Two Mysterious Tiny Katydids from the Ecuadorian Andes (Orthoptera: Tettigoniidae: Hexacentrinae)

Author: Braun, Holger

Source: Journal of Orthoptera Research, 25(2) : 97-106

Published By: Orthopterists' Society

URL: https://doi.org/10.1665/034.025.0209

Two mysterious tiny katydids from the Ecuadorian Andes (Orthoptera: Tettigoniidae: Hexacentrinae)

Holger Braun

División Entomología, Museo de La Plata, Paseo del Bosque s/N°, 1900 La Plata, Argentina. E-mail: braun@fcnym.unlp.edu.ar

Abstract

Two very small katydids living in upper montane rainforest and elfin forest at 2500–3200 m on the eastern Andean cordillera of south Ecuador are described: *Nubimystrix consuelo* gen. et sp. nov. and *N. amarui* sp. nov. They have strongly reduced wings and feature a confusing mixture of morphological characteristics, such as spiny fore tibiae, unconcealed tympana, and tiny auditory spiracles. Apparently these katydids represent a third South American genus of the small subfamily Hexacentrinae. Males of both species produce at night ultrasound calling songs with carrier frequency ranges from about 23 to 31 kHz. While the song of the first species consists of brief calls, males of the other call very continuously, so that especially the presence of the latter can easily be assessed using an ultrasound detector. With an acoustic record at 3210 m, *N. amarui* is also the highest-occurring katydid species in the investigated area. Some interrelated aspects of biogeography, ecology, and bioacoustics are discussed.

Key words

acoustic monitoring, bioacoustics, Ecuanedubini, elfin forest, high altitude, montane rainforest, new species, Parque Nacional Podocarpus

Introduction

Between August 1997 and January 2000 I investigated the katydid fauna of Parque Nacional Podocarpus and its surroundings in the very south of Ecuador (Braun 2002, 2008). At least 100 species were found. A group of three very small ones with spiny tibiae and strongly reduced wings could not be assigned to any subfamily back then. They obviously belonged to two unknown genera, one of which eventually turned out to be related to *Ecuaneduba* Gorochov 2006, a new genus that originally could not be placed in a subfamily either (Gorochov 2006). Shortly after, it was assigned to the Hexacentrinae (Gorochov 2007).

For one of the three species, found close to the northern border of Podocarpus National Park, was established the monospecific genus *Acanthoraculus* Braun & Morris 2009, and the two genera were united within the small tribe Ecuanedubini. It comprises altogether four species from Colombia and Ecuador, which currently are the only neotropical members of the Hexacentrinae, a group previously known solely from Africa, Southeast Asia, and Australasia (Braun *et al.* 2009, Cigliano *et al.* 2016).

Here are finally described the two other mysterious species from the northern part of Podocarpus National Park. Both live at high elevations, from around 2500 m up to 3200 m, coinciding with the upper distribution limit of katydids in the investigation area. Most puzzling were the unconcealed tympana of these species, combined with tiny auditory spiracles and other characteristics, each typical of a different subfamily. In conclusion, the two species seem to belong to the Hexacentrinae as well, coinciding with diagnostic characters of this group (Gorochov 2007), including long spines on fore and middle tibiae, and all three thoracic sternites bearing a pair of processes. They cannot be included in the Ecuanedubini though, differing by the open tympana and the only little modified pronotum in males, which covers the more strongly and differently reduced tegmina. Hence these unique species, despite belonging to a single new genus, merit a tribe of their own.

Investigation area and methods

Both species were found at three sites within a 5-km radius at the northern limits of Podocarpus National Park: Cajanuma, an access to the park a few kilometers south of the provincial capital Loja, with a cabin at 2735 m and a round trail along the cordillera ridge (investigated 2700–3380 m); then El Tiro, the mountain pass east of Loja on the road to Zamora (2720–2960 m); and finally the Cordillera El Consuelo, accessible from the Estación Científica San Francisco (1850 m), located about midway on the road between Loja and Zamora, the highest peak of the cordillera (3100 m) with a transmitter station (including an open concrete structure which served as a shelter during several excursions), this peak mostly being covered by clouds and invisible from the above-mentioned road.

The steep slopes are covered with upper montane rainforest (cloud forest) up to around 2800 m, in higher elevations elfin woodland perseveres in wind-protected vales. The nocturnal katydids were searched for at night, walking with a headlamp along the few available trails. A collecting permit was issued by the Instituto Ecuatoriano Forestal y de Áreas Naturales y Vida Silvestre (INEFAN), which was integrated in the Ministero del Ambiente del Ecuador in 1999.

Collected individuals were accommodated in dome-shaped gauze cages with a square base of 30 cm side length and a height of 15 cm. They were furnished with plant parts and provided with small cucumber pieces almost every day. Recordings of males calling inside the cages as well as field recordings were made with a Laar Bridge Box XL (BVL von Laar, Klein Görnow) at 400 kHz sampling rate and stored on DAT (digital audio tape) using a Sony Walkman (TCD-D7 and TCD-D100). Ambient temperatures were taken with a simple pocket thermometer. A Mini-3 heterodyne bat detector (Ultrasound Advice, London) was used for acoustic monitoring in the field as well as for surveillance of the caged males. At a subsequent field trip onto Fierro Urcu (January 2013) a D200 (Pettersson Elektronik) was used to listen for calling katydids. Sound analysis was done with Avisoft-SASLab Pro (R. Specht, Berlin). Recordings were also stored as WAV files: originally ten times slowed down

on DAT, read in with 22.05 kHz sampling rate in Cool Edit 2000 (Trial Version), and subsequently set to 220.5 kHz. Photographs of some morphological details were taken with a Micrometrix digital camera mounted on a Nikon SMZ1000 stereomicroscope, using the focus stacking software Combine Z5. Larger and additional images, sound recordings, and maps with geo-referenced localities of all known South American species of Hexacentrinae are available on Orthoptera Species File Online (Cigliano *et al.* 2016, subsequently abbreviated as OSF). The original specimen and recording codes are mentioned in this paper as well as in OSF to keep track of illustrations and sound files that correspond to particular specimens. At the next opportunity some of the additional paratypes will probably be transferred to the Colección de Invertebrados del Sur de Ecuador (CISEC), Museo de Colecciones Biológicas de la Universidad Técnica Particular de Loja.

Nubimystrigini trib. nov. (of Hexacentrinae)

Type genus: *Nubimystrix* gen. nov., described below.

Diagnosis.—Tiny brachypterous tettigoniids with, in lateral view, narrow head, spiny fore and middle tibiae, open tympana, and small auditory spiracle. Tegmina covered completely by pronotum, at most in males projecting a little beyond its rear margin. Meso- and metasternum each with a pair of tubercles.

Comparison with Ecuanedubini.—Members of *Ecuanedubini* have concealed tympana with slit-shaped ear openings, a more elongated and, in males, usually strongly modified pronotum, and a pair of thin spines on all three sternites.

