New species of awl-head katydids, *Cestrophorus* and *Acanthacara*, from the Andes of Ecuador (Orthoptera, Conocephalinae, Cestrophorini)

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Abstract

The Cestrophorini are small katydids of Ecuador's montane rainforest bearing a prominent awl-shaped fastigium verticis. They are unusual among Conocephalinae in lacking pre-tympanic ear chambers: their eardrums are exposed on their fore tibiae. There are presently two genera, *Cestrophorus* Redtenbacher, 1891 and *Acanthacara* Scudder, 1869. Awl-head habitat includes both climax forest and anthropogenically disturbed areas (e.g., pastures, roadsides) on lower slopes in the drainage of the volcanoes Aliso, Chiles and Tungurahua. At night, males perch on low vegetation and stridulate to attract females. To three extant species, we add a further seven, two in *Cestrophorus* and five in *Acanthacara*. Male calling songs were recorded and analyzed for all three *Cestrophorus* species and for three of the *Acanthacara* spp. We describe and discuss the waveforms of their sinusoid and transient sound pulses in time and frequency domains.

Keywords

Introduction

Dita Klimas and Glenn Morris made several trips to the Ecuadorean Andes (Fig. 1) between 1983 and 2003 in search of tettigoniid sound signals. Near Baños on pasture slopes of Volcán Tungurahua (Fig. 2) and in remnant wet forests southwest of Baeza[1] (Fig. 1), they found species of small conocephaline katydids (Fig. 3). These insects are characterized by a glistening black frons, a prominent, distally attenuated tip-deflected fastigium of the vertex recalling a cobbler's awl (Fig. 4) and, peculiar among conocephalines, superficial tibial tympana, i.e., eardrums not recessed within slitted chambers (Fig. 5). At present, these Andean 'awl-head' insects comprise just two genera: *Cestrophorus* Redtenbacher, 1891 and *Acanthacara* Scudder, 1869 in the tribe Cestrophorini Gorochov, 2015.

The holotype female of *Acanthacara acuta* Scudder, 1869 was collected in 1867 by the naturalist James Orton. As he recounts in *The Andes and the Amazon, Or Across the Continent of South America* (Orton 1870), his party journeyed eastward by horse from Quito, over the mountains on a rugged trail via Papallacta to Baeza and Cosanga, then across the Rio Cosanga and on downvalley toward Napo (Archidona, Tena). The Orton expedition's Orthoptera specimens were subsequently identified and named by Samuel H. Scudder (1869); on one of these specimens, a female, Scudder established a monotypic new taxon, *Acanthacara acuta* . This holotype, deposited in the Harvard Museum, lacks forelegs, making it evident why Scudder makes no mention of naked tympana.

In his 1891 monograph on Conocephalidae, Josef Redtenbacher names a conocephalid with superficial tympana: *Cestrophorus paradoxus* Redtenbacher, 1891. "*Ausgezeichnet durch das offene Trommelfell an den Vorderschienen*" [Distinguished by the open tympanum on the fore tibiae.] This species is based upon a lone male specimen labeled as from Madagascar. Label information is "Coll. B. v. Watt. Central Madagascar Dr. H. Dohrn". A very effective colored drawing of the specimen given in Karny's Genera Insectorum (1912, plate 8, item 16) is reproduced here (Fig. 6). On February 10 and 19, 1988, we (Dita Klimas and GKM) collected amongst a large calling deme of this species, males stridulating at dusk in understory vegetation along a trail beside the loud cascade of the Rio Aliso, near where it joins the Rio Cosanga—a locale very far from Madagascar. The two white maculae on the pronotal metazona of the males helped in detection and capture. One supposes Redtenbacher's choice of the name *paradoxus* may have something to do with his finding Madagascar an odd locality or perhaps he reacted to the open eardrums (Since Dohrn only travelled to western Africa, this is likely a case of mislabeling of a specimen coming from his collection in the museum at Stettin).

Recently, Gorochov (2015) described a male specimen of a second *Acanthacara* species, *A. ridiculosa* Gorochov, 2015, taken near the San Rafael Waterfall. This locality is east of the road junction

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1   An earthquake in March 1987 damaged the historic townsite of Baeza and led to the creation of a 'displaced Baeza' farther east; our collecting was upslope of the elder Baeza in remnant forest along a path beside a small gurgling stream.

Fig. 1. Part of a map, República del Ecuador, Instituto Geográfico Militar; scale 1:1,000.000. Baños, north of the volcano Tungurahua, is bottom left. Papallacta is top left, just north of Volcan Antisana; Baeza is down-valley to the east. Cosanga the town and Río Cosanga are near map center, a few km beyond Baeza in the direction of Archidona.

at Baeza, farther downvalley in the direction of Coca. Gorochov grouped *Acanthacara* and *Cestrophorus*, making the latter the type genus of a new tribe, Cestrophorini (Gorochov 2015).

We present nine species of Cestrophorini; all but one, *Cestrophorus amplitenuis* sp. nov., are from the drainage of volcanoes Aliso and Tungurahua, including probable males of *Acanthacara acuta*. We have examined a set of photographs of the *A. acuta* type female, kindly provided by Piotr Naskrecki

and of higher resolution than those previously available on the Orthoptera Species File Online (Cigliano et al. 2022); our females compare convincingly. The new species *C. amplitenuis* sp. nov. was located in Provincia Carchi, along a road (182) leading from Tofino (nr Tulcan) to the town of Maldonado[2]; a large population of singers were found roadside at night, several kilometers west of the *Espeletia*-dotted paramo of Volcán Chiles and a few kilometers east of Maldonado.

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2   Pedro Vicente Maldonado was a famous Ecuadorean scientist, cartographer, etc., of the 18th century. His name appears on two towns in Ecuador: this in Prov. Carchi, but also another in the neighboring Prov. of Esmeraldas.

Fig. 2. Volcán Tungurahua emerges from clouds, 1983.

Fig. 3. A live male of *A. incisa* collected roadside just below the small settlement Pondoa on northern aspect of Volcán Tungurahua, July 1985. Locality in a field name is a bad idea: when what you have christened "Baeza Blackface" is apparently taken later near Baños and you have to reference it as Baños' Baeza Blackface, confusion is likely, especially when these specimens sort into more species later.

Calling song analyses of three of these cestrophorines comprised a poster paper by GKM in 1987 at the VIth International Meeting on Insect Sound and Vibration at Odense, Denmark. At the time, these species were planned to belong to a new genus "*Gymnacoustes*", a reference to their naked tympana. The ISV poster's '*Gymnacoustes isoharmonicus*' (here reproduced as Fig. 17) is the species herein designated *Acanthacara ortoni* sp. nov., and the poster's '*G. unizip*' is *Acanthacara incisa* sp. nov. (Fig. 18). The species epithet *ditachus* resides now in the genus *Cestrophorus*.

A superficially similar undescribed conocephaline from montane areas on the slopes of Volcán Pichincha (near Quito) is readily distinguished from Cestrophorini by its possession of slitted pre-tympanal chambers and a large subnotal resonance chamber formed from the pronotal metazona. This insect is termed "Agraeciine x" by Morris and Mason (1995). This same species is misidentified as *Acanthacara acuta* in a recent paper (Jonsson et al. 2017).

Methods

Dita Klimas and GKM hunted perched katydids by sight at night, scanning by headlamp the vegetation bordering forest paths and taking photographs. The stridulation of tropical tettigoniids is not always useful in revealing a singer's location, but we were also aided by heterodyne devices ('bat detectors'). Specimens were captured by hand-herding into an insect net then transferred individually to small plastic jars. Some field recordings were made using a Sony Walkman tape recorder (WM D6C Stereo Cassette-Corder with an ECM 909 microphone) and are limited to the audio frequency range.

A subset of specimens were individually caged, maintained on pieces of apple, and transported alive via jet aircraft to Toronto, Canada. Here, as they called from a small cylindrical aluminum screen cage, their songs were recorded, with equipment reaching into the ultrasonic (Bruel & Kjaer ¼" microphone 4135 or 1/8" microphone 4138), onto a Racal Store 4 DS Instrumentation Tape Recorder running at 30″/s. The microphone output went initially to a B&K Impulse Precision Sound Level Meter 2204. This in-lab recording system responded to sound frequencies flat to 70 kHz. Room temperature was ~21 °C.

Analysis of analog tape recordings began with digitization. A Krohn-Hite filter (Model 3202) band-passing 125–15000 Hz was employed to anti-alias sound frequencies input to a computer sound card via Cool Edit. The Racal playback was slowed by a factor of 8, so a Cool Edit sample rate of 22050 Hz sufficed to digitize any real-time ultrasonics. Output from the Sony Walkman recorder running in real time was digitized at 48000 samples per second. Fourier transforms were then calculated using the windowing spreadsheet DADiSP (DSP Development Corp.). Figures of time and frequency domain analyses were made using Corel Draw.

