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Little walking leaves from southeast Ecuador: biology and taxonomy of *Typophyllum* species (Orthoptera, Tettigoniidae, Pterochrozinae)

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Abstract

Eight katydid species of the leaf-mimicking specialist genus *Typophyllum* were found in the southeast of Ecuador in an area comprising part of the eastern Andean cordillera and foothills toward the Cordillera del Cóndor in elevations between 850 and 3000 m. They are described along with the peculiar calling songs and other interesting aspects of their biology. Three of these species are new: *T. morrisi* **sp. nov.**, *T. onkiosternum* **sp. nov.** and *T. vignoni* **sp. nov.** A fourth species represented by a single male is possibly new as well. In males and females of a species considered as identical with *T. egregium* Hebard 1924, which was previously known from a unique female specimen, was found a remarkable variation of coloration, in addition to the striking sexual dimorphism typical for the genus, with the females being twice as large as the small males. The latter is related to the curious mating behaviour, which is documented for this species and *T. erosifolium* Walker 1870. The two other species found in the region are *T. bolivari* Vignon 1925 and *T. mortuifolium* Walker 1870. The calling songs of four species were recorded. In *T. erosifolium* and *T. morrisi* **sp. nov.** the sounds are almost pure sine waves at the lower boundary of ultrasound. In *T. egregium* and *T. onkiosternum* **sp. nov.** the spectrum of the carrier frequency is broader, which might be related to lower and denser vegetation at higher elevation. Based on the intraspecific variety found in *T. egregium* and *T. erosifolium*, which includes variation in tegmina shape and venation pattern, are established several syonymies among *Typophyllum* species from western South America. *T. erosifolium* is found to be identical with *T. peruvianum* Pictet 1888 syn. nov. Additionally are considered identical *T. inflatum* Vignon 1925 and *T. gibbosusm* Vignon 1925 syn. nov., *T. trigonum* Vignon 1925 and *T. quadriincisum* Vignon 1925 syn. nov., and finally *T. lacinipenne* Enderlein 1917 and *T. acutum* Vignon 1925 syn. nov. and *T. undulatum* Caudell 1918 syn. nov. The discussion treats the problematic taxonomy of the little walking leaves, bioacoustics, the pre-copulatory riding behaviour, the sophisticated mimesis, and very briefly the uncertain position within the katydid phylogeny.

Key words: Andes, bioacoustics, colour polymorphism, leaf mimicry, mating behaviour, new species, Reserva de Biosfera Podocarpus—El Cóndor, Pterochrozini, sexual dimorphism, tropical montane rainforest

Introduction

The neotropical Pterochrozinae include the probably most perfectly camouflaged katydids. Their distribution ranges from southern Mexico over Central America and the tropical part of South America, extending southward to Bolivia and southern Brazil, and to the north-eastern extension of Argentina (close to the Iguazú Falls, pers. obs. 2011/2012). They comprise almost 100 recognized species in 14 genera (Eades *et al.*). The most diverse genus is *Typophyllum* with currently 36 species from tropical South America, followed by the closely related genus *Mimetica* with 15 species from Central America and northern South America. At day reposing *Typophyllum* individuals are practically indistinguishable from a fallen leaf, unnoticeable in an environment full of "aerial leaf litter" accumulating on tree branches covered by bromeliads and other epiphytes. But at night, when they become active and extend their legs and raise the long antennae, with the aid of a lamp they can be uncovered as katydids. The males' distinctive calling songs (so far described for five species by Morris *et al.* 1989, Montealegre & Morris 1999, and Morris & Montealegre 2001) can also help finding these special insects in the understory of the rainforest, usually by means of an ultrasound detector. And very rarely a peculiar ensemble can be encountered: a female with a much smaller male riding sideways on one of the former's tegmina. *Typophyllum* males (with tegmen