***Nubimystrix* gen. nov.**

Type species: *N. consuelo* sp. nov., described below.

Etymology.—Loosely composed of Latin terms for cloud (referring to cloud forest habitat) and Greek word for mystery (alluding to mysterious systematic affiliation); gender: feminine.

Diagnosis.—Very small, fairly long-legged, dark brown to light greenish-brown katydids with spiny fore and middle tibiae and strongly reduced wings. Head narrow in lateral view, fastigium of vertex obtusely pointed, barely or slightly projecting beyond antennal sockets. Pronotal disc with portion formed by pro- and mesozona altogether narrow and narrowed in the middle, metazona broad, in males domed, in females dorsal contour of pronotum flat, in both sexes anterior portion of lateral lobes slightly concave. Tegmina in males entirely covered by pronotum, made up entirely by stridulatory apparatus, with bulging lateral margins, projecting laterally beyond the costal margins, these developed as delicate folds, fitting the tegmina to the insect's back, dorsal surface of left tegmen comprised of smooth and probably translucent mirror area. Females practically apterous (minute tegminal lobes, hardly visible looking from behind under pronotum). Auditory spiracles very small and completely exposed below ventral margin of pronotum (Fig. 2D). Prosternum with a pair of short, delicate and obtuse spines or tubercles, lateral lobes of meso- and metasternum ending in short, robust tubercles or bulges. All coxae ventro-distally produced into obtuse tips. Tympana unconcealed, only ventral margin slightly conchate. Fore tibiae over entire length with articulated spines on both ventral edges, and 1-3 similar spines on outer dorsal margin. Middle tibiae ventrally armed equally, dorsally with 3 internal spines and usually at least one external spine. Male cerci compact and two-tipped, with internal spine. Male subgenital plate with well developed delicate styli. Ovipositor of females moderately slender, tapering and pointed, about as long as abdomen, slightly upcurved.

***Nubimystrix consuelo* sp. nov.**
(Figs 1A-C, 2A,B,D,E, 3)

urn:lsid:Orthoptera.speciesfile.org:TaxonName:491428

Braun 2002, 79: Consuelo-Zwergschrecke; Braun 2008, 220: gen nov. "Consuelo-Zwergschrecke"

Etymology.—Reference to type locality: Cordillera El Consuelo; noun in apposition.

Specimens.—Male holotype (cbt039s04, sound recordings) and female paratype (-s05): Cordillera El Consuelo 2510 m, 6 August 1998, both deposited in the Museo de La Plata; additional paratypes: male (-s01) and female (-s02): same locality 2540 m and 2520 m, 7 September 1998; male (-s03, sound recordings): El Tiro 2710 m, 31 August 1999; all H. Braun leg., the last three specimens currently in collection of author.

Description.—General coloration brownish, with dark brown and light greenish markings, in males rear margin of pronotum light green (the greenish parts become pale yellowish in dried specimens). Portion of pronotal disc formed by pro-and mesozona fairly uniformly narrowed in the middle. In males inflated metazona very slightly translucent, tegmina tips flush with rear margin of pronotum, cubital vein of left tegmen dark (Fig. 2A). Fore tibiae dorsally with 1-3 spines on outer margin (only the most basal one below the ear present in all four specimens) and middle tibiae dorsally with 3-4 spines on inner and 1 spine on outer margin (a little above the middle). Male cerci with a short internal and a longer external tip, and a very small inward-directed ventral hook at the very base (only visible from behind, Fig. 2E). Pronotum length 5 mm in males and 4 mm in females, hind femur 11.5-12.5 mm, ovipositor 7.5-8 mm.

Song.—At night males produce short calls, each representing one syllable and consisting of 6-10 impulses (Fig. 5A,B; unknown whether generated at opening or closing movement of the tegmina). In the field an individual male usually produces at most one or two calls per minute. A caged male sang at 20 °C (which is much higher than night temperatures in natural habitat) continuously with up to 27 calls per minute, interrupted by few pauses. The carrier frequency spectrum is moderately broad and ranges from about 23 to 31 kHz (Fig. 5C).

Habitat and distribution.—Understory of cloud forest, 2460–2840 m, known from three localities in the northern part of Parque Nacional Podocarpus and the adjacent Reserva Biológica San Francisco.

***Nubimystrix amarui* sp. nov.**
(Figs 1D-F, 2C, 4)

urn:lsid:Orthoptera.speciesfile.org:TaxonName:492065

Braun 2002, 79: Elfenwald-Zwergschrecke; Braun 2008, 220: gen nov. "Elfenwald-Zwergschrecke"