Repositories are the Museo de La Plata (MLP) and the Academy of Natural Sciences in Philadelphia (ANSP). Additional pictures, including all holotypes, will be available on Orthoptera Species File Online (Cigliano et al. 2022).

Taxonomy

Cestrophorini Gorochov, 2015

Small agraeciine-like conocephalines with fully exposed tympana. Tegmina in males covering up to the entire abdomen or reduced to about pronotum length; in females, rudimentary or absent. Coloration light yellowish brown to greenish, with whitish, dark brown, or black markings and patterns. Fastigium of vertex

Fig. 4. Scanning electron micrograph (SEM) of male *A. ortoni* fastigium verticis.

Fig. 5. SEM of superficial tympanic membrane on proximal tibia of *A. ortoni*.

acutely pointed, from just projecting beyond antennal scapus to quite long, slightly downcurved or almost straight. Acoustic spiracle tiny, exposed below ventral margin of pronotum. Prosternum unarmed. Ovipositor of females about as long as head and pronotum combined, slightly upcurved (lower margin strongly curved, upper margin little curved or almost straight), moderately broad with acuminate tip. Inhabiting Andean foothills of Ecuador.

Cestrophorus Redtenbacher, 1891

Etymology.—From original description: Greek κέστρο – Latin *subula* [shoemaker's awl] and φέρω – *fero* [bear, carry], surely referring to the notable fastigium: "*fastigium verticis articulo primo antennarum fere duplo longius, subulatum, decurvum*" (Redtenbacher 1891).

    Diagnosis.—Small, robust to moderately compact. In males, pronotum posteriorly widened and metazona usually at least slightly elevated; male tegmina covering abdomen completely or leaving only tip exposed, left tegmen uniformly with coarse venation and long cubital vein occupying considerably more than half of total width. Male cerci short, broad, dorsally with obtuse medial lobe, below that terminating in acuminate inward curved spine, and ventrally at the base with another upcurved spine. Male subgenital plate with very short styli, almost looking like latero-terminal tips rather than separately articulated styli, sometimes completely reduced.

Cestrophorus paradoxus Redtenbacher, 1891
Figs 6, 8A, B, 11, 12

Material examined.—ECUADOR • ♂; Río Aliso; 4 Jul. 2003; G.K. Morris leg.; MLP • 6 ♂♂; Río Aliso; 10 Feb. 1988; G.K. Morris leg.; ANSP • 6 ♂♂; Río Aliso; 19 Feb. 1988; G.K. Morris leg.; ANSP • 5 ♂♂; Río Aliso; 4 Jul. 2003; G.K. Morris leg.; ANSP • 1 ♀; Río Aliso; 19 Feb. 1988; G.K. Morris leg.; ANSP • 1♀; Cosanga; 10 Feb. 1988; G.K. Morris leg.; MLP.
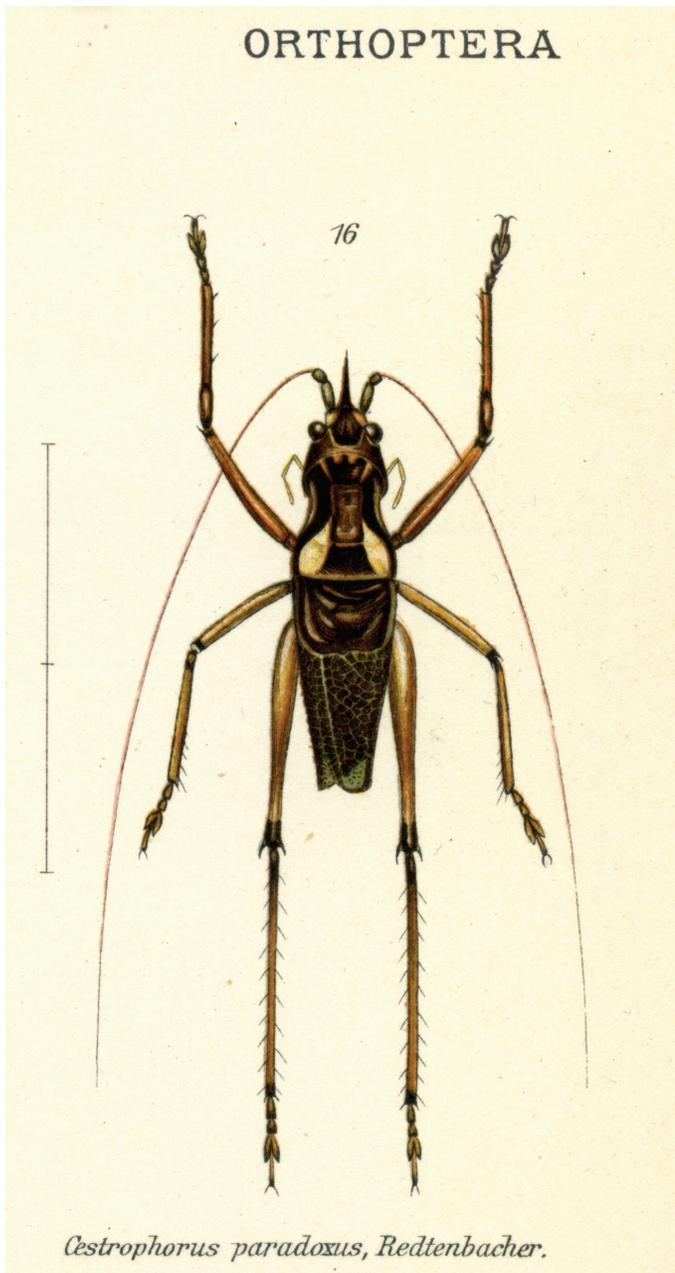
Fig. 6. *C. paradoxus*. Illustration of male adult from Karny H., 1912. Genera Insectorum Orthoptera Fam. Locustidae, Subfam. Agraeciinae (Plate 8, item 16).

Redescription.—Robust with fastigium projecting well beyond scapus. Males with contrasting coloration: fastigium blackish, dorsal surface of pronotum medially dark, in prozona and metazona blackish, in metazona broadly trapezoideal and fringed by a pair of ovoid elongate whitish lateral maculae (Fig. 8A), thin distal portion of hind tibiae blackish. Male tegmina greenish, broadened beyond width of pronotum and covering abdomen completely. Male cerci approximately broadly triangular in dorsal and lateral view, obtuse medial lobes with inconspicuous obtuse and recurved hook, almost touching in the middle, cercus terminating in sharp upcurved spine, and at the base with long and more or less perpendicularly upcurved spine (up to beyond the height of the dorsal hook).

Fig. 7. *C. amplitenuis* pair mating in the field; part of a large deme of singers in shrubby roadside vegetation at the type locality near Ecuador's northern border with Colombia. Female lacks wings.

Measurements.—Male: midline pronotum 4.6 mm, fastigium verticis 1.8 mm, tegmina 9.2 mm; female: midline pronotum 3.8 mm, fastigium verticis 1.7 mm (based on two specimens, no apparent variation in size).

Note.—All specimens—in February 1988 and again in July 2003—were taken from beside a forest path tracing the south bank of the Río Aliso upstream; the site is reached by a (very) secondary road branching west from the main highway just before the town of Cosanga. About 3 km along this sideroad is the lodge Cabañas San Isidro; a few km farther on, a posted sign at an iron bridge identifies the Río Aliso.

Cestrophorus ditachus sp. nov.

https://zoobank.org/39B53563-0D85-42CA-8DF2-80F9C45018AB
Figs 8C, D, 13

('*Gymnacoustes ditachus*' Morris, 1987)

Material examined.—**Holotype:** ECUADOR • ♂; old Baeza; 11 Jul. 1985; G.K. Morris leg.; SN-2, MLP. **Paratypes:** ECUADOR • 1 ♂; old Baeza; 10 Jul. 1985; G.K. Morris leg.; 85-1, Glassy Tegmina, ANSP • 1 ♂; Tungurahua; 25 Feb. 1985; G.K. Morris leg.; GLASSY TEG, SN-3, ANSP • 1 ♀; Cosanga; 19 Feb. 1988; G.K. Morris leg.; MLP • 1 ♀; Cosanga; 19 Feb. 1988; G.K. Morris; ANSP.

Etymology.—Named for its two-part, two-pulse-rate, song structure, readily apparent to the human ear in real time. Greek δι di [two], ταξηοσ tachos [speed]. This insect is also named (inadvertently but deservedly) for Dita Klimas, katydid field photographer extraordinaire.

Diagnosis.—More slender and uniformly colored than *C. paradoxus*, with shorter tegmina. General coloration pale greenish; in males, metazona of pronotum with brown trapezoidal spot fringed by elongate whitish lateral spots. Male tegmina leaving abdomen tip exposed. Females uniformly greenish and apterous. Male cerci with obtusely triangular dorsal lobe (internally with inconspicuous toothlet at the tip) and robust inward-curved acuminate spine, baso-ventral spine with broad base and tapering in perpendicularly upcurved tip; above it on same lobe, another short spine (difficult to see). Styli completely reduced.

