo: Primavera: 1 male, 4 females (paratypes), G.K. Morris, VII 19 1985.

We propose the following new combination (see discussion for details):
Uchuca peruviana (Caudell) comb. nov.
Dectinomima peruviana Caudell, 1918: 21
Uchuca pallida (Caudell) comb. nov.
Dectinomima peruviana Caudell, 1918: 22

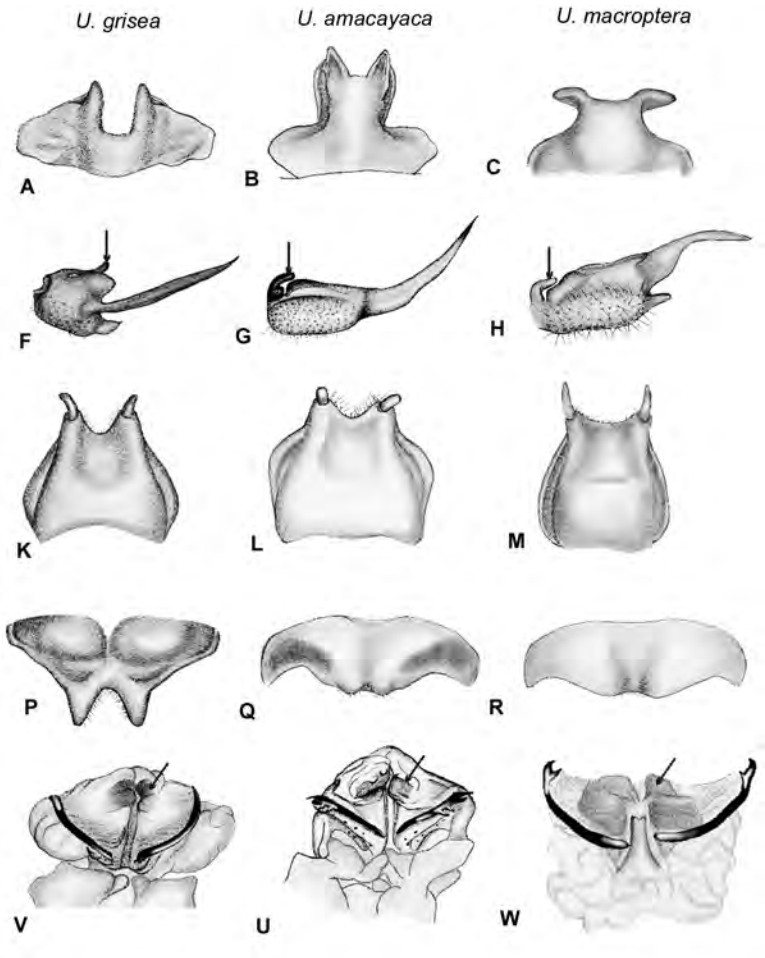

Fig. 5. Genital structures of *Uchuca* spp. Rows (from top down) female subgenital plates, male cercus, subgenital plate, Xth tergite, phallus. Arrows in figs. F-J indicate the digitate process of the cercus. Arrows in figs. V-Y show the sclerotized area of the phallus. A, F, K, P, V (relaxed): *U. grisea*. B, G, L, Q, U: *U. amacayaca* (structures drawn from a specimen in alcohol). C, H, M, R, W: *U. macroptera* (relaxed). D, I, N, S, X: *U. haltikos* (structures preserved in alcohol). E, J, O, T, Y: *U. similis* (from a dry specimen). E: female of *U. similis* is unknown.

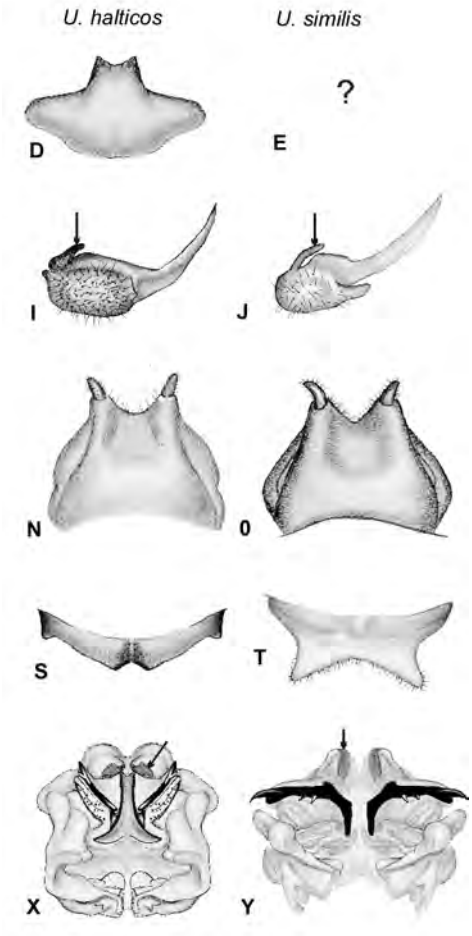

Fig. 5. (continued; see opposing page)

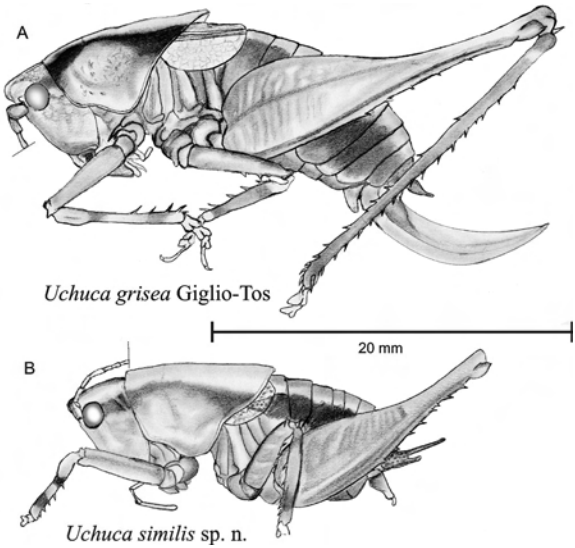

Fig. 6. Habitus of the female of *Uchuca grisea* (A) and the male of *U. similis* (B). Specimens. courtesy of the Museo de Instituto di Zoologia Sistematica dell'Universita di Torino (A), Italy. MusËe de Paris France (B).