Etymology.—Dedicated to Amaru, son of my friend Felix Matt,

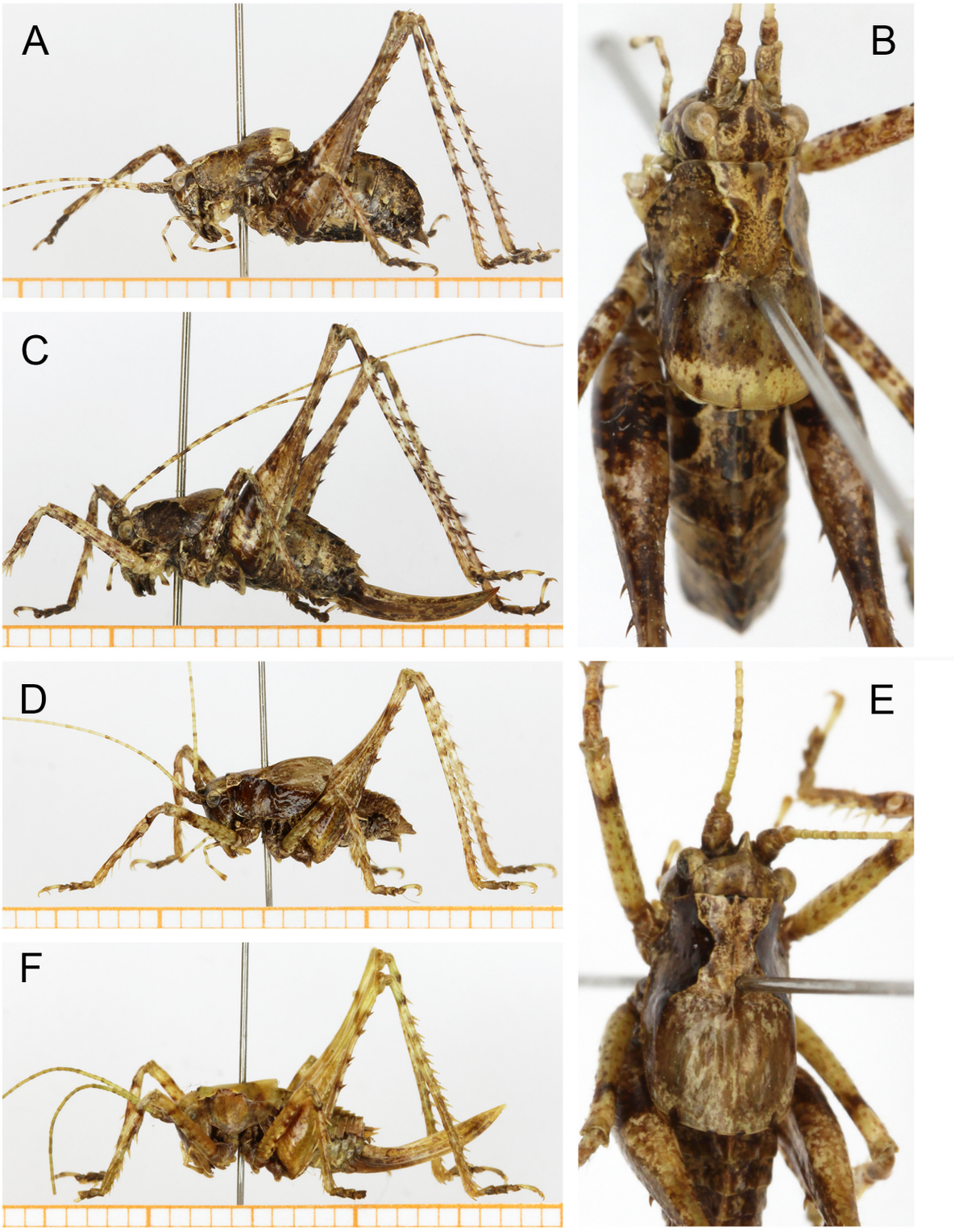

Fig. 1. The two *Nubimystrix* species. *N. consuelo* (A-C): **A,B.** male holotype in lateral and dorsal view, **C.** female paratype (cbt039s05); *N. amarui* (D-F): **D,E.** male holotype (abdomen shrunk), **F.** female paratype (possibly subadult, cbt040s03). For color version, see Plate IV.

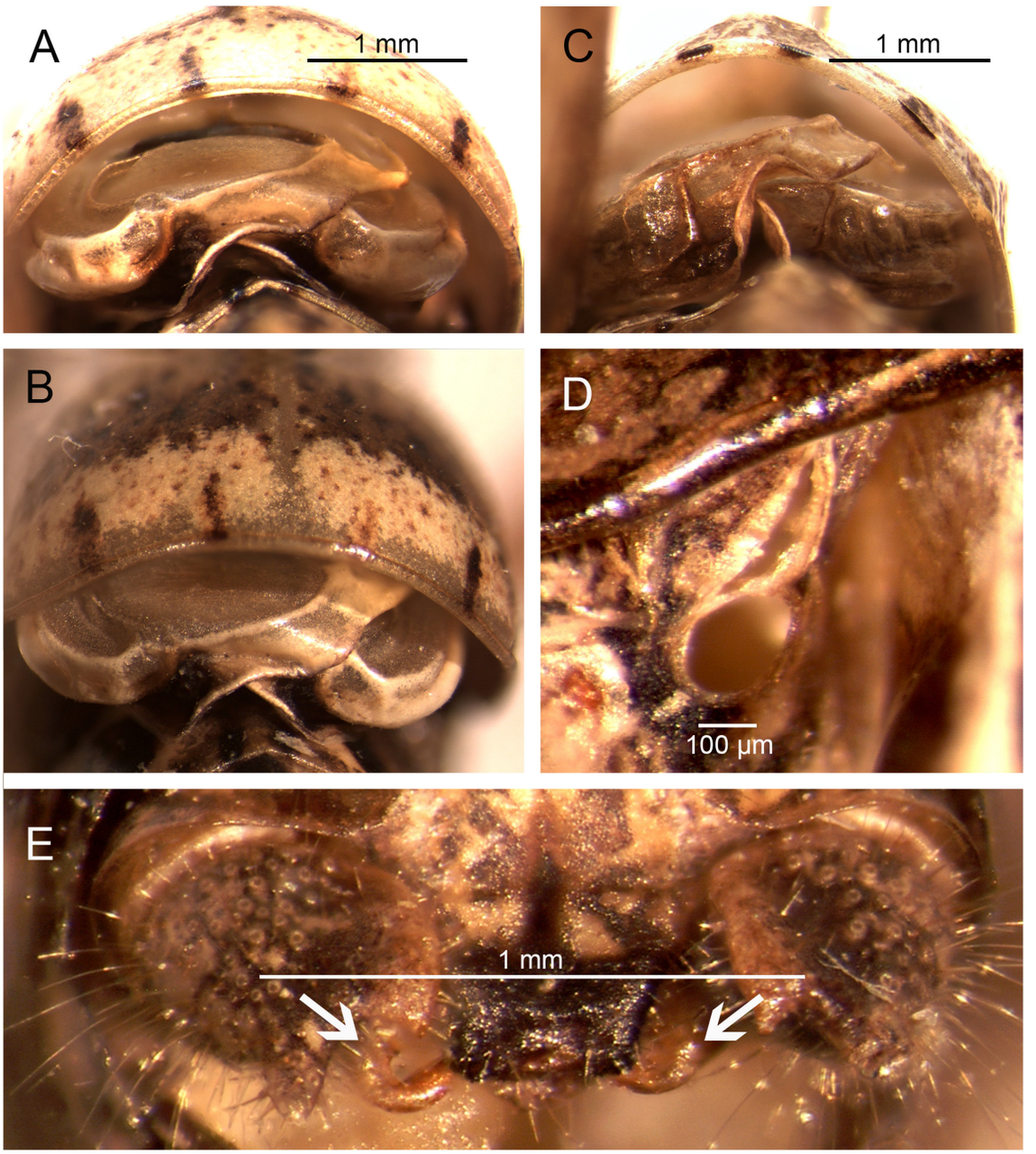

Fig 2. Morphological details of males of the two *Nubimystrix* species (holotypes). **A,B**. *N. consuelo*: posterior view of pronotum and tegmina under slightly different angles; **C.** *N. amarui*: idem; **D.** *N consuelo*: left auditory spiracle, fully exposed below pronotum margin; **E.** *N. consuelo*: caudal view of the cerci showing the small internal basal hooks, corresponding to the basal ventral process in external lateral view in Fig. 3 (top right middle).

who came along with us on two field trips onto the Fierro Urcu in January 2010 and 2013 (see discussion), showing great interest in grasshoppers and katydids.

Specimens.—Male holotype (cbt040s01, sound recordings): El Tiro, 2830 m, 15 June 1999, and female paratype (possibly subadult, -s03): El Tiro, 2720 m, 4 August 1999, both deposited in the Museo de La Plata; additional paratypes: two males (-s02, -s04, sound recordings): El Tiro, 2880 m and 2710 m, 3 and 31 August 1999; one female nymph (-s05): El Tiro, 2710 m, 31 August 1999; all H. Braun leg., the last three specimens currently in collection of author.