Measurements.—Male: midline pronotum 4.3 mm, fastigium verticis 1.7 mm, tegmen 7.5 mm, hind tibiae 8.6 mm; female: mid-
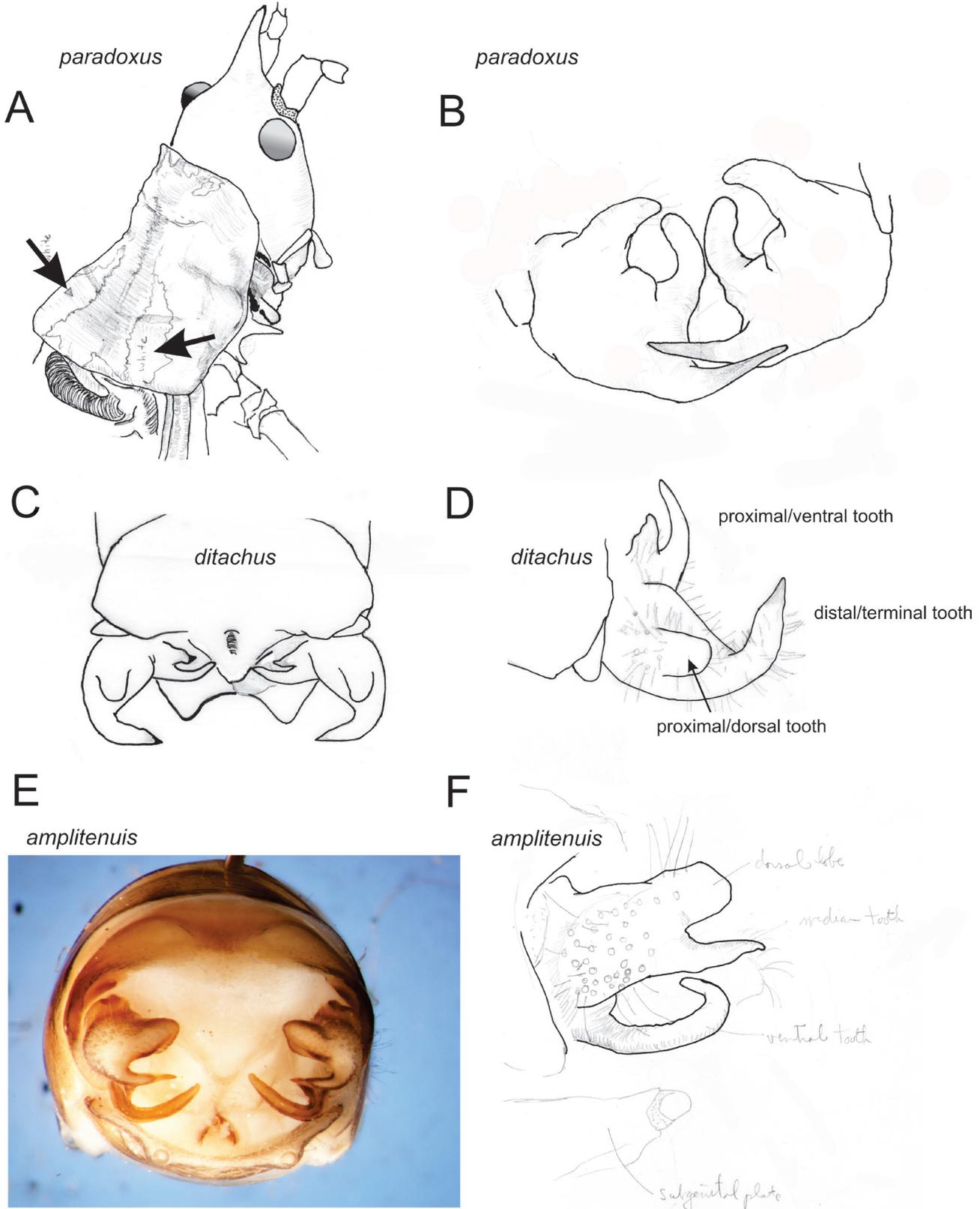
Cestrophorus spp.

Fig. 8. *Cestrophorus* spp. male genitalia compared. **A.** White pronotal maculae of *C. paradoxus*; **B.** Parameres of *C. paradoxus* 'upside-down dancing anteaters'; **C.** Dorsal aspect *C. ditachus* parameres; **D.** Lateral view of *C. ditachus* paramere; **E.** Photo of terminalia of *C. amplitenuis*; **F.** Lateral aspect of *C. amplitenuis* paramere.

line pronotum 4.1 mm, hind tibiae 9.7 mm, ovipositor 8.7 mm (based on holotype and one paratype).

Field notes.—We hunted in light rain at the [historic pre-earthquake] townsite of Baeza, along a muddy rock-strewn trail fenced by barbed wire, uphill beyond the hospital and cemetery on the night of July 10, 1985. We recorded and captured one male 'agraeciine' of "pearly pale cast", [like *C. paradoxus*] with white maculae prominent laterad on its pronotal metazona, its very pale greenish tegmina shorter than the abdomen, and its eardrums not recessed behind slits [field name 'glassy tegmina']. This specimen is now the holotype male. On July 11, GKM recorded another singer up the eastern branch of the trail above Baeza but failed to capture him.

On July 25, 1985, we drove from Quito and parked part way up Volcán Tungurahua at signed "ecological reserve" hut under construction, below Pondua. Many *C. ditachus* sp. nov. were heard singing from shrubby vegetation scattered about a pasture (never a bovid seen). GKM "recorded a male singing from well above my head in a clump of bamboo and one small hardwood tree. After recording, we bent the bamboo down and searched the foliage with our lights," finding and capturing the presumed singer. "As we left the immediate vicinity of the road and climbed several hundred feet, the incidence of [*C. ditacus sp. nov.*] singers declined to zero. They had ceased calling by 10:30 pm. Chilly and soon one could only hear single quiet lisps recurring at intervals of several seconds, presumably *Acanthacara incisa.*"

Cestrophorus amplitenuis sp. nov.
https://zoobank.org/F43EDD15-D715-4F3A-AADD-9426CB04ADFF
Figs 7, 8E, F, 14

Material examined.—**Holotype:** ECUADOR • ♂; Prov. Carchi, hwy 182, e. of Maldonado; 16 Apr. 1990; G.K. Morris leg.; MLP. **Paratypes:** ECUADOR • 1 ♀; Prov. Carchi, hwy 182, e. of Maldonado; 16 Apr. 1990; G.K. Morris leg.; ANSP • 7 ♂♂, 2 ♀♀; Prov. Carchi, hwy 182, e. of Maldonado; 16 Apr. 1990; G.K. Morris leg.; ANSP • 4 ♂♂; Prov. Carchi, nr. road btwn Maldonado and Tulcan, s. of Rio La Plata, 3100 m., primary forest; 26–31 Jul. 1988; Glenn, Pedersen & Wechsler leg.; ANSP on loan to GKM.

Etymology.—Named in reference to the 'dying fall' of each call's amplitude: each song emission begins as intense sinusoids that then diminish (Fig. 14 B,C). Latin *amplio* [made large], *tenuis* [thin].

Diagnosis.—As *C. ditachus,* more slender than *C. paradoxus*. Fastigium short and projecting only a little beyond scapus. General coloration light amber; in males. dorsal surface of pronotum medially dark brown, with whitish lateral fringes, especially in metazona. Male tegmina slender, almost as long as abdomen but leaving tip exposed. Females apterous. Male cerci with obtusely truncated dorsal lobe and acuminate terminal spine; ventro-internal process uniformly thin, fairly long, and slightly twisted.

Measurements.—Male: midline pronotum 4.4 mm, fastigium verticis 1.1 mm, tegmen 7.3 mm, hind tibia 9.1 mm; female: midline pronotum 4.0 mm, fastigium verticis 1.2 mm, hind tibia 9.5 mm, ovipositor 6.7 mm (based on holotype and one paratype).

Field notes.—A road (182) runs west along the Colombian border from Tulcán to Maldonado and beyond. The insects were taken roadside roughly 50 km west of Tulcán. After Tofino, the road climbs the slope of Volcán Chiles into paramo dotted with tall columnar "grey friar" plants. Their flowers are like small sunflowers in clusters. The road was (still is?) a single lane of rough winding dirt that favors switchbacks. We descended into a col of the volcano and passed a strangely colored lake with the strong smell of sulfur in the air. The light was beginning to fade as we crossed a height of land on the west side of the volcano and began to steadily descend. After proceeding downhill for several kilometers, we left the paramo but were not yet into forest. We stopped here to listen, the road bordered by shrubs and sedge, and heard singing.