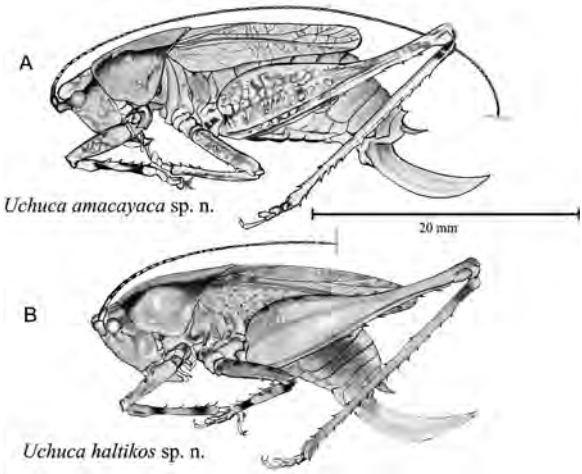

Fig. 7. Habitus of the female. A. *Uchuca amacayaca* B. *U. haltikos*.

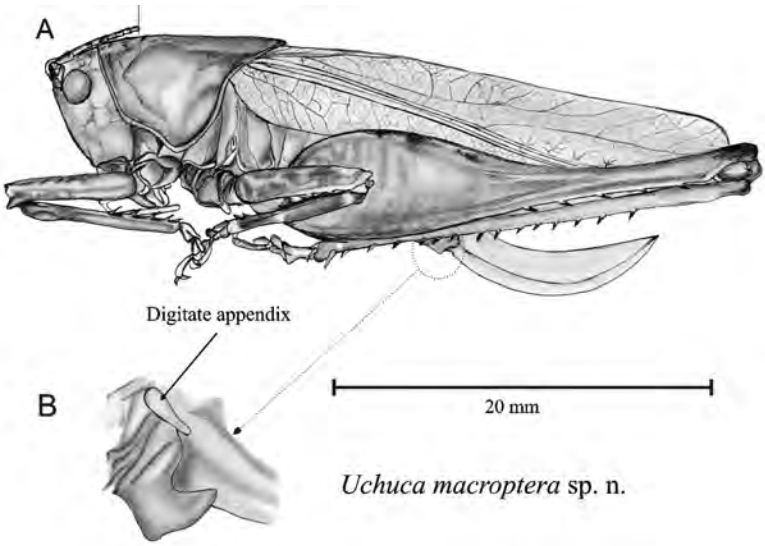

Fig. 8. *Uchuca macroptera*. A. Habitus of the female. B. Female terminalia, lateral view showing the subgenital plate and the digitate appendix (drawn from a relaxed specimen).

BIOACOUSTICS

Dectinomima jenningsi

Two adult males (specimens A, B) were kept in captivity for more than eight months and successfully recorded at 25.4°-25.8°C. Calling song was a rapid succession of pulse train groups (Fig. 12A), each group of variable length (range 0.27-0.54sec, mean 0.38 sec, n=55) and including ~8 to 12 pulse trains. These songs recurred at fairly regular intervals (0.029 sec, n=8). At 9 cm distance, during sustained calling, the sound pressure level of specimen A reached 87 dB with each call. Specimen B registered 90 dB at 9.5 cm.

Each call is resolved as a series of phonatomes (all the sound produced during one cycle of wing movment);each phonatome was comprised of a very short minor pulse train following a major pulse train. Each major train consists of 86 to 97 rapid-decay (transient) pulses. These pulses occur at a rate of 2666/s (specimen A) and 2376/s (specimen B). The major pulse train lasts about 0.036 s (n=9, specimen A) and 0.037 (n=14, specimen B). The phonatome rate at 25.4°C was ~25/s.

The frequency spectrum presents a band between 25 and 35 kHz (taken as energy within 20 dB of the carrier peak maximum), with its maximum intensity at 30.6 kHz, and without harmonics. Spectral analysis of specimen B showed the same features, but with maximum carrier intensity at 28.3 kHz.

Dectinomima sagittata

One male of *D. sagittata* produced a disturbance sound while being collected, its faintness to human ears suggesting this species may, as does *D. jenningsi*, lack significant output in the audio range. The morphology of *Dectinomima* files (Fig. 3, 4 ~370-600 teeth) is an oddity: tooth density and the total number of teeth

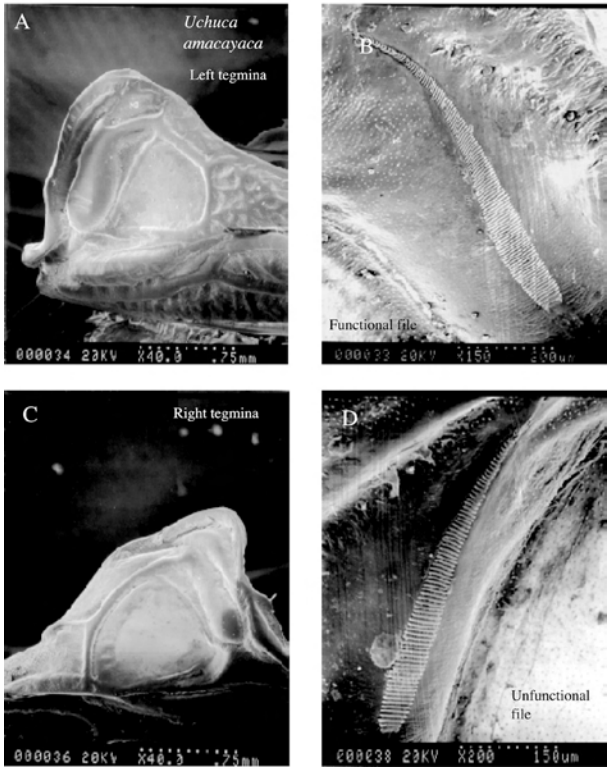

Fig. 9. SEM of *Uchuca amacayaca:* A. Left tegmen showing stridulatory area (dorsal view). B. Functional stridulatory file of the wing shown in A. C. Right tegmen showing stridulatory area and scraper. D. Nonfunctional file of the wing shown in

are higher than for any other species of katydid known to the authors. Files of pure-tone singer conocephaloid katydids such as *Copiphora gracilis* and *Panacanthus cuspidatus* show a maximum of 280 and 312 teeth, respectively (Montealegre-Z. and Morris 2004). The teeth are quite uniformly spaced throughout the length of the *Dectinomima* file, but tooth spacing increases in the distal portion. Such file morphology is consistent with the generation of a high-*Q* signal (Montealegre-Z & Morris 1999).