Description.—Coloration dark brown with light green, immatures more greenish (green color fading in dried specimens). Portion of pronotal disc formed by pro-and mesozona stepwise narrowed in the middle, overall more constricted than in the other species, contours of light disc against dark lateral lobes approaching the shape of an hourglass in dorsal view (Fig. 1E). In males inflated metazona almost transparent, covering tegmina amply, stridulatory area of left tegmen unicolor as far as visible. Fore tibiae dorsally

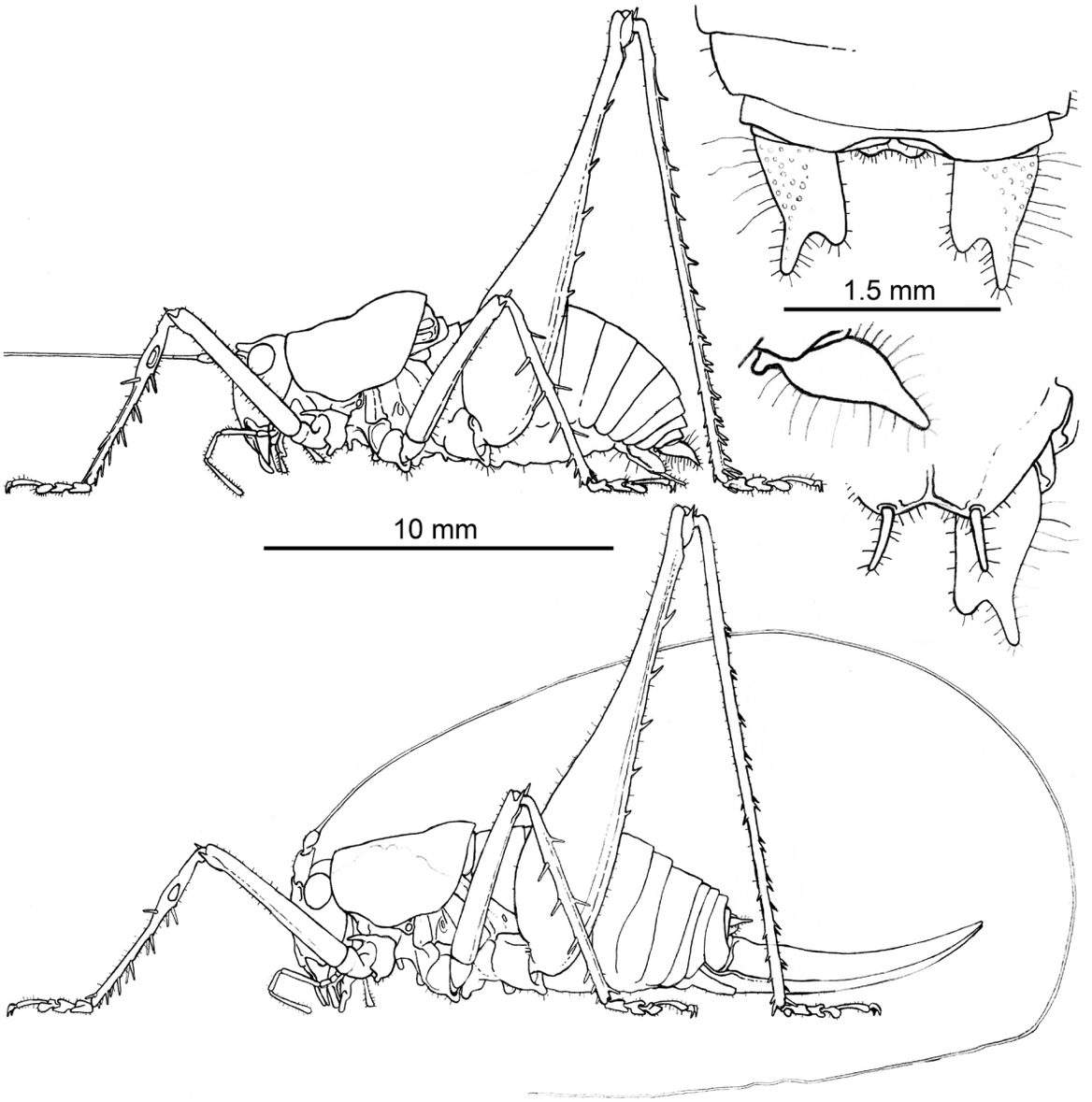

Fig. 3. *Nubimystrix consuelo*: male, body length 13.5 mm, antennae 23 mm, cerci in dorsal, external lateral and ventral view (paratype cbt039s01) and female, total length including ovipositor 20 mm (paratype cbt039s05, same specimen as in Fig. 1C) (pencil drawings of freshly dead specimens from August/September 1998, slightly edited).

with two spines on outer margin, middle tibiae dorsally with four spines on inner margin (including apical spur) and two spines on outer margin. Male cerci with a short dorso-internal and a more robust ventro-external tip, and approximately in the middle with a small internal hook that is directed back- and upward (Fig. 4, middle right). Pronotum length 5 mm in males and 4 mm in females, hind femur 10-10.5 mm, ovipositor 7.5-8 mm.

Song.—At night males call very continuously, with long pulse trains, mostly consisting of a series of double pulses, and sometimes single or triple pulses, and also single and double or double and triple pulses mixed (Fig. 5D,F). The pulse trains can last up to 4 seconds, and usually approximately one is produced every minute, sometimes up to 6-9 per minute. The repetition rate of the single, double or triple pulses is about 10 per second at 5 °C in the natural habitat, and 26-27 per second at 18 °C with a caged male (in scientific station at much lower elevation). The carrier frequency spectrum is like in the previous species, with identical range from about 23 to 31 kHz, and most energy between 25 and 30 kHz (Fig. 5E).

Habitat and distribution.—Understory at upper limit of cloud forest and patches of elfin woodland, 2710-3210 m, known from the same three localities in the northern part of Parque Nacional Podocarpus as the other species.