Acanthacara Scudder, 1869

Etymology.—Not mentioned in the original description; probably derived from Greek άκανθα – *ácantha* [thorn] and, as in *Cestrophorus*, certainly referring to the vertex being "prolonged into a sharply pointed, long and curved thorn" (Scudder 1869).

Diagnosis.—Habitus more slender compared to *Cestrophorus*, with more delicately thin and elongate fastigium verticis. Tegmina not much longer than the narrower and more elongate pronotum; in males, the left tegmen with distinctively developed stridulatory area with transparent fields, the vein with the stridulatory file underneath relatively short. Male cerci not conspicuously broad at base and male subgenital plate with distinct styli.

Redescription.—Small and slender, yellowish brown, brachypterous coneheads with strongly oblique face and prominent, almost straight or slightly recurved acuminate fastigium. Body length 17–22 mm; fastigium length almost twice the eye diameter. Pronotum shallow and rounded, dorsal contour flat or almost flat, posteriorly produced and in males diverging overtop bases of short tegmina that are of equal length or little longer than the pronotum, leaving at least half of the abdomen uncovered in live individuals. Stridulatory area of left tegmen subdivided in transparent fields usually free from venation: a speculum lies right behind the short cubital vein, and an adjacent lateral field lies left of this 'mirror'. The cubital vein is fairly bulgy and occupies half or a little more of the total dorsal width of the tegmen. Females are apterous. The tiny acoustic spiracles are directed latero-posteriorly. All genicular lobes except the outer one of the fore tibiae armed. Male cerci at base moderately wide, with more or less prominent distal dorsal process and below that with another inward-directed process that sometimes has a more delicate ventral appendage. Male subgenital plate with short but distinct styli. Coloration ochre or light brown with extensive black markings on face and with darker brown and blackish markings and patterns on pronotum, abdomen and legs. Living in montane woodland.

Notes.—All following diagnoses refer to males. Apart from the development of male tegmina, the species can be distinguished by the shape of male cerci. Measurements of the new species correspond to the holotypes (there is no significant variation among specimens of a particular species and there is little difference in the body size of all species). It is difficult to assign females to corresponding males. Below the species accounts, a key to all seven species is provided.

Acanthacara acuta Scudder, 1869
Figs 9A, 10A

Material examined.—ECUADOR • 1 ♂; Río Aliso, nr San Isidro Resort, 2000 m; 2–6 Jul. 2003; G.K. Morris leg.; MLP • 1 ♂; Baeza; 10 Jul. 1985; ANSP • ♂; Cosanga; 10 Feb. 1988; G.K. Morris leg.; ANSP.

Diagnosis.—Tegmina slightly longer than pronotum; venation at costal margin sometimes greenish. Pronotum sparsely pubescent and with contrasting coloration: lateral lobes dark, dorsal portion light with dark median markings on front and rear margin, sometimes separation of dark lobes and lighter dorsal por-
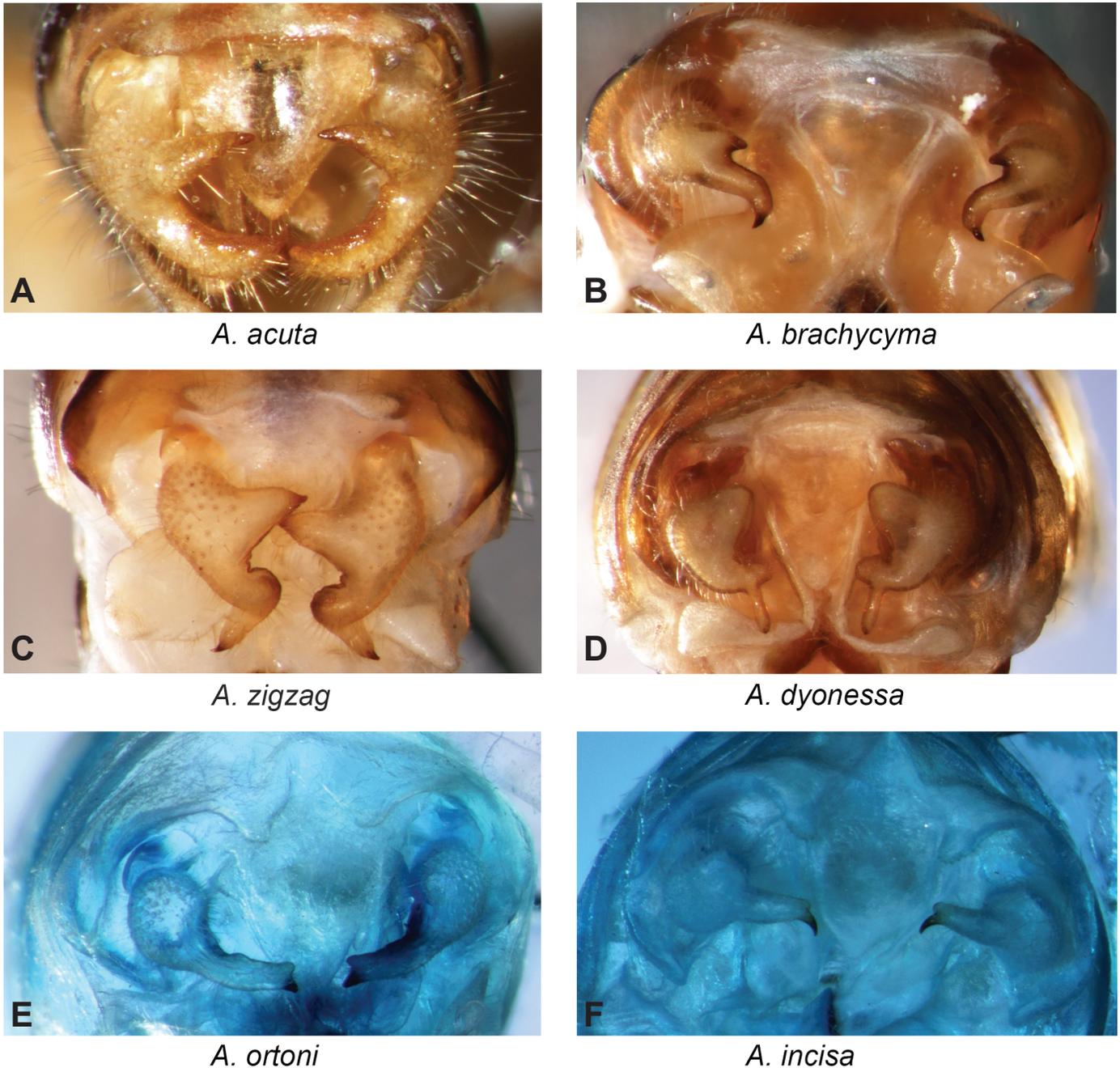
Fig. 9. *Acanthacara* spp. male genitalia compared.

tion developed as light medially restricted lateral stripes on disc. Last tergite shallowly emarginate. Cerci in dorsal portion elongate, inward-curved, and pointed; below that, another, slightly stronger and also inward-directed pointed branch, with dorsally slightly more sclerotized ridge, so the cerci look bifurcate in caudal view. Styli very short but distinctive, 1–2 times as long as wide.

Measurements.—Pronotum 4.2 mm, tegmina 5.1 mm, hind tibiae 9.1 mm.

Notes.—Our three males are so similar to the female holotype of *A. acuta* that we consider them conspecific. Fastigium shape and coloration details of the body match very well (the type is unfortunately lacking all legs except its right middle leg). The female was collected by the naturalist James Orton somewhere between Quito and the Napo region (Scudder 1869). His expedition spent time in Baeza and then camped at a locality about 6 km further south on the banks of the Cosanga River (Orton 1870). This is the very area where our specimens have been found, as well as the ones of the following two new species, which differ in coloration. According to measurements of pronotum and hind femora in the original description, the holotype appears to be adult, not a last-instar nymph as Gurney (1972) suspected.