Uchuca amacayaca

A single male was recorded indoors at 24°C in Palmira, Colombia, using ultrasonic-effective equipment. Two males collected at PNN Amacayacu in the Colombian Amazon, sang only at the biological station, where some recordings amplitude modulation patterns were achieved using a U30 bat detector (zero-crossing).

The song of *U. amacayaca* is a regular series of extremely short notes (Fig. 13A) that can be heard very faintly with the unaided human ear. One of our recorded males produced a succession of such calls (notes) with a call period of about 1.1s; these calls had an average duration of 0.7 s (n=7 consecutive calls), a

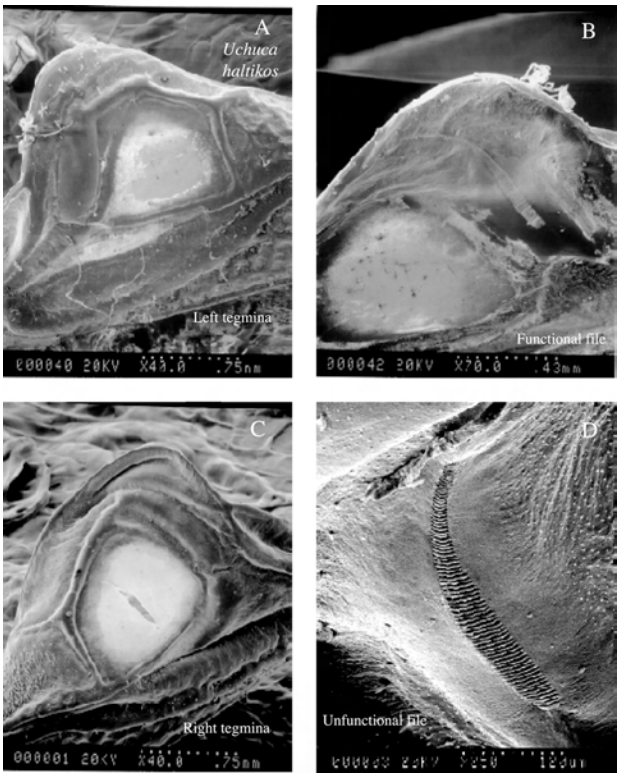

Fig. 10. SEM *Uchuca haltikos:* A. Left tegmen showing stridulatory area (dorsal view). B. Functional file of the wing shown in A. C.Right tegmen showing stridulatory area and scraper. D. Nonfunctional file of the wing shown in C.The distal end of the file (the flattened region) appear like a dark region of the file in B.

call rate of about 0.7 per sec. The intensity of the songs is rather low for tettigoniids: only ~81dB 10 cm dorsal (Fast setting).

Slowed by a factor of 4, each note presents a musical quality to the human ear. Each consists of a single sustained sinusoidal pulse (Fig. 13B). Each pulse lasts about 2.74 ms (n=5 songs). A pulse is made up of nearly 90 (mean=90.6, n=5) sinusoidal waves (Fig. 13BC). Over about 25 waves the pulse gradually approaches maximum amplitude; this amplitude then decreases steadily and slightly over the next 55 waves. Strong decay of the pulse involves approximately the last 16 waves. Calculation of *Q* from this decay (Fig. 13B) gave a mean value of 18.2 (n=7, range 16.7-20.7). Figure 9 AB shows the file of the left tegmen of one male.

Unlike *U. haltikos* (see below) the song of this species does not present subequally strong harmonics. The number of teeth on the file, 109 (n=1) in a length of 0.72 mm, comfortably exceeds the number of waves observed in the uniform amplitude portion of the pulse (90.6, n=5), so it is reasonable to suppose that each such wave is the product of one tooth-scraper interaction. If so, the number of teeth engaged in one pulse would be about 83.1%.

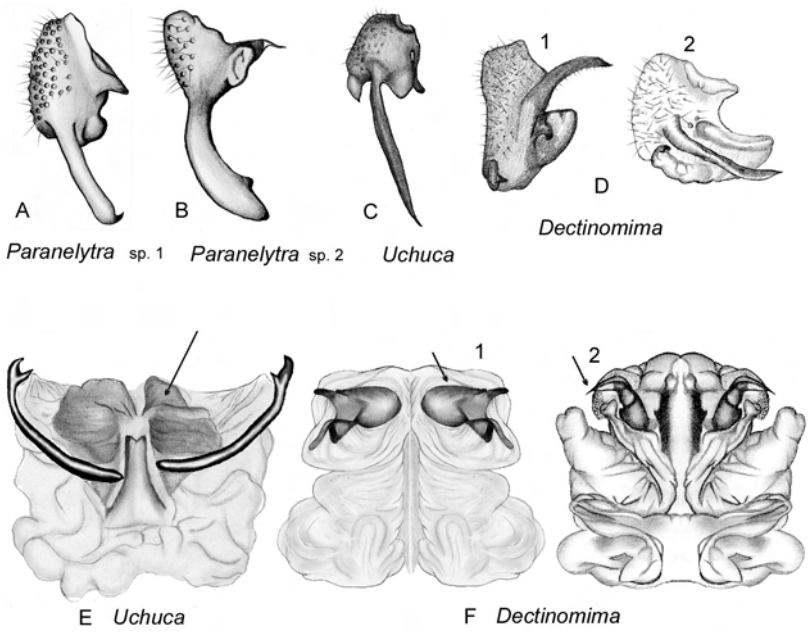

Fig. 11. Genital structures of *Dectinomima, Uchuca* and other possibly related genera. A, B. *Paranelytra,* right cercus of two undescribed species(ANSP). C. Right cercus of *U. grisea*. D. Right cercus of *Dectinomima sagittata*. E. Relaxed phallus of *U. amacayaca*. F. Relaxed phallus of *D. sagittata,* the arrow shows the membranous sclerotized area.