Discussion

Comparison with other Hexacentrinae.—In comparison with the ten genera from Africa, SE Asia and Australasia currently included in Hexacentrinae (Cigliano *et al.* 2016), members of the three South American genera *Ecuaneduba* and *Acanthoraculus* (Ecuanedubini) as well as *Nubimystrix* feature a unique combination of characteristics. All other hexacentrines do not have dorsal spines on the fore tibiae and only some of them have single short spines on the middle tibiae,

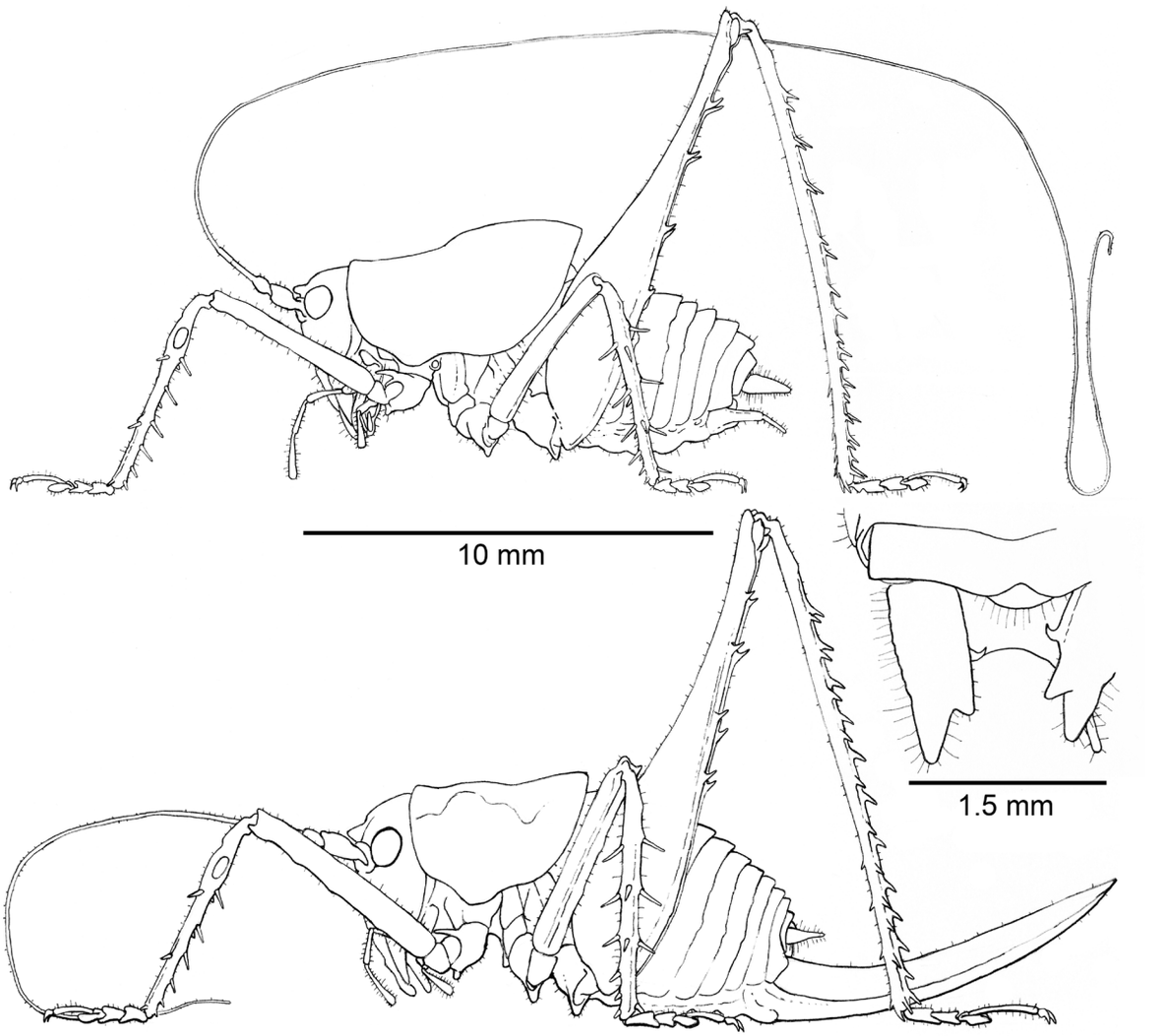

Fig. 4. *Nubimystrix amarui*: male, body length 12 mm, abdomen tip in dorsal view, and female, 10.5 mm excluding ovipositor (habitus pictures to same scale, holotype and paratype cbt040s03, same specimens as in Fig. 1D-F) (pencil drawings of freshly dead specimens from June-August 1999, slightly edited).

whereas *Ecuaneduba* and in particular *Acanthoraculus* and *Nubimystrix* sport 1-3 well developed dorsal spines on the fore tibiae and 4-6 on the middle tibiae (Braun *et al.* 2009, Gorochov 2006, 2007, Hugel 2010, Karny 1907, Rentz 2001, Tan 2012, Willemse 1961, photos of specimens in OSF). Almost all Old World hexacentrines have well developed wings, except the five species of the Malesian genus *Glenophisis*, where the tegmina at most barely cover the abdomen, and *Nepheliphila raptor* from Mauritius, whose tegmina are only about as long as the pronotum in males, and reduced to tiny lappets in females (op. cit.). In all three South American genera the tegmina are considerably reduced, with the stridulatory apparatus covered by the pronotum in males, and even more reduced or absent in females (adult females of Ecuanedubini are unknown). In Nubimystrigini the tegmina of males are practically reduced to the stridulatory apparatus, whereas in Ecuanedubini the remaining tegmina surface serves to enclose a subtegminal air space, with the entire structure covering the anterior portion of the abdomen. Most Old World hexacentrines have moderately large exposed auditory spiracles, except the four species of the genus *Aerotegmina* from Tropical East Africa and the already mentioned *Nepheliphila raptor*, where they are similarly small as in the South American species. In almost all hexacentrines the ear openings at the base of the fore tibiae are slit-like and oriented dorsad, except for the Nubimystrigini, where the tympana are fully exposed in lateral view. The male paraprocts, each of which should have a digitiform process or distinct apical lobe diagnostic of the subfamily (Gorochov 2007) are shrunk and practically invisible in the holotypes, the only males on hand at this moment (my collection is split between Germany and Argentina). To avoid any damage it was refrained from re-softening or dissecting these small and delicate specimens.

Biogeography.—The occurrence of the two new species on the eastern Andean cordillera of south Ecuador fits in the distribution of the other four South American species of Hexacentrinae. *Ecuaneduba gambitaensis* and *E. inzaensis* are known from unique males from the Andes of Colombia (Cordillera Oriental at 2600 m and inter-Andean at 2200 m respectively), *E. aequatorialis* from a population on the eastern foothills in northern Ecuador (1300-1900 m), and *Acanthoraculus milagro* from the Cordillera El Consuelo where also the new species occur, but in an area at lower elevation (2120-2230