***Acanthacara brachycyma* sp. nov.**
https://zoobank.org/B40DA89A-98F9-41D6-AE7A-01C907CD5E8A
Figs 9B, 10B, 15

Material examined.—**Holotype:** ECUADOR • ♂; San Isidro, nr Cosanga; 2–6 Jul. 2003; G.K. Morris; MLP. **Paratypes** • 7 ♂♂; San
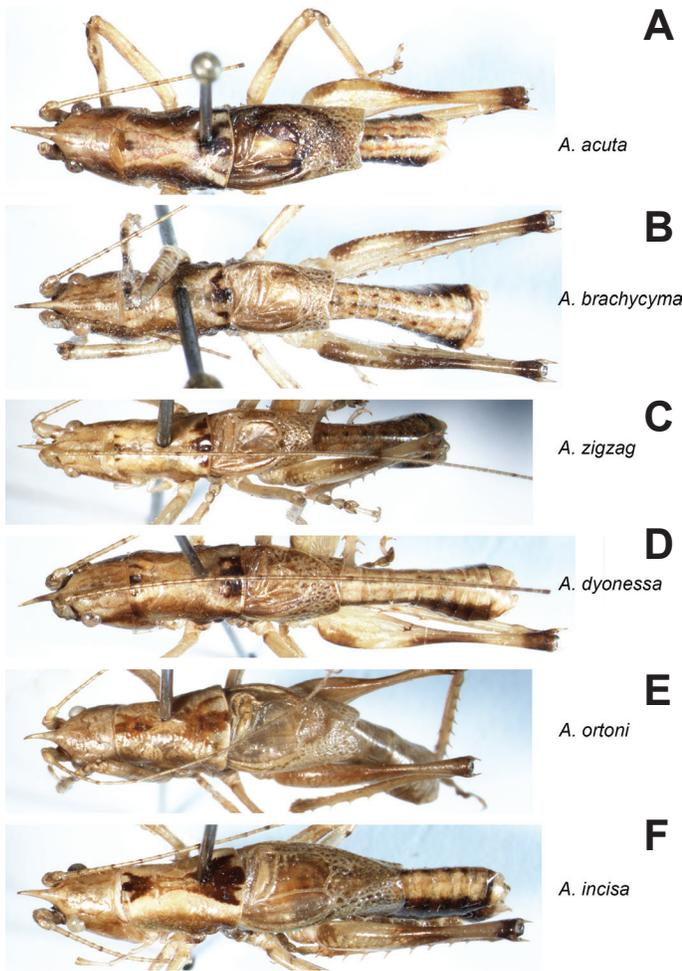
Fig. 10. *Acanthacara* adult males compared in dorsal aspect.

Isidro, nr Cosanga; 2–6 Jul. 2003; G.K. Morris leg.; ANSP • 1 ♂; Cosanga; 10 Feb. 1988; G.K. Morris leg.; ANSP • 1 ♀; San Isidro, nr Cosanga; 2–6 Jul. 2003; G.K. Morris leg.; MLP • 7 ♀♀; San Isidro, nr Cosanga; 2–6 Jul. 2003; G.K. Morris leg.; ANSP.

Etymology.—Greek βραχύς – brachys [short] and κύμα – kyma [wave], a reference to the predominantly ultrasonic spectrum of the song (noun in apposition).

Diagnosis.—Fastigium almost straight, very tip slightly down-curved. Tegmina about as long as pronotum, stridulatory area of left tegmen with translucent fields occupying almost ¾ of total length, the bulgy vein with stridulatory file underneath barely longer than mirror width. Pronotum with small blackish median spot on anterior margin (sometimes surrounded by a pair of smaller spots) and up to five spots on the rear margin, the middle one being the most prominent and the most lateral ones contiguous with the dark coloration of the lateral lobes. Last tergite shallowly bilobate. Cerci with a small dorsal tip and terminating in a ventrally directed process. The dorsal tip is directed medially and obtusely pointed. The ventral process is S-shaped, curving first inward and then downward, with an acute tip.

Notes.—Very similar to *A. ridiculosa* Gorochov, 2015 and distinguished by the following differences: no reticulation on mirror area of left tegmen (dense venation network in *ridiculosa* according to photo in Gorochov 2015, fig. 69, cannot be illumination artifact); rear margin of last tergite shallowly emarginate without distinct lateral tips, rather with very broad lateral lobules (more or

less distinctly rounded tips in *ridiculosa*, see ventral view in fig. 71 (Gorochov 2015) for true contour, probably no shrinkage artifact); the secondary (dorsal) tip or process on the cerci is very short when viewed from all possible angles, directed inward, and in approximately same plane as terminal zigzag process (in *ridiculosa*, sticking out in dorsal view, apparently quite long in ventro-lateral view of fig. 72); the zigzag process is distinctly thinner than rest of cercus and fully S-shaped: curved first perpendicularly inward—not quite horizontally but slightly downward—and then halfway-rearward and perpendicularly downward (in *ridiculosa*, not thin over noticeable length, tip close to compact base, the inward-curved part relatively shorter in dorsal view in fig. 70). There are broad, thin and transparent, remotely cup-shaped structures below the cerci into which the latter could be stored, perhaps belonging to the paraproct, without any elongate or pointed processes (in *ridiculosa*, corresponding structure with conspicuous processes visible in fig. 70 and looking acutely pointed in ventral view in fig. 71). Subgenital plate shallowly emarginate, with two lobes between the styli and with very short styli that are hardly twice as long as wide (the subgenital plate of *ridiculosa* has a straight rear margin and the styli considerably longer according to figs 71, 72).

Measurements.—Pronotum 4.3 mm, tegmina 4.0 mm, hind tibiae 9.3 mm.

Acanthacara zigzag sp. nov.

https://zoobank.org/21093D8A-D9B0-486E-A67C-ABA40D71DD7D

Figs 9C, 10C

Material examined.—**Holotype**: ECUADOR • ♂; old Baeza; 10 Jul. 1985; G.K. Morris; MLP. **Paratypes**: ECUADOR • 3 ♂♂; old Baeza; 10 Jul. 1985; G.K. Morris leg.; ANSP • 1 ♂; old Baeza; 23 Apr. 1989; G.K. Morris leg.; ANSP.

Etymology.—Named for the alternating acute-angle direction changes of the male cerci.

Diagnosis.—Very similar to preceding species, with slightly longer cubital vein (longer than width of mirror) and different cerci. Fastigium almost straight. Tegmina of same length as pronotum; pronotum with 1 or 3 small blackish spots on anterior margin and 3 larger spots on rear margin. Last tergite ending in two lobes. Cercus with pointed medial branch, rectangularly inward-directed; below that, another inward-directed process with thinner and downward-directed appendage terminating in acute spinule. The structures below the cerci, mentioned for the previous species (see notes on comparison with *A. ridiculosa* above), here have obtuse posterior tips.

Measurements.—Pronotum 4.0 mm, tegmina 4.3 mm, hind tibiae 7.6 mm.

Acanthacara dyonessa sp. nov.

https://zoobank.org/D5BC4C3E-F9DF-4F7C-99D5-3996BDA5EA9D

Figs 9D, 10D

Material examined.—**Holotype:** ECUADOR • ♂; old Baeza; 8 Apr. 1989; G.K. Morris; SN-2; MLP. **Paratypes:** ECUADOR • 2 ♂♂; Río Huagra Yacu near Baeza; 9 Apr. 1989; G.K. Morris leg.; ANSP • 1 ♂; Baeza; 23 Apr. 1989; G.K. Morris leg.; ANSP • 1 ♂; Baeza; 11 Jul. 1985; G.K. Morris leg.; ANSP.

Etymology.—Greek *dyo* [dive], *nessa* [duck] – referring to shape of male cerci resembling a diving duck.

Diagnosis.—Fastigium slightly longer than in other species. Tegmina as long as pronotum. Pronotum with small blackish spot

on front margin and more or less extensive spot on rear margin. Cerci with bulky and obtuse in- and upward-directed tip, below that with another half as bulky inward-directed process, which has a thin digitiform and pointed ventral appendage. Styli very short and looking like lateral tips of the subgenital plate.

Measurements.—Pronotum 4.5 mm, tegmina 3.9 mm, hind tibiae 9.6 mm.

Acanthacara ortoni sp. nov.
https://zoobank.org/5DFD1F3D-770C-4185-9DEA-AF923FD609A8
Figs 4, 5, 9E, 10E, 16, 17

('*Gymnacoustes isoharmonicus*' – Morris 1987, field name: Baeza Blackface)

Material examined.—**Holotype:** ECUADOR • ♂; Tungurahua, Pondoa; 16 Jul. 1985; G.K. Morris leg.; 85-2; MLP. **Paratypes:** ECUADOR • 1 ♂; Tungurahua, Pondoa; 16 Jul. 1985; G.K. Morris leg.; 85-1; ANSP • 1 ♂; Tungurahua, Pondoa; 16 Jul. 1985; G.K. Morris leg.; 85-3; ANSP • 1 ♂; Tungurahua, Pondoa; 16 Jul. 1985; G.K. Morris leg.; 85-4 [field recorded 1 of 3, 85-1, 85-2, 85-3]; ANSP.

Etymology.—Dedicated to the aforementioned James Orton (1830–1877), Professor of Natural history at Vassar College in New York State, naturalist in South America (Orton 1916, Miller 1982). On his first trip there in 1867 he crossed the continent west to east, starting in Ecuador, securing biological specimens along the way. Among them were 22 new species of orthopterans, including 9 species of katydids (described in Scudder 1869, 3 names of grasshoppers are now considered synonyms). On the way home from his third expedition, after a series of mishaps which affected his health, he unfortunately died during a passage across Lake Titicaca at only 47 years old.

Diagnosis.—Similar to the next species. Tegmina slightly longer than pronotum; dark markings on pronotum indistinct. Last tergite terminally truncate or with broad and shallow emargination (perhaps shrinkage artifact). Cerci with obtuse dorsal tip; below that with curved and tapering inward-directed process, ending with sharp and recurved spine, and above this with small and inconspicuous obtuse tip. Styli about twice as long as wide.