Virtually all of the acoustic energy in this call is ultrasonic, except for a very low-intensity fundamental frequency near 18 kHz. The dominant frequency component of this species, containing all significant call energy, is a second harmonic at 36.6 kHz (Fig. 13D); there is also a fourth harmonic detected at 73.2 kHz, though its intensity >40 dB below the carrier, would make it undetectable under field noise conditions.

Uchuca haltikos

The song of our single recorded male was heard in real time as a regular series of very short, discrete notes (Fig. 14A). At 21°C these occurred on average 1.6 s apart (n=19 consecutive calls), a call rate of about 0.6 per sec.

Each note is a single, nearly pure tone, pulse (Fig. 14BC), its musicality apparent to the human ear when slowed by a factor of 8. This pulse, of about 118 waves, lasts for less than 3.2 ms and it builds and falls away almost symmetrically. The amplitude envelope climbs very gradually so that only after 20 waves is the pulse approaching its maximum, and it still increments slightly to mid-pulse. A consistent feature, at least of this particular male, was that throughout the pulse, the composite wave shows characteristic alternating amplitudes (Fig. 14C), manifesting the mechanical interaction of the scraper (the driving force) on successive file teeth (Bennet-Clark and Bailey 2002). The driving force acts during almost all the pulse, with the free decay of the resonator involving only a few

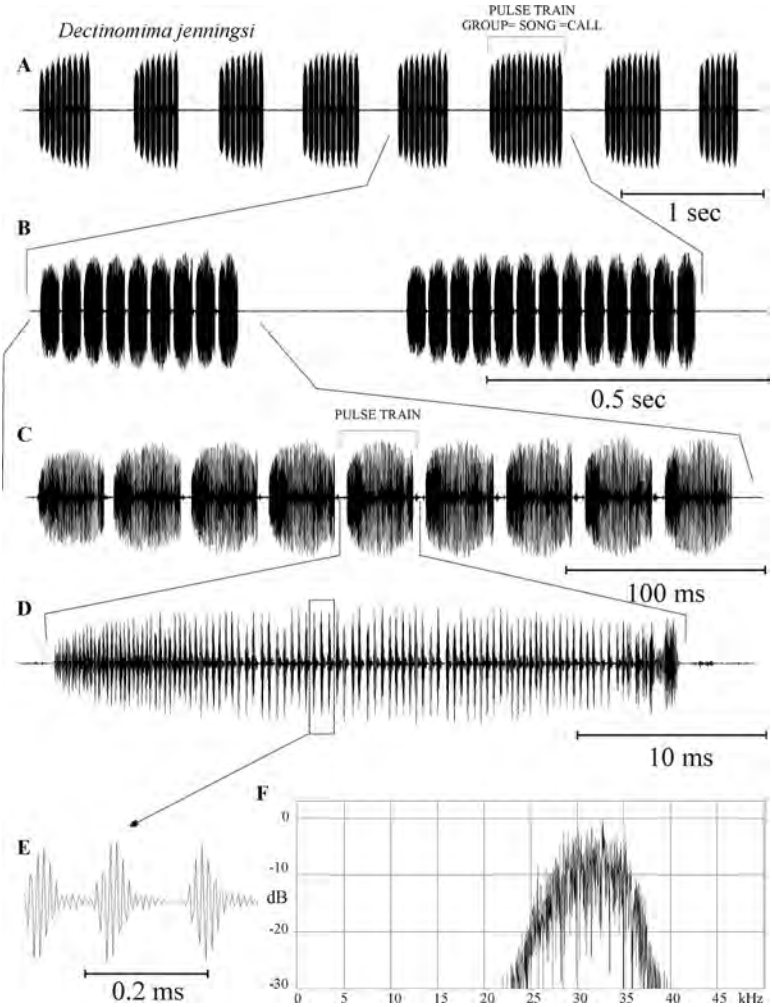

Fig. 12. Song structure of *Dectinomima jenningsi:* A. A succession of calls (songs). B. Two calls at higher resolution. C. One call consisting of 9 pulse trains. D. A phonatome (major pulse train followed by minor opening sound). E. Three transient pulses from mid-train at high resolution. F. Power spectrum of the pulse train shown in D.

cycles at the end, in this particular case about 8. The quality value (Q), calculated from this time domain decay, is 15.2 (n=5, range 13.5-17.5).

Almost all this insect's song energy is ultrasonic. There are two harmonically related carrier components of similar intensity, one 42.3 kHz, the second harmonic of a fundamental at 21.2 kHz. On average, the fundamental was 5 dB below its harmonic, so that this peak might be considered the dominant carrier. There are also inconsequential third and fourth harmonics, 63.2 kHz and 84.3 kHz; the third is > 30 dB below the dominant second (Fig. 14D).

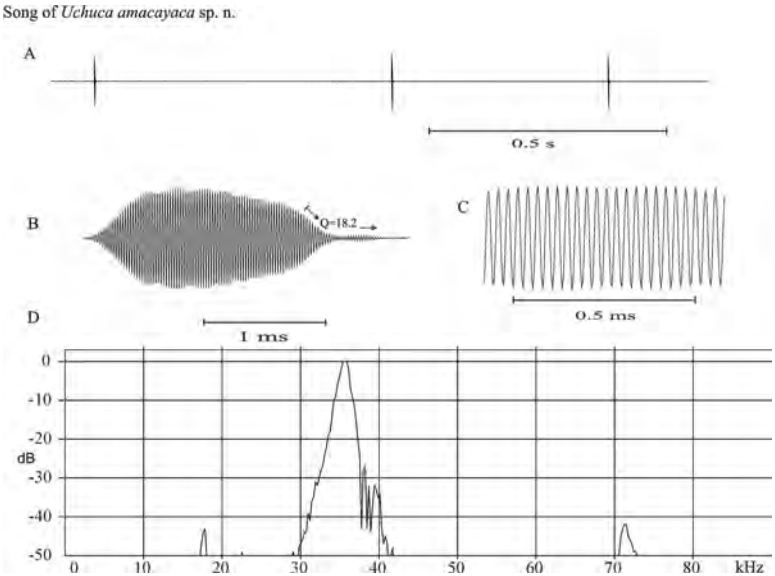

Fig. 13. Song of *Uchuca amacayaca:* A. Three consecutive songs. B. Amplitude envelope of one song in A. C. Portion of near-maximum amplitude of the pulse in B at higer resolution. D. Power spectrum of the pulse in B.