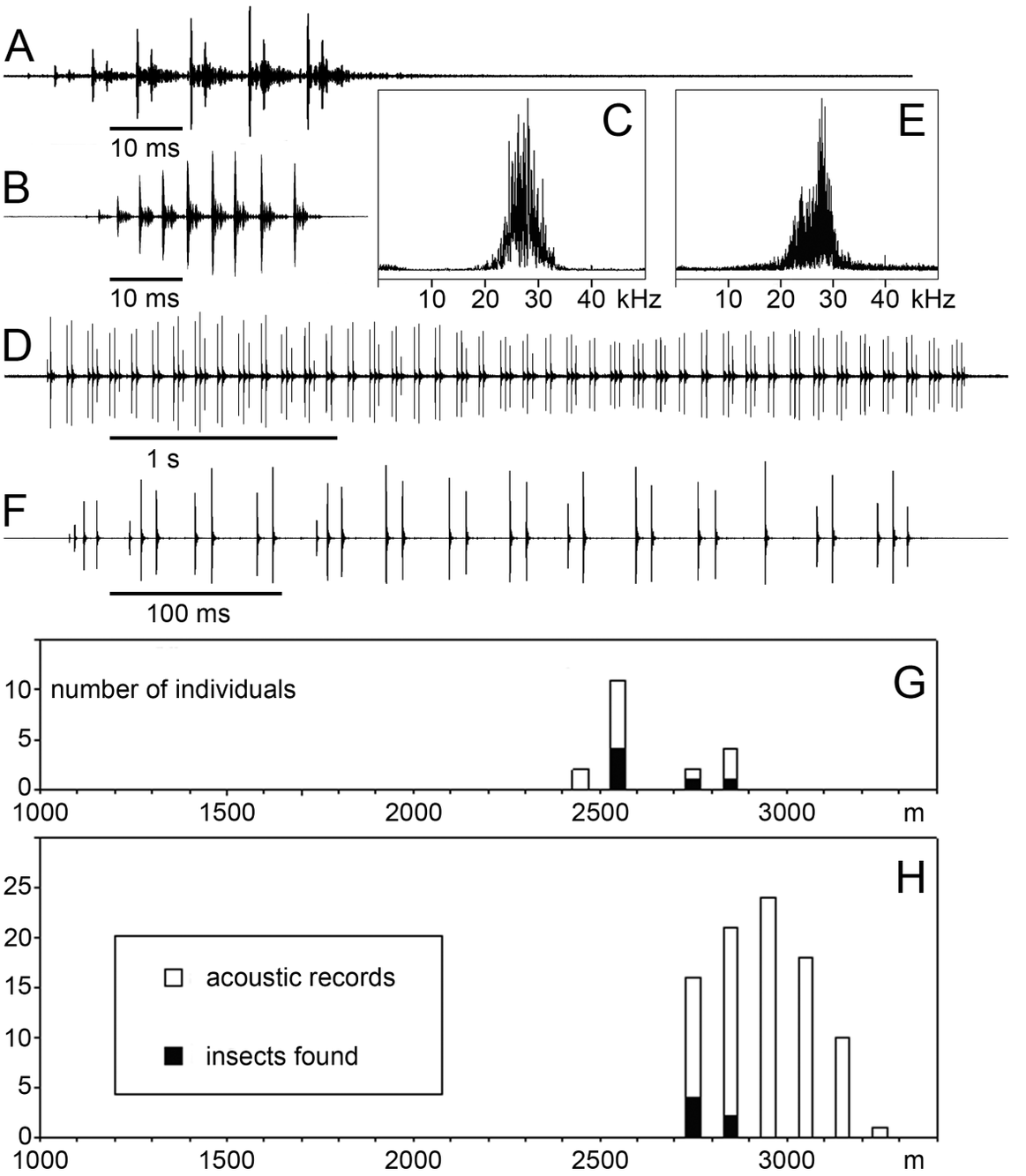

Fig. 5. Calling songs and altitudinal distribution of the two *Nubimystrix* species. *N. consuelo* (A-C,G): **A.** field recording, 14 °C, the low-amplitude impulses are probably echoes (cbt039x03r01); **B.** cage recording, 20 °C (holotype, cbt039s04r07); **C.** linear spectrogram taken from A. *N. amarui* (D-F,H): **D.** field recording, long pulse train, 5 °C (cbt040s02r02); **E.** linear spectrogram taken from D; **F.** cage recording, short pulse train, 18 °C (holotype, cbt040s01r03). **G.** records of *N. consuelo* along the investigated altitudinal gradient from 1000 to 3400 m divided in 100-m intervals (acoustic records based on one survey per locality); **H.** the same for *N. amarui*.

m) (Braun *et al.* 2009). A fairly similar distribution exists in the Tabariini, a small group of three currently monospecific genera of apterous and very long-legged katydids of spider-like appearance, the only South American representatives of the otherwise Old World subfamily Mecopodinae. The three species are known from the Andes and Andean foothills from Colombia to central Peru. As already speculated (Braun *et al.* 2009, Chamorro-Rengifo 2009), ancestral populations of one or two hexacentrine species as well as a mecopodine species must have remained in northern South America after the final separation from Africa in the mid Cretaceous 90-100 MYA. The katydids ended up on the Andes which at that time just had begun uplifting. In the middle Miocene through early Pliocene the Eastern Cordillera of Colombia was still at only about 40% of its current altitude, with elevations then increasing more rapidly between 5 and 2 MYA, reaching modern elevations by around 2.7 MYA (Gregory-Wodzicki 2000). The katydids were probably adapted to montane habitats and populations were divided during the uplift. Climatic fluctuations with glacial and interglacial periods and

substantial shifts of tree line during late Pliocene and Pleistocene, as well as volcanic activity, might have contributed to the subdivision of originally continuous populations of cloud forest species (*e.g.*, Kieswetter & Schneider 2013 and references cited therein). Higher elevations of the Tropical Andes are poorly investigated in respect to the often exclusively nocturnal katydids, as indicated by the numerous undescribed species found in the investigation area (Braun 2002, 2008). So it is likely that other undiscovered species of *Nubimystrix* live in high-elevation cloud forest and patches of elfin woodland along the cordilleras.

A similar geographic distribution as Ecuanedubini and Tabariini is displayed by the grasshopper genus *Jivarus*, with 29 species occurring on the Andes from southern Colombia, throughout Ecuador, to the very north of Peru (Cigliano & Amédégnato 2010). These fairly small, brachypterous and diurnal grasshoppers are found in elevations from 1500 to 4200 m, mostly between 2500 and 3500 m, usually in paramo habitats. At Cajanuma, one of the three *Nubimystrix* localities, a female of *Jivarus ronderosi* was found in low vegetation on the cordillera ridge at almost 3000 m (January 2010, photos in OSF). Some of these *Jivarus* species occur sympatrically, but most have small ranges and many seem to be parapatric or form populations that are isolated from one another. A similar situation is conceivable for *Nubimystrix* and possibly the Ecuanedubini, although perhaps with not quite as many species as in these grasshoppers. In any case, it would be worthwhile to do fieldwork at additional sites with undisturbed woodland between 2500 and 3000 m on the Andes of Colombia, Ecuador, and northern Peru. This should include acoustic monitoring with an ultrasound detector from dusk until night temperatures drop too low. *Nubimystrix amarui* was still calling at only 5°C (Fig. 5D).