Measurements.—Pronotum 4.7 mm, tegmina 5.2 mm, hind tibiae 8.4 mm.

Acanthacara incisa sp. nov.
https://zoobank.org/5B7E4485-BDD8-4EF1-A73F-86C6939C6954
Figs 3, 9F, 10F, 18, 19

('*Gymnacoustes unizip*' Morris 1987, field name: Baños Blackface)

Material examined.—**Holotype:** ECUADOR • ♂; Tungurahua; 25 Jul. 1985; G.K. Morris leg.; MLP. **Paratypes:** ECUADOR • 1 ♂; Tungurahua; 25 Jul. 1985; G.K. Morris leg.; SN-5, 85-5, Rec.; ANSP • 2 ♂♂; Tungurahua; 26 May 1983; G.K. Morris leg.; ANSP.

Etymology.—Referring to the significant midline emargination of the posterior margin of abdominal tergite IX. In an excess of caution, we are careful to avoid a species name relating to song—e.g., unizip, as given in the ISV poster—for both the preceding *A. ortoni* and *A. incisa*. The two sing in earshot of each other and solitary vs. doubled zips easily distinguish their songs, but some confusion in field naming might have led to misapplication of song to these species.

Diagnosis.—Similar to previous species. Tegmina almost twice as long as pronotum. Pronotum with blackish spot on prozona

and posteriorly diverging blackish spot on metazona, both spots connected by more narrow dark coloration in between. Last tergite with deep narrow cleft, wider in distal portion, and the lobes formed by this division with inward-directed tips sporting tiny teeth. Cerci with obtuse dorsal tip as in previous species; below that, with curved inward-directed process; ending also sort of two-tipped, with the lower tip developed as short spinule. Styli almost twice as long as wide.

Measurements.—Pronotum 5.0 mm, tegmina 6.3 mm, hind tibiae 8.4 mm.

Key to species of *Acanthacara* based on males

1   Cerci more or less uniformly bifurcate, with pointed dorsal branch and more prominent pointed ventral branch, both branches directed medially ....*A. acuta* Scudder, 1869

–   Cerci with obtuse or pointed dorsal tip and differently modified ventral portion... 2

2   Cerci with more or less pointed dorsal tip and ventral branch ending in a downward projecting and acuminate tip.................................... 3

–   Cerci with obtuse or little developed dorsal tip, ventral process directed medially; if there are downward-projecting processes, they are clearly set apart from the rest of the ventral branches and much thinner than the latter 5

3   Mirror of left tegmen with venation network ....
....*A. ridiculosa* Gorochov, 2015

–   Mirror of left tegmen without reticulation... 4

4   Cerci with small pointed inward-directed dorsal tip and long ventral process, which is first directed medially and then turns into a downward-projecting acute tip, the horizontal portion being longer than the downward tip......................................*A. brachycyma* sp. nov.

–   Cerci with robust pointed inward-directed dorsal tip, the ventral process first directed medially and slightly forward, and then sharply bent perpendicularly downward, ending in an acute tip; the surface of the horizontal portion with microscopic sclerotized toothlets and downward portion longer than horizontal portion in caudal view ...
....*A. zigzag* sp. nov.

5   Tegmina as long or shorter than pronotum, cerci with broadly rounded dorsal tip and distinctive ventral branch, consisting of a sturdy and obtuse medially-directed process with a thin downward-projecting appendage, the latter originating slightly before the obtuse tip of the former..*A. dyonessa* sp. nov.

–   Tegmina longer than pronotum, dorsal tip of cerci indistinct, ventral branch directed medially and tapering into two-tipped end, the ventral tip developed as an acute spine (without downward projecting part).. 6

6   Last tergite uniformly light ochreous with caudal margin entire ....
....*A. ortoni* sp. nov.

–   Last tergite with black anterior third and deep medial emargination
.... *A. incisa* sp. nov.

Cestrophorine signal structure

The mechanical basis of forewing stridulation by katydids is a scraper contacting file teeth to make tegminal speculae oscillate at 'multiplied' frequencies (e.g., *Xiphelimum amplipennis* Morris, Braun & Wirkner, 2016). The diverse sound-pulse patterns thus produced are usefully (for taxonomists) species diagnostic. For each species, time-domain song structure resolves as a relatively stereotyped series of discrete sound pulses, manifesting as distinctive spectra in the frequency domain. Simple sinusoid pulses, sus-

tained in amplitude over several oscillations, will appear spectrally as one to a few peaks of stronger central tendency, i.e., higher Q. More complex transient pulses, grouped in trains, each rapidly decaying from a maximal onset, will appear spectrally as a band of melded peaks tending to a band, i.e., to lower Q. Each transient pulse in a train is surely the acoustic effect of one file-tooth scraper interaction, but a more prolonged sinusoid pulse suggests driven specular oscillators generating at one tooth per wave, coupled or uncoupled (Montealegre-Z et al. 2006).

The call of *C. paradoxus* (Fig. 11) repeats as lisps paired in time (Fig. 11A); each lisp is a train of ~30 very temporally discrete and transient pulses (Fig. 11B). Each pulse is apparently the result of a single tooth-scraper event (pluck or impact?). Close inspection of these complex-wave transients (Fig. 11C) shows them to be remarkably consistent in wave shape, each giving rise (via Fourier analysis) to a low-Q spectral band with a species-characteristic distribution of frequency peaks and subpeaks. (Even tiny spectral subpeaks can be a stable feature of the singer, only shifting as an effect of aspect: see *Conocephalus nigropleurum* Morris & Pipher, 1967.) In *C. paradoxus,* the lisp analyses as a band of sound energy between 8 and 13 kHz, entirely within the audio range (Fig. 11D). This species' calls are readily heard by human ears and devoid of effective ultrasonics (Fig. 11D, 12).

The song of *C. ditachus* (Fig. 13A) is also very audible and, like that of *C. paradoxus,* has a time-domain pattern of stereotypic transients in trains. But it compares to *C. paradoxus* and to the other five cestrophorine species songs as higher in duty cycle and unique in complexity, i.e., there are two rates of transient pulses that present as two different pulse trains to comprise a dual-pattern call. The field-recorded insect of Fig. 13 called steadily from overhead, perched in a sapling. His song pattern repeats every 2 s or so as 5 to 10 high-rate transient pulse trains interspersed with a single longer train of markedly slower rate of pulse repetition (Fig. 13B, C). The two different rates, readily apparent to a human listener, one rate almost 5 times the other, result in only slight differences in high resolution pulse waveforms (Fig. 13D, E) and spectral subpeaks (Fig. 13F, G). A dominant frequency peak for both song parts lies near 7.8 kHz, and there is no sound energy in the high audio 10–18 kHz. However, ultrasonics are still possible since this record was made with equipment limited to the audio range.

Each call of *C. amplitenuis* is a sinusoidal sustained pulse (Fig. 14A, B), a steady series of identical lisps well-separated by >2 s. The amplitude envelope of this pulse wave-train varies, giving it a ragged appearance (Fig. 14B). In keeping with a strongly simple sinuosity, the spectral energy is concentrated in a relatively narrow high-Q peak at about 11 kHz (Fig. 14D). Ultrasonics in the song are trivial. The big difference between the songs of *C. amplitenuis* and *C. paradoxus* may be understood as the tooth interaction rate: in the former species, there is no down time between tooth contacts, so the speculae are sustained in amplitude as an ongoing sinusoid (Fig. 14C). *C. paradoxus,* by contrast, engages its scraper such that each energy transfer has time to completely dissipate before the next tooth is met. Presumably, the sound-radiating speculum of *C. amplitenuis* makes a prolonged-pulse sinusoid by contacting one tooth for each emitted wave.