DISCUSSION

Systematics

General considerations: *Uchuca* and *Dectinomima*

Caudell (1918: 23) considered the possibility that *Uchuca* and *Dectinomima* were the same taxon, but the characters he anticipated might resolve this issue (differential tegminal development) do not help. *Uchuca* has species both brachypterous and macropterous. Tegmina in both sexes of *Uchuca* are more developed than in *Dectinomima* (with the exception of *U. grisea* and *U. similis)*. But the possession of long vs short wings is not a sufficient criterion on which to define the monophyly of a group (Heller 1990: 133) and the reduction of tegmina has likely occurred independently many times in Tettigoniidae. By other external characters proposed by Caudell (1918) and other authors, *Dectinomima* is not separable from *Uchuca* (appendix 1).

Analysis of the type material of Giglio-Tos and Caudell *(Uchuca* and *Dectinomima)* and the of the male of *Dectinomima sagittata,* helps to clarify that these are distinct genera. The male genitalia, especially the cercus and titillators, provide good evidence that they are related but separate taxa and may be the best way to establish the phylogenetic relationships between these and related genera.

The titillators of *Dectinomima*, diverging and distally deflected in both species, are formed in *D. sagittata* into upper and lower finger-like projections; in *D. jenningsi* they are undivided, unitary and exceptionally sharply pointed (Fig.

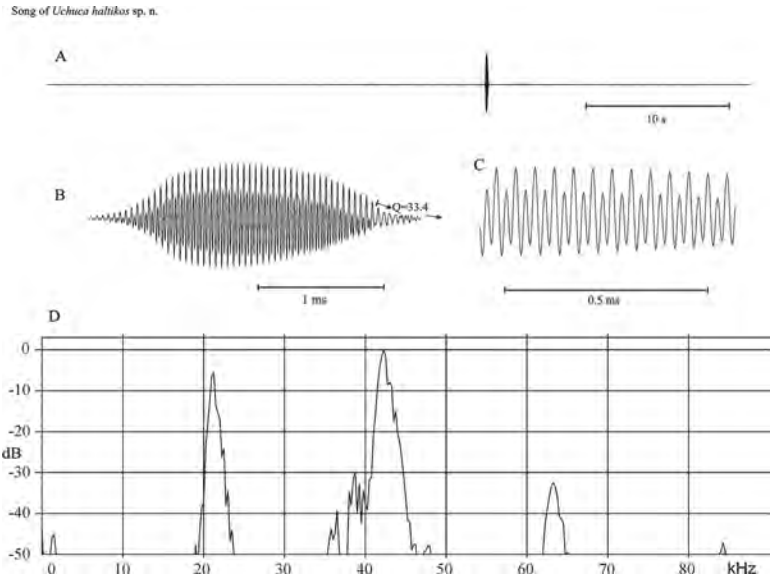

Fig. 14. Song of *Uchuca haltikos:* A. One calling songs. B. Amplitude envelope of one song in A. C. Portion of maximum amplitude of the pulse in B. D. Power spectrum of the pulse in B.

11F arrow). *Uchuca* does not have its titillators developed in this way: they are rod-like (rib-shaped) and apically bifurcate (Fig. 11E). In both genera titillators are of course embedded in surrounding membranous areas of the phallus and the posterior face of the titillator is exposed in both genera, but in *Dectinomina* both faces of the titillators are detached from the surrounding membrane, while in *Uchuca* the anterior face is partially implanted within this membrane (Fig. 11EF). Dissimilarity in genital traits, especially titillators, may not indicate a distant relationship, as would be true for any autapomorphy. And these genera may also be related by synapomorphic traits of the genitalia, e.g., digitate process of cerci (Fig. 11CD). Until a comprehensive revision of the genus *Dectinomima* is complete and the male genital traits of previously described species studied, it will not be possible to argue definitively which lineage present a more plesiomorphic condition.

We studied Caudell's type material of *Dectinomima* and note that *D. pallida* and *D. peruviana* differ considerably from *D. jenningsi* in the genitalic structure of both female specimens; so we conjecture that they *(D. pallida* and *D. peruviana)* should be included in *Uchuca*. The female subgenital plate and 10th tergite, suggest that *D. peruviana* might be closely related to *U. grisea*. In general, the shape of the body of *D. jenningsi* and *D. sagittata* differs from that of *Uchuca* spp. Moreover, even though size is not a good basis on which to separate taxa in most cases, it is important to note the proportions of *Dectinomima* spp. and *Uchuca* spp.: in the former, individuals are much larger and moderately more robust (see respective tables for measurements).

The genera *Paranelytra* Karny (from South America) and *Spinisternum* Willemse (from the Old World, see Willemse 1942, 1966), exhibit a phallus lacking any reinforcing sclerotization (titillators). There is rather, a thin layer of chitin covering the upper membranous surface of the phallus. This character state seems to be the most plesiomorphic condition phallus reinforcement in this group.

On the basis of the male cerci, *Uchuca* shows more relation to males of *Paranelytra* from Colombia (Morris and Montealegre in preparation) than to males of *Dectinomima*. This character state (cerci) in our male of *Paranelytra* also seems to be the most plesiomorphic condition when compared with *Uchuca* (Fig. 11A-C).

We think that the genus *Eppia*, traditionally seen as a relative of *Dectinomima*, should not be included in this complex. It appears to be more akin to *Neoconocephalus* and *Bucrates* in male genitalia, and it is just those traits that make this genus so different from *Uchuca, Dectinomima* and related genera. Naskrecki (2000) considers it likely that *Eppia* is related to *Bucrates,* and we agree. One can also find primary homology in the cerci of *Dectinomima* and *Sphyrometopa,* but the phallus of the latter shows only the partial sclerotization commonly found in *Eppia, Bucrates, Neoconocephalus, Pyrgocorypha* etc. The relation of *Dectinimima* and *Sphyrometopa* is not clear and therefore has to be reviewed.

For the time being, the phylogenetic relationships of this generic complex will remain speculative and will probably only be clarified when other related and presently unknown lineages are described.