Ecology.—The two *Nubimystrix* species, with only 11-13 mm body length, are among the tiniest katydids found in the investigation area comprising an altitudinal gradient from 1000 to 3400 m. That insects living on mountains are mostly small has been known for a long time (Mani 1962), and this is attributed to low temperatures, with additional seasonal constraints on development in higher latitudes (Mani 1962, 1968, Mousseau 1997). It also was described long ago (for Orthoptera: Chopard 1938), that high-altitude insects typically have reduced wings, or are totally apterous, like the *Nubimystrix* females. Possible explanations I had outlined elsewhere (Braun 2011).

Nubimystrix amarui is the highest-occurring katydid species in the investigation area, with an acoustic record at 3210 m at the Cajanuma site (Fig. 6, maximum local elevation 3380 m). It was not heard on the Cerro Toledo (3400 m) in the southwest corner of Podocarpus National Park, 34 km south of Cajanuma (29 October 1999). Only five other species in the area were recorded from above 2900 m: *Typophyllum egregium* (to 2980 m), *Disceratus nubiger* (3000 m), and three undescribed species belonging to *Mystron* (3000 m), *Acanthacara* (3000 m), and an undescribed genus related to *Acanthacara* (2940 m). Of all five species as well as *Nubimystrix amarui* the altitudinal distribution could be assessed quite completely by means of acoustic records. Two additional katydid songs (typical broad-band signals with high carrier frequency, in one case ultrasound) were recorded above 2900 m, but the singers could not be tracked down (Cajanuma at 2905 m and Cerro Toledo at 3020 m, "incognito songs" type 20 and type 21, Braun 2002, 125, Fig. 6.3.18).

On the Fierro Urcu (3788 m), a mountain about 50 km north of the area where the *Nubimystrix* species were found, woodland extends to higher elevations than in Podocarpus National Park. In a nocturnal survey in a fairly large patch of elfin forest at 3520 m, at not particularly low temperatures, no katydid was seen, and none was heard calling while listening with the ultrasound detector (5 January 2013, 19:00-21:45 h). Other insects (moths, beetles, stick insects), spiders, harvestmen, as well as different species of frogs were present.

Maybe January was too late (the records of *N. consuelo* span from August 6 to October 17, the ones of *N. amarui* from June 15 to August 31, of the aforementioned species of *Disceratus*, *Mystron*, and *Acanthacara* there are also no records in the months following October for want of fieldwork in higher elevations). No seasonality was found in the phenology of more common katydids in lower elevations. So the upper distribution limit of katydids on the equatorial Andes seems to be at 3100-3200 m.

On the Andes of Argentina and Chile, katydids are reported from considerably higher elevations. On the Aconcagua (6962 m), the highest mountain outside of Asia, individuals of *Apteropedetes anaesegalae* (Tettigoniinae) were found at 4250-4300 m (Gurney & Liebermann 1975) and on the volcano San José even at 4500 m (specimen in Australian National Insect Collection, photos in OSF). On the volcano Lascar *Platydecticus simplex* (Tettigoniinae) was found at 3700–4000 m (Rentz & Gurney 1985). These katydids are even tinier than the *Nubimystrix* species, with only 7-8 mm body length in males, and in contrast to the Ecuadorian katydids they are active during the day (Gurney & Liebermann 1975), which seems to be true for all insects in alpine zones of high mountains (Mani 1968; night temperatures at 4000 m in the Andes of NW Argentina are very low and can drop sub-zero also in summer, pers. obs. January 2011). Another species of Tettigoniinae, *Acrodectes philopagus*, is reported from the Sierra Nevada in California, at 4200–4300 m (Rehn & Hebard 1920), and yet two others, *Hyphinomos fasciata* and *H. svenhedini*, from the Himalayas at 4570-4870 m and 4570-5500 m respectively (Uvarov 1921, Ramme 1950, original data 15,000-16,000 and 15,000-18,000 ft).

Directly at the equator katydids are evidently restricted to considerably lower elevations than montane species from higher latitudes. The latter can rely on extended periods with high daytime temperatures, completing their reproductive cycle in summer, with the next generation overlasting the winter as diapausing eggs. In contrast, on the equatorial Andes there is little seasonality, with typical weather conditions comprising prolonged cloud cover and frequent rain, with only short and unreliably occurring sunny times. Embryonic development in the eggs possibly proceeds without diapause, whereas the development from nymphs to adults is probably slow due to overall low temperatures. This would mean that most of the population is around on their six legs at any time, rendering it susceptible to sporadically occurring cold snaps. Brief events of cold weather with occasional frost, characteristic for the Andean slopes of Bolivia and southern Peru, can rarely reach further north (Fjeldså *et al.* 1999), and perhaps preclude the survival of katydids of the Tropical Andes at elevations beyond 3200 m. In tropical Africa the upper distribution limit of katydids seems to be yet lower, located at 2600–2700 m on Mount Kilimanjaro (Hemp 2013).

Bioacoustics.—The presence of both *Nubimystrix* species can easily be ascertained by means of an ultrasound detector and the males' conspicuous calling songs, and allowed an acoustic assessment of the altitudinal distribution of the two nocturnal katydids (Fig. 5G,H). A call of *N. consuelo* was subsequently found on a field recording of *Typophyllum egregium* from October 1997, ten months before the first individual was actually discovered (recording available in OSF under *T. egregium*). With the long and continuously produced

Fig. 6. At upper distribution limit of *Nubimystrix amarui*: the katydids occur in patches of elfin woodland visible in middle distance; mossy branches (Cajanuma, January 2010).

calls of *N. amarui* only the bat detector needs to be switched on to immediately establish if the species is around. More nocturnal acoustic surveys in high-elevation woodland would not only yield new distribution records and still unknown species, but could also serve to document possible elevational distribution shifts caused by global warming. The monitoring of insect communities along altitudinal gradients and at high elevations in the Tropical Andes is considered a research and conservation priority (Larsen *et al.* 2011). The *Nubimystrix* species as well as other montane katydid species (including the ones mentioned above), most of them characterized by males calling with high duty cycles (Braun 2002), would be suitable study organisms.

The soft costal margins fit the tegmina of males snugly to the insect's back, very similar to the Ecuanedubini (Braun *et al.* 2009), although at the rear end not as perfectly fitting as in *Acanthoraculus*. This subtegminal cavity forms a closed box and no acoustic short-circuiting can occur with the air volume between tegmina and pronotum. The metazona, which is very thin and transparent in the male of *Nubimystrix amarui*, probably acts as sound radiator. How the localization of calling males by females could work, remains a little bit puzzling. In Pseudophyllinae, another subfamily with small auditory spiracles, the tympana are concealed, and the ears usually open via thin slits on the dorsal surface of the fore tibiae. The enclosed air volumes could act as Helmholtz resonators, responding maximally when the openings are directed toward the sound source. In *Nubimystrix* the tympana are totally unconcealed. For the ears to work as pressure difference receivers, wide auditory spiracles would be necessary, with the narrowing auditory trachea connected to the inner surface of the tympana acting as sound amplifying exponential horn (Jonsson *et al.* 2016). However, with moderately high ultrasound, a small auditory spiracle might be sufficient (Fernando Montealegre-Z., pers. comm.).