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length in the smaller species only 13-15 mm) are among the smallest Pterochrozinae. The conspecific females are twice as big. Their tegmina are thus not only much larger than the ones of males, but also differ in venation pattern and shape. Of three of the species presented here were found representative numbers of individuals (9-20), and these show additional intraspecific variation in coloration and in female tegmina shape. However, most *Typophyllum* species have been described from either unique females (22) or unique males (10), and so far apparently only from 10 out of the 36 currently valid species both sexes have been known. Accordingly most authors were apparently unaware of the striking sexual dimorphism, and just as little of intraspecific variation and colour polymorphism. All this makes morphological diagnoses problematic and original verbal descriptions without illustrations practically useless. The eminent French specialist on these "sauterelles-feuilles" (leaf katydids), Paul Vignon, who published almost twenty articles on the "ptérochrozées" between 1922 and 1931, concluding with a richly illustrated revision of the entire group, and who could study only very few conspecific male and female museum specimens, was obviously not yet fully aware of the extent of this diversity in appearance of single species. Subsequent to Vignon's monograph only five more species of *Typophyllum* have been described (Hebard 1933, Piza 1976, Montealegre & Morris 1999, and Xiberras & Ducaud 2014a). In two very recent contributions (Xiberras & Ducaud 2014a and b), that come with beautiful plates, are described two species as new, the previously unknown male of another one, and three species names are synonymised. The purpose of this article is the description, i.e. illustration, of eight species from an area in south Ecuador, comprising the eastern Andean cordillera and its foothills extending east toward the Cordillera del Cóndor, along with what could be discovered about the biology of these little walking leaves. Three of these species are described as new, two of them based on males and females, while five species names are considered to be synonymous.

Investigation area and methods

Fieldwork was done during several stays in the provinces Loja and Zamora-Chinchipe in southern Ecuador: August 1997–January 1998, July–December 1998, May 1999–January 2000, July 2002, January 2009, and April 2009. The investigation area comprises several sites in the Parque Nacional Podocarpus and its immediate surroundings, a site near its eastern border, and another site at lower elevation about 70 km northeast of the national park. The main site is the Reserva Biológica San Francisco and its surroundings, contiguous with the northern border of the national park, and accessible from the scientific station ECSF (Estación Científica San Francisco), midway on the road from Loja to Zamora. This site was extensively investigated from 1750 m in the Río San Francisco valley to the highest peak of the Cordillera del Consuelo at 3100 m. Another site, El Tiro, at the highest point of the pass road above Loja, was investigated 2700–2960 m. Further south is the Nudo de Cajanuma (surveyed 2720–3340 m). In the southwestern part of the national park near the village of Yangana are the Cerro Toledo (2480–3420), and Quebrada Honda (around 2500 m). In the central northern part of the national park, south-east of ECSF, were explored the valleys of Río Sabanilla (1300–1650 m) and Río Bombuscaro (1000–1200 m), as well as a site called Romerillos in the upper valley of Río Jamboe (1750–1850 m). East of the national park were investigated two sites at the Río Nangaritza south of Zurmi near the community Las Orquídeas: west of the river (1200–1850 m) and east of the river close to the border to Peru (1250–1430 m). And at the Río Zamora, a little upstream of El Pangui, is Maralí (850–1500 m). In Orthoptera Species File Online (Eades *et al.*), subsequently abbreviated OSF, are available maps with point data based on the collected specimens. Fieldwork between 1997 and 2000 in and around Podocarpus as well as in 2009 in Alto Nangaritza was approved by collecting permits of the Ministero del Ambiente del Ecuador. Maralí is a private property.

The surveyed sites comprise undisturbed montane rainforest and at higher elevations elfin forest in wind-protected vales. Search for these nocturnal katydids was carried out at night using a headlamp, walking along paths and trails, or moving through ravines and creeks.

Sound 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). Additionally, a Mini-3 heterodyne bat detector (Ultrasound Advice, London) was used for acoustic monitoring. Collected individuals were accommodated in dome-shaped gauze cages with a square base of 30 cm side length and a height of 15 cm. These cages were furnished with small bromeliads or frequently renewed twigs or leaves. The occupants were also provided with small cucumber slices almost every day. Most recordings were made at 10-20 cm distance from caged males. There as well as with field recordings the temperature was taken with a simple pocket thermometer. With field observations the elevation was measured with an altimeter. For sound analysis was used the program 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 in Cool Edit 2000 (Trial Version), and then set to 220.5 kHz.