Uchuca, collected in the amazon basin and placed into plastic jars became known to collectors as 'head-bangers' from their habit of leaping upward against the jar lid making an audible sound. Few other species showed such behavior so consistently. Jumping behavior is an important strategy of escape and explains the marked development of hind femora in all species of both genera. A leaper needs to maintain long legs with very long femora, which makes running cumbersome (Hische 1950). Many characters of *Dectinomima* spp. and *Uchuca* spp. are correlated with the ability of these insects to make long leaps: fore and mid legs are short, hind femora are strongly developed and most species are incapable of flying. Leaping prowess might be correlated with poor flying as an alternative escaping strategy. This disproportionate elaboration of the hind femur has evolved several times in Tettigoniidae, e.g. Tettigoniinae.

Interspecific variation in *Uchuca*

Species of *Uchuca* show wide variation in the morphology of their genitalia: the phallic complex and other male genital traits, the subgenital plate of the female (Fig. 5). Male cerci present two main states: the first, basal sclerotized appendage dark brown, weakly pollicate and simultaneously lacking a ventral lobe groups

U. halticos and *U. amacayaca* (Fig. 5GI). This grouping is reinforced by the fact that both species present a functional stridulatory (truncate) file, terminating abruptly well short of the wingbase (Figs. 9B,10B), something not previously encountered in a katydid; this then, is a synapomorphic trait for this species group. The second cercal state is a paler sclerotized appendage strongly pollicate, occurring simultaneously with a ventral lobe. This characteristic situates *U. grisea, U.*

similis and *U. macroptera* in another branch. *Uchuca grisea* and *U. similis* seem to be also closely related, not only by sharing this cercal state, but also by having the tenth tergite medially strongly triangularly incised, ending in two semitriangular lobes (Fig. 5PT). *Uchuca macroptera* is placed with confidence in *Uchuca,* but is not assigned to either of these clades yet because it presents characters of both, together with flight capability (unusual in species of this genus), and the autapomorphy of the laterotermi nal appendix beside the subgenital plate in females (Fig. 8B). The taxonomic status of this species is difficult to determine until other species of the genus are described.

Increasing the number of characters used in the analysis can reinforce a hypothesis of relationship. With the accessible data we have achieved some insight into the relationships among *Uchuca* spp. and between *Uchuca* and *Dectinomima*. In this instance only genital traits provided criteria for discriminating among apparently incorrect phylogenetic hypotheses advanced in the literature.

Bioacoustics

The physical basis of pure-tone sound generation requires that the number of carrier frequency waves in a song closing sound match the number of teeth on the file (Bennet-Clark 1989, Dambach and Gras 1995). Pure tone singers should have a file with regularly spaced teeth and a sharply tuned resonator.

Assuming each pulse is made on one closing traverse of the file, and each wave represents passage over a single tooth, the number of waves in a pulse of *U. amacayaca* indicates an engagement of about 83% of available file teeth. It is possible in this species (even though the file is very short, being suddenly truncate at its basal end) that the pulse is made on a simple resonant, tooth-per-wave basis. The file would then be utilized beginning after the first 30 teeth, whose extreme narrowness suggests their non-functionality.

In *U. haltikos* the number of teeth on the stridulatory vein (119) appears to coincide with the total number of waves of the carrier frequency in a song pulse (~118). In accordance with a 1:1 ratio between wave and tooth-contact, this species would exhibit complete tooth engagement: it would utilize every file tooth. But, as described above, its pulse consists of regularly fluctuating peak wave amplitudes (also manifest as the subequal harmonically related spectral peaks). It seems more likely then, that *U. haltikos* is producing two waves of different peak amplitude for each tooth contact.

Suga (1966: 1046) reported a species of Pseudophyllinae, *Leurophyllum (Drepanoxiphus) modestus,* in which the total number of waves was greater than the number of teeth present on its file. And he pointed out the possibility that two waves might be produced by one tooth-strike. The production of two waves per tooth-scraper contact is also noted elsewhere in Tettigoniidae (Sales and Pye 1974: 106, Morris 1980 for *Copiphora rhinoceros).*

More insight into this mechanism is offered by Bennet-Clark & Bailey 2002. During stridulation, in addition to radiation by any wing membrane resonators, sounds are generated each time the scraper makes or breaks tooth contact. If these sounds, typically of higher frequency, occur in phase with the vibration of the tegminal resonator they will be harmonically related to the resonator's fundamental frequency, and their high frequency components will be manifest in the resulting emission. Superimposed, these frequencies can generate the observed

alternating amplitude peak pattern of the wave. If this is what occurs in *U. haltikos,* pulses would be generated by about 60 teeth, implying an engagement of only about 50% of the total tooth number. This proportion of file functionality is more in accordance with that of other katydid species.

In both species of *Uchuca* studied here pulses build up exponentially to a maximum. The force put into the system from the driving mechanism (tooth-scraper make and break) affects this build-up. But when these tooth-related sounds cease the wing radiator continues on its own in a natural decay: so the very end of the pulse presents a free decay (Fig. 14B) (Bennet-Clark 1999ab, Bennet-Clark and Young 1992, Bennet-Clark). *Q* is best calculated from the final portion of the emitted pulse.

Unlike the *Uchuca* songs, in *D. jenningsi*, every phonatome consists of transient pulses (typically 86-97, Fig. 12). This is manifest in the spectral analysis as a broad 20-kHz band (measured 30 dB down from the maximum) centered on 29.5 kHz. High-speed video recordings show that in this insect pulse train emission coincides with scraper travel across almost all the file. So each closing stroke generates a train of about 90 pulses while the scraper is passing over about 400 file teeth. If most file teeth are contacted it follows that several teeth (~4?) must contribute to the creation of each pulse.

A mechanism involving the storage and release of elastic energy within the scraper and associated veins may be used by some Tettigoniidae (Morris & Pipher 1972, Montealegre & Morris 1999). Perhaps during pulse train generation, the bent scraper of *D. jenningsi* moves to a stop across a small group of (4?) file teeth, imparting incrementing energy to the rising-amplitude waves of each pulse. For the remainder of the pulse the scraper is paused behind the last tooth, bending in its connection to the rest of the moving wing, and so gathering more elastic energy. A changed angle slips it free and so the process repeats for the next tooth group, and the next, along the file. The remarkably high tooth density of this species, coupled with increased speed through cuticular elasticity, may thus be a way of generating higher carrier frequencies.