Acknowledgements

Perhaps this is a good place to commemorate the late Theodore "Ted" Cohn, to whom I am deeply grateful for encouragement during my first steps into tettigoniid taxonomy. After having examined a specimen of the "Consuelo Nubimystrix", which I had sent him in 2000 or early 2001, the response in one of his elaborate e-mails included the following phrase, conserved in my thesis: "it looks like a really peculiar phaneropterine, and cannot be a listrosceline." In January 2013 my old friend Felix Matt organized a nice field trip with overnight camping on the Fierro Urcu, to take a closer look at high-elevation woodland, which had drawn my interest at another common excursion three years earlier. Finally, I thank the two reviewers for useful suggestions and corrections.

References

Braun H. 2002. Die Laubheuschrecken (Orthoptera, Tettigoniidae) eines Bergregenwaldes in Süd-Ecuador – faunistische, bioakustische und ökologische Untersuchungen. Doctoral thesis, University of Erlangen-Nürnberg, 142 pp.

Braun H. 2008. Orthoptera: Tettigoniidae - Checklist Reserva Biológica San Francisco and Parque Nacional Podocarpus (Prov. Zamora-Chinchipe and Loja, S. Ecuador). Ecotropical Monographs 4: 215-220.

Braun H., Chamorro-Rengifo J., Morris G.K. 2009. Curious katydids from the Andes of Colombia and Ecuador: three new species, a new genus and acoustic baffles. Journal of Orthoptera Research 18: 225–235.

Braun H. 2011. A brief revision of brachypterous Phaneropterinae of the tropical Andes (Orthoptera, Tettigoniidae, Odonturini). Zootaxa 2991: 35-43.

Chamorro-Rengifo J. 2009. Redescription of two species of the genera *Encentra* and *Tabaria* (Tettigoniidae: Mecopodinae) of Colombia. Zootaxa 2003: 46-52.

Chopard L. 1938. La biologie des orthoptères. Encyclopédie Entomologique. Paul Lechevalier, Paris, 541 pp.

Cigliano M.M., Amédégnato C. 2010. The high-Andean *Jivarus* Giglio-Tos (Orthoptera, Acridoidea, Melanoplinae): systematics, phylogenetic and biogeographic considerations. Systematic Entomology 35: 692-721.

Cigliano M.M., Braun H., Eades D.C., Otte D. 2016. Orthoptera Species File Online. Version 5.0/5.0. Available from: http://Orthoptera.SpeciesFile.org [accessed October 2016].

Fjeldså J, Lambin E., Mertens B. 1999. Correlation between endemism and local ecoclimatic stability documented by comparing Andean bird distributions and remotely sensed land surface data. Ecography 22: 63-78.

Gorochov A.V. 2006. A new katydid genus of unclear systematic position from Ecuador (Orthoptera: Tettigoniidae). Zoosystematica Rossica 15: 47-50.

Gorochov A.V. 2007. Notes on taxonomy of the subfamily Hexacentrinae with descriptions of some taxa (Orthoptera: Tettigoniidae). Zoosystematica Rossica 16: 209-214.

Gregory-Wodzicki K.M. 2000. Uplift history of the central and northern Andes: a review. Geological Society of America Bulletin 112: 1091-1105.

Gurney A.B., Liebermann J. 1975. A new species of shield-backed katydid from Cerro Aconcagua, Argentina, with notes on other species and their habitats (Orthoptera, Tettigoniidae, Decticinae). Journal of the Washington Academy of Sciences 65: 102-107.

Hemp C. 2013. Annotated list of Ensifera (Orthoptera) and further records on Caelifera (Orthoptera) of Mt Kilimanjaro, Tanzania. Zootaxa 3613: 301-342.

Hugel S. 2010. New and little known predatory katydids from Mascarene islands (Ensifera: Meconematinae and Hexacentrinae). Zootaxa 2543: 1-30.

Jonsson T., Montealegre-Z. F., Soulsbury C.D., Robson Brown K.A., Robert D. 2016. Auditory mechanics in a bush-cricket: direct evidence of dual sound inputs in the pressure difference receiver. Journal of the Royal Society Interface 13: 1-11.

Karny H.H. 1907. Revisio Conocephalidarum. Abhandlungen der K.K. Zoologisch-botanischen Gesellschaft Wien 4: 1-114.

Kieswetter C.M., Schneider C.J. 2013. Phylogeography in the northern Andes: complex history and cryptic diversity in a cloud forest frog, *Pristimantis w-nigrum* (Craugastoridae). Molecular Phylogenetics and Evolution 69: 417-429.

Larsen T.H., Escobar F., Armbrecht I. 2011. Insects of the Tropical Andes: diversity patterns, processes and global change. In: Herzog S.K.R., Martínez R., Jørgensen P.M., Tiessen H. (Eds) Climate Change and Biodiversity in the Tropical Andes, pp. 228-244. Inter-American Institute of Global Change Research (IAI) and Scientific Committee on Problems of the Environment (SCOPE), 348 pp.

Mani M.S. 1962. Introduction to high altitude entomology. Insect life above the timberline in north-west Himalaya. Methuen & Co. Ltd. London, 302 pp.

Mani M.S. 1968 Ecology and biogeography of high altitude insects. Junk N.V. Publishers, The Hague, 527 pp.

Mousseau T.A. 1997. Ectotherms follow the converse to Bergmann's Rule. Evolution 51: 630-632.

Ramme W. 1950. Neues zur Gattung *Hyphinomos* Uvarov (Orth. Tettig.). Entomologisches Nachrichtenblatt Österreichischer und Schweizer Entomologen 2:76-79.

Rehn J.A.G., Hebard M. 1920. Descriptions of new genera and species of North American Decticinae (Orthoptera: Tettigoniidae). Transactions of the American Entomological Society 46: 225-265.

Rentz D.C.F. 2001. The Listroscelidinae, Tympanophorinae, Meconematinae and Microtettigoniinae. Tettigoniidae of Australia 3. CSIRO Publishing, Collingwood, Victoria, 524 pp.

Rentz D.C.F., Gurney A.B. 1985. The shield-backed katydids of South America (Orthoptera: Tettigoniidae, Tettigoniinae) and a new tribe of Conocephalinae with genera in Chile and Australia. Entomologica Scandinavica 16: 69-119.

Tan M.K. 2012. New species of *Glenophisis* (Orthoptera: Tettigoniidae: Hexacentrinae) from Singapore, with key to species. Zootaxa 3185: 64-68.

Uvarov B.P. 1921. Three new alpine Orthoptera from Central Asia. Journal of the Bombay Natural History Society 28: 71-75.

Willemse C. 1961. Description of some new Orthoptera from the Indo-Malayan region (Tettigonioidea). Publicaties van het natuurhistorisch Genootschap in Limburg 12: 28-35.