The three *Cestrophorus* spp. call loudly in the audio and lack any appreciable ultrasonic spectral component. But songs of the three *Acanthacara* all have significant ultrasonic spectral components. *A. brachycyma* has its most intense output at 30 kHz (Fig. 15D). This species groups short sinusoidal sustained pulses (Fig. 15B, C) into brief 4 or 5-pulse trains (Fig. 15A). Calculation from the sine
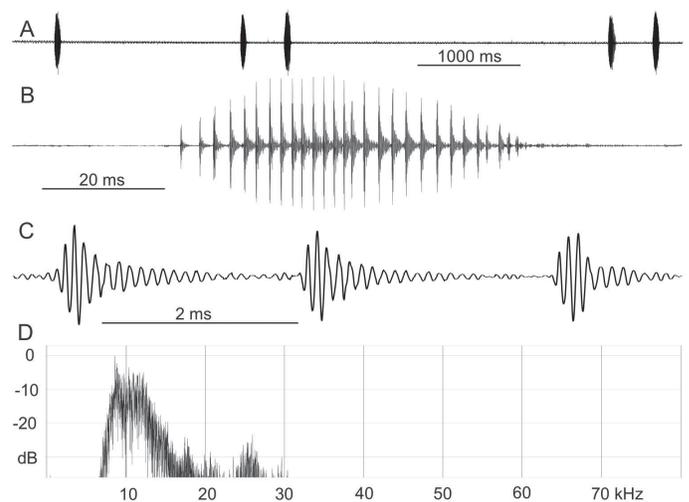

Fig. 11. Song of *C. paradoxus* is an ongoing sequence of lisp pairs. **A.** Sequence at low time resolution showing two complete pairs; **B.** A lisp at higher resolution reveals its composition as a long train of >25 discrete rapid-decay pulses; **C.** Three pulses showing stereotyped waveform detail; **D.** Power spectrum of *C. paradoxus* with frequencies confined to the audio range in a narrow band 8–13 kHz.
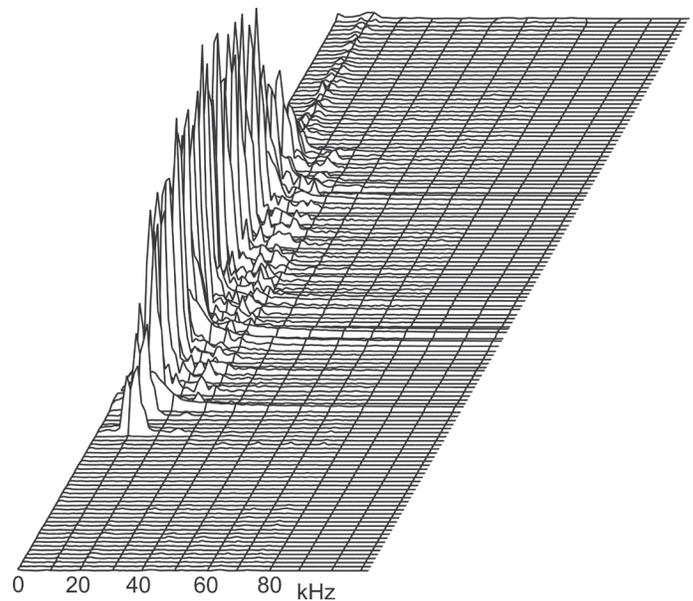

Fig. 12. Waterfall record of one *C. paradoxus* 60-ms pulse train/lisp indicating absence of ultrasonics.

wave yields (of course) a frequency of just about 30,000 Hz. (In 1 millisecond there are 12/.4 waves; in 1 second 1000 X (12/.4) = 30,000 waves). As with *C. amplitenuis,* this might be an instance of contacting one file tooth per each sinusoid wave to create each sustained pulse, i.e., tooth touch rate matches carrier frequency.

The call of *A. ortoni* is heard by a human listener as a sequence of double zips produced at a call rate of 2.2/s at 20.8°C (Fig. 16A). Each double-zip call lasts about 40–50 ms. The first zip begins as a short pulse train of transient pulses (Fig. 16B) fusing into a sustained high-intensity pulse that time-resolves into a characteristic two-cusped sinusoid waveform (Fig. 16C) that is
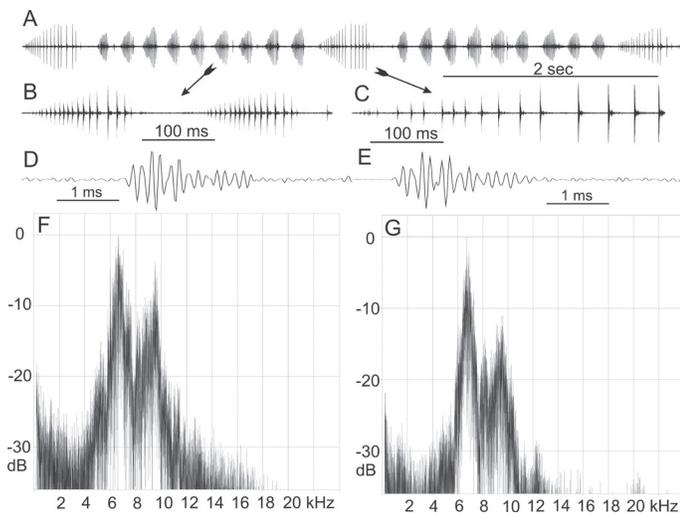
Fig. 13. Field-recorded song (Sony Walkman, audio range only) of *C. ditachus*: trains of pulses characterized by two different pulse rates, slower (SPR) and faster (FPR). **A.** Two complete calls taken from an ongoing sequence. Single SPR train prefaces a 9 FPR-train sequence; **B, D.** FPR trains at higher time resolutions showing waveform of rapid-decay pulses; **C, E.** SPR train at higher time resolution showing waveform of rapid-decay pulses; **F, G.** Audio-limited spectra of FPR and SPR respectively; spectra unaffected by scraper speed, peaking at 6–10 kHz.
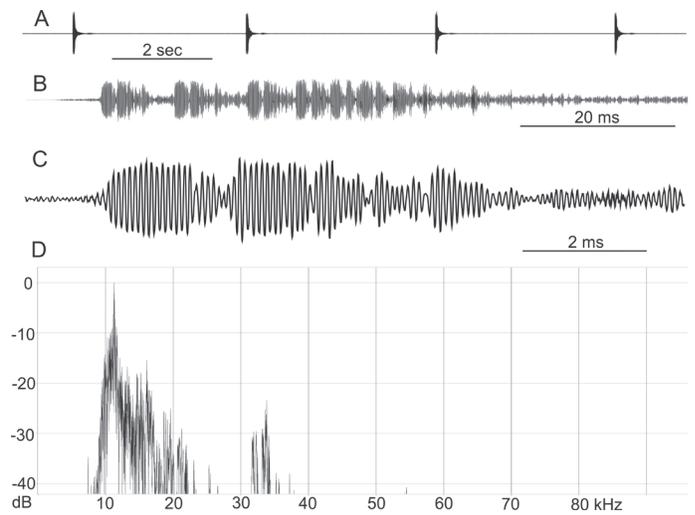

Fig. 14. Song of *C. amplitenuis*. **A.** Regular well-spaced call series; **B. C.** The same call at two levels of time resolution; each emission a prolonged sinusoid wavetrain of quite variable amplitude envelope falling-away; **D.** Audio peak near 11 kHz, spectrum almost without ultrasonics; the sinusoid-tending call is also apparent in the relatively high peakedness, of the spectrum. Lab recording at 21.3°C.
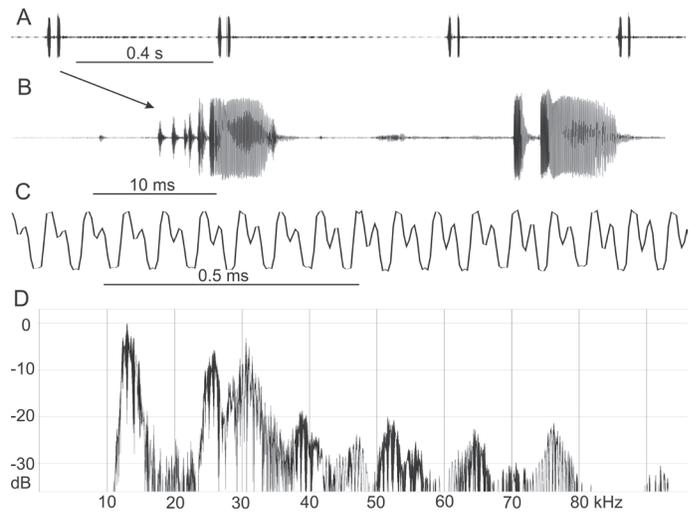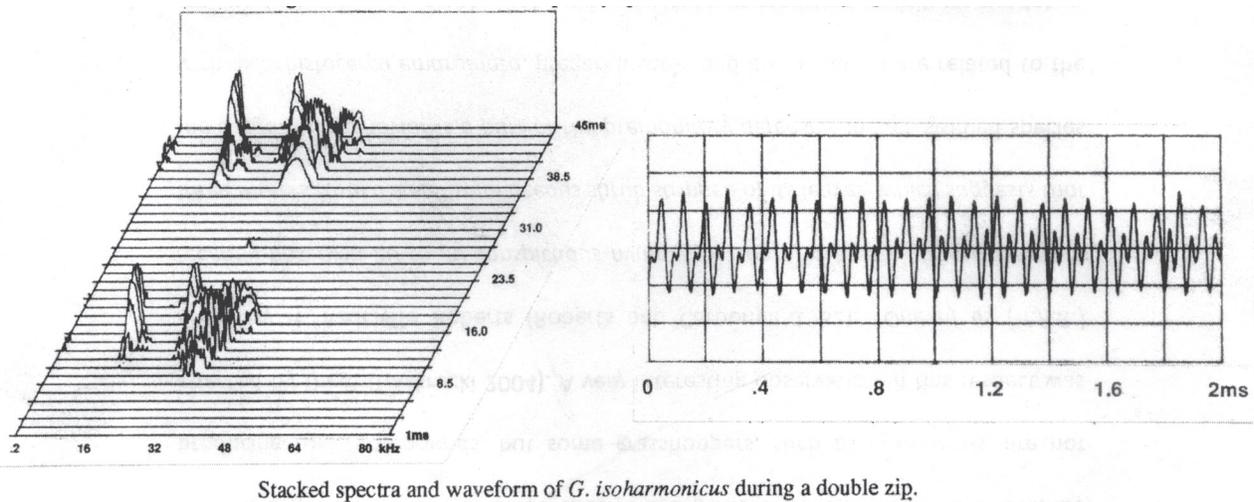

Acanthacara brachycyma

Fig. 15. Song of *A. brachycyma*. **A.** Two calls from an ongoing sequence of paired lisps; each lisp of 5 or so pulses; **B.** One complete lisp at higher time resolution; **C.** High resolution of a single sound pulse shows it to be highly sinusoidal; **D.** Spectrum dominated by ultrasonic peak at 30 kHz.