A high phonatome rate and calling songs with transient pulses is not found in the species of *Uchuca* studied acoustically in the present work. But such song features are observed in undescribed species of *Uchuca*, occurring at high elevations in Ecuador (Brown 2002).

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Table 1. Characters proposed by the authors to distinguish *Dectinomima* and *Uchuca*.

Uchuca

1. *Wings*. Brachypterous or macropterous.
2. *Stridulatory apparatus*. File with less than 120 teeth. In some species the file is truncate basad.
3. *Male cerci*. Always with an elongate acuminate projection, becoming laminate. Basally cercus has another sclerotized appendage, which, interspecifically, varies in size (Fig.5 F-J).
4. *Titillators*. Strengthened by two rigid semi-curved sclerotized rod-shaped structures,projecting dorso-lateral and converging ventrally. These rigid bars are apically acuminate and may be either smooth or dentate on the ventral edge (Fig.5 V-Y).
5. *Tenth tergite of the female*. Bilobulate or bi-acuminate, medially shallowly or narrowly notched.
6. *Subgenital plate of the female*. Deeply emarginate posteriorad; lateral margins terminate distad in two straight lobes, directed dorsomesad, between which a rather deep mesodistal emargination is formed (Fig. 5K-O).

Dectinomima

1. *Wings*. All species brachypterous, tegmina always hidden by pronotum.
2. *Stridulatory apparatus*. File with more than 400 teeth. The file is continuous and does not present any proximal truncation.
3. *Male cerci:* With an irregular internal swelling mesodorsally and elongate mesointernal tapered projection curved anterior or posteriorad. Apically the cercus shows another projection moderately concave, acute and curved upward.
4. *Titillators:* With two sclerotized appendages, curved ventrally and apically acute (Fig.1). In the upper part (basally) of the titillators a pair of sclerotized filaments, covered by a transparent membrane.
5. *Tenth tergite of the female*. Truncate, medially deeply and narrowly notched.
6. *Subgenital plate of the female*. Elongate, narrow or basally broad; distally sulcate laterally and broad or minutely incised apically (Fig. 1E,K,O).

Table 2. Principal distinguishing features of *Dectinomima* spp.*

D. jenningsi

1. Prosternum armed
2. Facial markings absent
3. Male subgenital plate (apex) bilobulate
4. Acuminate projection of cerci directed posteriorad
5. Female subgenital plate minutely emarginate

D. sagittata

1. Prosternum unarmed
2. Facial markings present
3. Male subgenital plate (apex) truncate
4. Acuminate projection of cerci directed anteriorad
5. Female subgenital plate broadly emarginate

(*) We did not include D. pallida and *D. peruviana* in this table as we consider them to belong to *Uchuca;* see discussion for more details.

Table 3. Measurements of *Dectinomima jenningsi* (mm)

	Males (2)			Females (3)		
	average	Sdtdev	range	average	Sdtdev	range
Body	29.3	0.99	28.6-30.0	29.5	0.71	29.0-30.0
Pronotum	9.5	0.14	9.4-9.6	10.15	0.07	10.1-10.2
Tegmina	4.1	0.07	4.0-4.1	—	—	—
Fore femur	7.0	0.21	6.8-7.1	8	0.42	8.7-8.3
Fore tibia	8.1	0.14	8.0-8.2	9.15	0.35	8.9-9.4
Mid femur	7.0	0.00	7.0-7.0	8.1	0.28	7.9-8.3
Mid tibia	8.5	0.00	8.5-8.5	9.15	0.64	8.7-9.6
Hind femur	20.9	0.00	20.9-20.9	23.25	0.07	23.2-23.3
Hind tibia	21.1	0.21	20.9-21.2	22.95	0.07	22.9-23.0
Cercus	1.7	0.00	1.7-1.7	—	—	—
Ovipositor	—	—	—	10.6	0.57	10.2-11.0
Subg. plate	4.0	0.35	3.7-4.2	1.7	0.14	1.6-1.8

Measurements of *Dectinomima sagittata* (mm)

	Males (2)			Females (6)		
	average	Sdtdev	range	average	Sdtdev	range
Body	27.3	1.2	28.5-26.2	32.4	2.2	27.8-34.3
Pronotum	11.7	0.1	11.8-11.5	12.8	0.5	12.1-13.6
Tegmina	3.5	0.1	3.4-3.5	— —	—	
Fore femur	7.4	0.2	7.6-7.2	8.3	0.2	8.0-8.7
Fore tibia	8.7	0.1	8.8-8.6	9.6	0.6	9.0-10.6
Mid femur	7.4	0.2	7.6-7.2	8.7	0.4	8.1-9.4
Mid tibia	8.8	0.1	8.9-8.7	9.7	0.7	9.1-11.0
Hind femur	21.4	0.1	21.5-21.2	24.6	0.9	23.6-25.9
Hind tibia	21.5	0.1	21.6-21.4	24.8	1.1	22.9-26.3
Cercus	3.0	0.1	3.1-3.0	—	—	—
Ovipositor	—	—	—	11.0	0.4	10.6-11.6
Subg. plate	4.1	0.1	4.0-4.2	3.3	0.5	2.3-3.7

Table 4. Measurements of *Uchuca grisea* and *U. similis* (mm)

	U. similis	*U. grisea*			
	Males (1)	Males (1)	Females (2)		
			average	stdev	range
Body	16.4	23.6	22.9	0.7	23.3-22.4
Pronotum	7.3	8.6	9.3	0.3	9.5-9.1
Tegmina	3.0	4.63	4.9	0.3	5.0-4.7
Fore femur	4.5	5.77	6.5	0.2	6.7-6.4
Fore tibia	5.8	6.69	7.8	0.3	7.6-8.1
Mid femur	4.5	5.62	6.9	0.3	7.2-6.7
Mid tibia	5.0	6.07	7.6	0.6	7.1-8.1
Hind femur	12.1	16.36	19.9	0.5	20.2-19.5
Hind tibia	11.0	15.35	19.2	0.8	19.7-18.6
Cercus	3.3	3.78	—	—	—
Ovipositor	—	—	10.1	0.7	10.5-9.6
Subg. plate	2.4	3.12	2.0	0.1	2.1-2.0