Numerous photographs of almost all collected specimens are available in OSF, along with original drawings in larger size, as well as sound recordings. The links under the species names lead to the corresponding species pages.

The species. Vignon (1925a) subdivided the genus into four species groups. The first group (Première Section) includes species where the tympanal chamber walls of the fore tibiae do not project beyond the dorsal surface of the tibia in lateral view, and whose hind tibiae are not significantly enlarged. To this group belong more than half of the described species. In the second group (Deuxième Section) the bases of the hind tibiae are considerably enlarged, and it will include six species. Diagnostic for the third group (Troisième Section) are the expanded anterior tympanal chamber walls, which project well beyond the dorsal surface of the tibia, like in *Mimetica* species. It includes four species. The fourth group lacks the previously mentioned characters, and, in contrast to all other species, the radial vein of the tegmina is curved downward (in closed wings) or forward (in spread wings). A single species is left in this group. Members of all four groups were found in the investigation area.

Typophyllum egregium Hebard 1924

(Figs. 1, 2, 3, 4)

http://lsid.speciesfile.org/urn:lsid:Orthoptera.speciesfile.org:TaxonName:5513

Hebard 1924: 219, Vignon 1931: 126, Beier 1960: 359, Braun 2002: 66 (*Typophyllum* sp. 2, "Berg-Spaziergehblättlein"), Braun 2008: 216 (Fig. 1: male), 220, Chamorro-Rengifo *et al.* 2014: 595.

Examined specimens. Female holotype, Ecuador, Tungurahua, 2130 m [7000 ft], Academy of Natural Sciences, Philadelphia (pencil drawings December 2003); 13 males and 7 females from four localities in Parque Nacional Podocarpus and its periphery, leg. H. Braun between 4 October 1997 and 17 September 1999 (currently in collection of author): Cordillera del Consuelo: male cbt002s01 (sound recording) 2200 m; male cbt002s13 (sound recording), 2300 m; female cbt002s14, 2410 m; female cbt002s15, 2840 m; male cbt002s17 (sound recording), 2830 m; male cbt002s21 (sound recording), 2500-3000 m; El Tiro: male cbt002s19, 2880 m; Cajanuma around 2750 m: male cbt002s02 (sound recording), male cbt002s03 (sound recording), male cbt002s04, male cbt002s05, male cbt002s06, male cbt002s07, female cbt002s08, female cbt002s09, female cbt002s10, female cbt002s11, male cbt002s18 (sound recording); Quebrada Honda 2480 m: male cbt002s20 (sound recording), [the female nymphs cbt002s12 and cbt002s16 belong to *Typophyllum onkiosternum* **sp. nov.** described below]

Notes. "The type of this striking species is unique" wrote Hebard (1924) in the original description, and this seems to have remained so up to the present. The new-found females are very similar to this specimen, and taking into consideration the intraspecific morphological variation of the genus *Typophyllum*, they most probably are conspecific. The volcano Tungurahua (5023 m), where the type was found at around 2100 m, is about 300 km north of the investigation area and also part of the eastern Andean cordillera. Hopefully this population has survived the recent volcanic activity starting in October 1999, with several subsequent eruptions, and still high activity with emission of ash in September 2014 (according to online newspaper articles in El Comercio and El Universo, Ecuador).