Fig. 16. Song of *A. ortoni*. **A.** Four double-zip emissions; **B.** Higher resolution of first call of record above; **C.** Cusped waveform characteristic of the interplay of two nearly equal harmonics; time sample taken from the prolonged pulse that ends each zip. This wave feature is the basis of the stillborn name '*isoharmonicus*' as used by GKM in his 1987 ISV Poster in Denmark; see Fig. 17 below; **D.** Spectrum shows subequal first (13.5 kHz) and second (27 kHz) harmonic peaks and then lower intensity harmonic peaks that occur well into the ultrasonic. A broad peak around 31 kHz is not part of the harmonic series. The academic editor expressed concern that the *A. ortoni* signal shown here may be slightly overloaded; we think rather that trace C shows the effect of the sampling rate failing to characterize the wave train smoothly at high time resolution. The recording in Fig. 17 is not subject to any possible overload distortion and shows the same harmonic interplay giving a cusped waveform.

dominated by harmonics (Fig. 16D). The second zip of Fig. 16B shows two of these sustained sinusoids, the second of much longer duration. The carrier fundamental at 12.6–13.2 kHz is subequal in intensity to its second harmonic at 25.4–26.0 kHz. The harmonically related frequencies (Fig. 16D) repeat well into the ultrasonic (13 X 2 = 26, X3 = 39, X4 = 52, X5 = 65, X6 = 78 kHz).

Stacked spectra and waveform of *G. isoharmonicus* during a double zip.

Fig. 17. Figure from 1987 ISV meeting abstract booklet showing a different *A. ortoni* specimen's song analysis; the waveform shown at high resolution is characteristic of subequal harmonics. There remains the possibility that this call is not properly associated with *A. ortoni* but is the call of *A. incisa*; see below.
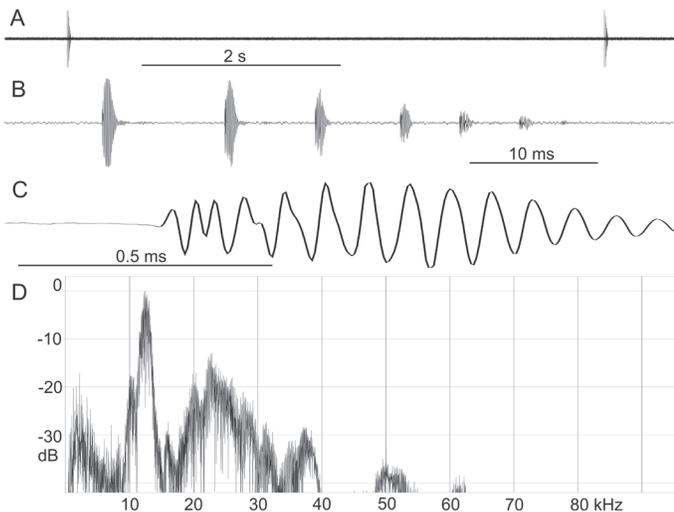

Fig. 18. Song of *A. incisa*. **A.** Two single-lisp calls, seconds apart, taken from a sustained sequence; **B.** At higher time resolution, each call is seen to be a train of 5–6 pulses of fading intensity; **C.** A single pulse at very high resolution reveals its sinusoidal nature; **D.** The power spectrum suggests higher Q generator components with a strongly high-Q peak near 13 kHz and some lesser but significant ultrasonics of 20–28 kHz.
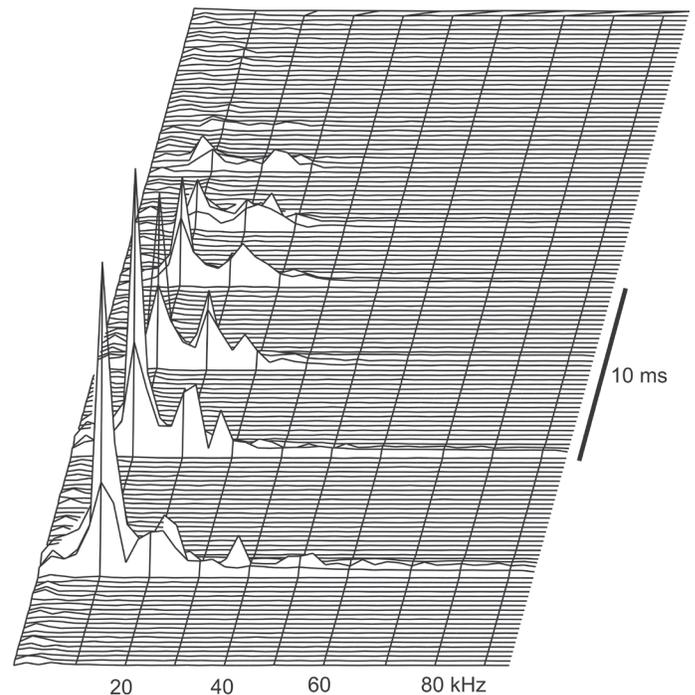

Fig. 19. One call of *A. incisa*; 7 pulses in a waterfall display.

A waterfall display of the double zip of *A. ortoni*, together with its cusped subequal harmonic waveform, is shown for a second specimen of *A. ortoni* (Fig. 17). This latter record formed part of the Insect Sound and Vibration (ISV) poster given in Denmark in 1987. At the ISV meeting, the species was designated as *Gymnacoustes isoharmonicus,* now a *nomen nudum*. The same sort of patterned time domain is characteristic of the Costa Rican katydid *Copiphora rhinoceros* (Morris 1980). The stridulatory basis of these higher harmonics would seem to involve oscillation of tegminal speculae with only the fundamental coinciding with each tooth interaction.

The call of *A. incisa* is a train of a half-dozen short sinusoid pulses successively falling in intensity, given as a single lisp every few seconds (Fig. 18A–C, Fig. 19). A single high-Q (narrow) spectral peak dominates the audio near 13 kHz. Low-frequency and weak ultrasonics, 20 dB down, exist at 20–25 kHz (Figs 18D, 19).

The species-distinctive songs of these cestrophorine species are a typical mix of the familiar frequency domain and time domain physical features that recur in most tettigoniid genera: high-Q, broadband, audio, ultrasound, harmonic, inharmonic, pulses sustained, and pulses transient. But these typical cono-

cephalid songs are listened to with unusual conocephalid ears: foreleg eardrums that are superficial and unoccluded and an acoustic spiracle (stigma) that is very small. Among conocephaloids, a naked ear is apparently unique to Cestrophorini and contrasts with the diverse tympanal coverings—"slits, resonators, pinnae" (Bailey 1990)—of other conocephaloids. So why don't *Acanthacara* and *Cestrophorus* have pretympanal pinnae (sensu lato)?

Beyond mechanical protection, a suggested acoustic function of these pretympanal structures is as ultrasonic wave guides, adding precision to the pressure gradient localization of short-wavelength—ultrasonic—sounds (Bailey 1990, Gwynne 2001). A publication in train (Montealegre-Z, pers. comm.) reports that pinnae of the conocephaloid *Copiphora gorgonensis* are structured to provide enhanced sound detection at high ultrasonic frequencies (>60 kHz), matching the echolocation range of co-occurring insectivorous bats. Perhaps the absence of tympanal coverings of Cestrophorini reflects much reduced bat predation for these small montane species.

It remains puzzling why the unoccluded tympana are combined with such small auditory spiracles. A narrow ear canal reduces sound velocity and, along with its asymmetric bifurcation near the individual tympana, creates different sound paths for each ear, all of which could help to pinpoint the direction of the sound (Veitch et al. 2021). Interestingly, the same rare combination of naked tympana and tiny spiracles is found in two species of Hexacentrinae (genus *Nubimystrix*), known also exclusively from the Andes of Ecuador and living in similar habitat (Braun 2016).

Acknowledgements

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