Table 5. Measurements of *Uchuca amacayaca* (mm)

	Males (2)			Females (3)		
	average	Sdtdev	range	average	Sdtdev	range
Body	23.0	1.3	22.0-23.9	25.0	0.9	24.5-26.0
Pronotum	8.2	0.5	7.8-8.5	8.4	0.5	7.8-8.8
Tegmina	13.7	1.0	13.0-14.4	15.4	1.4	14.1-17.0
Fore femur	5.6	0.3	5.4-5.8	5.8	0.3	5.5-6.1
Fore tibia	6.5	0.3	6.2-6.7	6.9	0.3	6.8-7.2
Mid femur	5.8	0.3	5.6-6.0	6.2	0.2	6.0-6.5
Mid tibia	6.8	0.3	6.6-6.9	7.4	0.3	7.1-7.8
Hind femur	18.5	0.7	18.0-18.9	19.7	0.8	18.8-20.2
Hind tibia	16.7	0.5	16.3-17.0	18.4	0.6	17.8-18.9
Cercus	5.3	0.1	5.2-5.3	—	—	—
Ovipositor	—	—	—	10.4	0.3	10.2-11.7
Subg. plate	3.4	0.2	3.3-3.6	3.0	0.1	2.8-3.0

Table 6. Measurements of *Uchuca haltikos* (mm)

	Males (7)			Females (6)		
	average	Sdtdev	range	average	Sdtdev	range
Body	22.0	1.1	20.3-23.9	25.3	1.6	23.9-28.5
Pronotum	9.1	0.8	7.8-10.1	9.2	0.8	7.8-10.4
Tegmina	12.5	1.0	11.6-14.4	15.6	1.9	13.8-19.2
Fore femur	6.0	0.3	5.4-6.4	6.4	0.5	5.5-6.9
Fore tibia	7.0	0.4	6.2-7.4	7.6	0.6	6.8-8.7
Mid femur	6.4	0.5	5.6-7.3	6.9	0.5	6.0-7.4
Mid tibia	7.4	0.5	6.6-8.4	8.0	0.5	7.1-8.7
Hind femur	19.4	0.7	18.0-20.1	20.9	1.1	18.9-22.8
Hind tibia	18.3	1.1	16.3-19.1	20.4	1.6	17.8-22.7
Cercus	4.6	0.5	4.1-5.3	—	—	—
Ovipositor	—	—	—	10.8	0.5	10.2-11.7
Subg. plate	3.3	0.2	3.1-3.6	3.0	0.1	2.8-3.1

Table 7. Measurements of *Uchuca macroptera* (mm)

	Males (4)			Females (7)		
	average	Sdtdev	range	average	Sdtdev	range
Body	21.4	0.8	20.3-22.0	25.5	1.9	23.9-28.5
Pronotum	9.4	0.5	9.0-10.1	9.6	0.6	9.0-10.4
Tegmina	12.1	0.6	11.6-12.9	15.7	2.2	13.9-19.2
Fore femur	6.2	0.2	6.0-6.4	6.7	0.3	6.1-6.9
Fore tibia	7.3	0.1	7.1-7.4	7.9	0.5	7.3-8.7
Mid femur	6.5	0.1	6.3-6.5	7.2	0.3	7.1-7.4
Mid tibia	7.8	0.2	7.6-8.0	8.2	0.3	7.6-8.7
Hind femur	19.7	0.3	19.3-20.1	21.5	0.7	21.2-22.8
Hind tibia	18.9	0.3	18.5-19.1	21.2	1.0	20.1-22.7
Cercus	4.3	0.2	4.1-4.4	—	—	—
Ovipositor	—	—	—	10.9	0.5	10.2-11.7
Subg. plate	3.3	0.2	3.1-3.4	3.0	0.2	2.8-3.1

Appendix 1. Distinction between *Dectinomima* and *Uchuca,* based on characters used by authors in the respective original descriptions and further revisions (Gigliotos 1898, Caudell 1910, Karny 1912ab).

UCHUCA

1. Frons: Smooth
2. Frontal fastigium: Acute
3. Vertexial fastigium: Broader than the scapus, dorsally flat, rounded anteriorad, ventrally compressed laterad and bearing an elongate keel. Seen frontally, the lateral margins are strongly divergent and touch the frontal fastigum
4. Scapus: Dilated interiorad, scarcely protruding
5. Pronotum: Convex, anterior margin truncate and the posterior one acutely rounded
6. Lateral lobes of the pronotum: Deep, with acute ventral margin and humeral sinus almost inconspicuous
7. Prosternum: Bispinose
8. Meso and metasternum: Ending in elongate angles
9. Fore and mid femora: Ventrally dentate on the anterior margin
10. Hindfemur: Strongly swollen basally, with short spines on the proximal half
11. Foretibia: Dorsally flattened
12. Hind tibia: With terminal spines in both margins.
13. Forewings: ?
14. Genicular lobes: ?
15. Male subgenital plate styli: Present
16. Ovipositor: Sickle-shaped

DECTINOMIMA

1. Frons: ?
2. Frontal fastigium: ?
3. Vertexial fastigium: Fastigium proximally broad but not broader than the scapus, not narrowed, without any ventral tooth, but separated from the frontal fastigium by a superficial sulcus.
4. Scapus: ?
5. Pronotum: Pronotum convex, without lateral carinae, rounded anteriorad, posterior margin strongly rounded and outstanding
6. Lateral lobes of the pronotum: Lateral lobe with oblique ventral margin, humeral sinus superficial
7. Prosternum: Armed with large spines
8. Meso and metasternum: Triangular, with rounded lateral lobes, which end in acute angle
9. Fore and midfemora: With spines on anterior margin
10. Hind femur: Hind femur very thickened, armed on both ventral margins with 5 to 6 spines.
11. Fore tibia: ?
12. Hind tibia: ?
13. Forewings: Strongly reduced, barely exceed the posterior pronotal margin, scarcely visible
14. Genicular lobes: Outer genicular lobe of fore and mid legs sharply pointed, others with spine
15. Male subgenital plate styli: ?
16. Ovipositor: Strongly compressed laterad, deeply bent basally, then with straight dorsal edge and ventral edge proportionally curved and ending sharply.