Description. The internal and external tympanal chamber walls of the foretibia are equally developed and not expanded, and also the bases of the hind tibia are not expanded, placing this species in the first of the four groups of Vignon (1925a). Figures 1, 2 and 4 show the small males and large females, which do not show really distinctive characters, apart from the shape of the sexually dimorphic tegmina. However, there is considerable variation, especially in females, where the distal half of the anal margin can be undulated or uniform (Fig. 3), and the tip can be elongated or not (Fig. 4). The male's right tegmen has a transparent speculum (Fig. 4E). Hindwings are small, of about two-thirds the length of the tegmina. As in other *Typophyllum* species nearly all body parts can have small tubercles and tiny granules or are wrinkled to individually varying degree. Hairs are fairly sparse and mostly very short. Some females have a tiny knob at the tip of the maxillary palp. The pronotal disc is widened posteriorly, more pronouncedly in males, with a tiny notch in the hind margin. The prosternum has short delicate spines (slightly shorter than diameter of tip of maxillary palp); the mesosternal and the metasternal spines are slightly longer and less delicate. Often there are small medial lappets on second and third abdominal tergites (probably vestiges of moss camouflage in nymphs).

Coloration. Highly variable (Fig. 1). Most frequently uniformly medium or dark brown, sometimes uniformly light green (Fig. 4A), and sometimes two colours mixed: green with dark brown or reddish brown portions, light brown with dark brown markings, or dark brown with very light legs and antennae.

FIGURE 1. *Typophyllum egregium*: four males with different coloration, photos staged during day (specimens cbt002s13, -s02, -s20 and -s04).

Measurements. Tegmen length in males 13–15 mm and in females 22.5–24.5 mm (in holotype 32 mm), hind femora in males 12–14 mm and in females 16–17.5 mm (in holotype 17 mm), antennae in males up to 45 mm, in females slightly longer.

Acoustic behaviour. The males' calling song (Fig. 19A) consists of isolated "double zips", partly in the audio range and fairly loud (in contrast to pure-tone low ultrasound songs of most other *Typophyllum* species). Each of the two syllables is preceded by a very low pulse which corresponds probably the opening stroke of the tegmina. These syllables are each resolved into about 30 (20–35 depending on the individual) initially crescending transient impulses corresponding to the individual tooth-scraper impacts. These rapidly decaying impulses result in a still moderately narrow spectrum with a peak at 18 kHz. While in the natural habitat calls are separated by pauses of several minutes, after seven days in confinement one male was calling like a lunatic in his cage with up to six calls within 45 seconds at 23°C (at the upper limit of the distribution range at 3000 m the medium temperature at midnight is 8°C and lowest temperatures measured with field recordings were 9.5–11.5°C). Calling is restricted to night, with very sporadic calls on gloomy afternoons within the clouds.

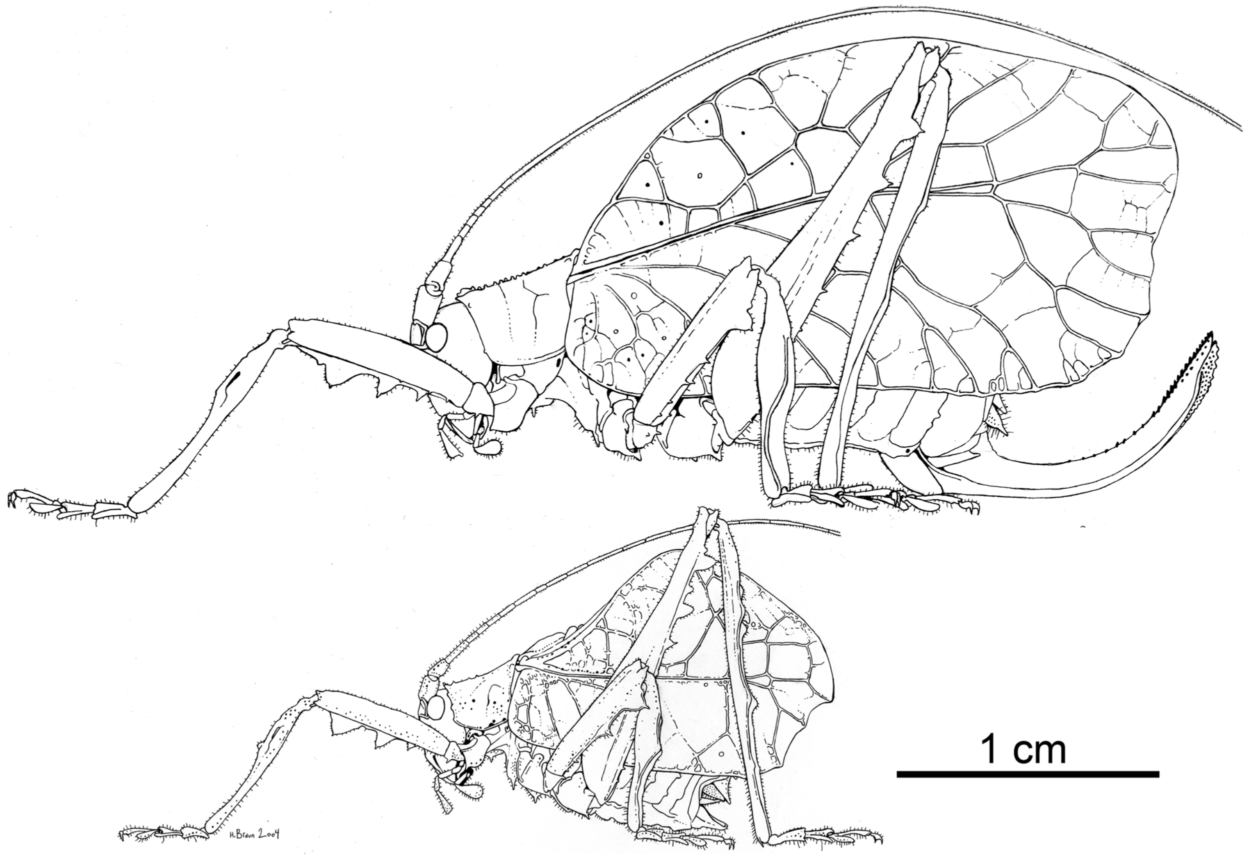

FIGURE 2. *Typophyllum egregium*: female and male habitus (specimens cbt002s09, light green morph with apically rounded tegmina, and cbt002s01, brown), note difference in size and tegmen venation.

Mating behaviour. Males and females kept together in cages showed a number of instances of the piggyback behaviour where the male spends one to mostly several days riding on one side of the female's tegmina before copulation. The small male usually sits perpendicular on the tegmen surface with his body axis more or less parallel to the main veins (Sc/R) and the head directed to the wing tip. Once a male rode for one day on the female, the subsequent copula lasted five hours, then the individuals separated. Another time a different male spent five days riding on the same female before they separated without copula. Some other time three males climbed within two hours onto a female (one on each side of the wings and the third on top—surely an artefact of crowded conditions); after three days the last mounted male mated and stayed in contact with the female via the spermatophore for at least 10 hours, then the forth night the second male mated, and in the subsequent night the third (and first to have mounted), where the copula lasted at least 3.5 hours. In yet another instance copula occurred after the male rode for two days on the female. Females often walked around with their riders and unlike the males they ingested food. The observed copulations occurred mostly late at night and lasted sometimes to noon the following day. Size of the spermatophores was approximately 7 mm x 3 mm x 3 mm and the females began to feed on them immediately after copula. After successful mating the individuals always separated.

Distribution. In this species the numerous acoustic records allowed a complete assessment of its altitudinal distribution range in the investigated area (Fig. 20A). It occurs in a wide range from apparently 1500 m to 3000 m on both slopes of the cordillera, with the lowest observation at the interandean western side at 2750 m due to the lower limit of survey there. It cannot be completely excluded that the song was not confused with some other species with a double-zip audio call at lower elevations; the lowest record of an insect was at 2120 m. *T. egregium* was found in the valleys of Río San Francisco and Río Sabanilla, at El Tiro, Cajanuma and in Quebrada Honda. The uppermost living individuals inhabit small fragments of elfin forest in wind-protected vales. Along with the type locality the geographical distribution comprises the eastern Andean cordillera at least from central Ecuador to the border with Peru.

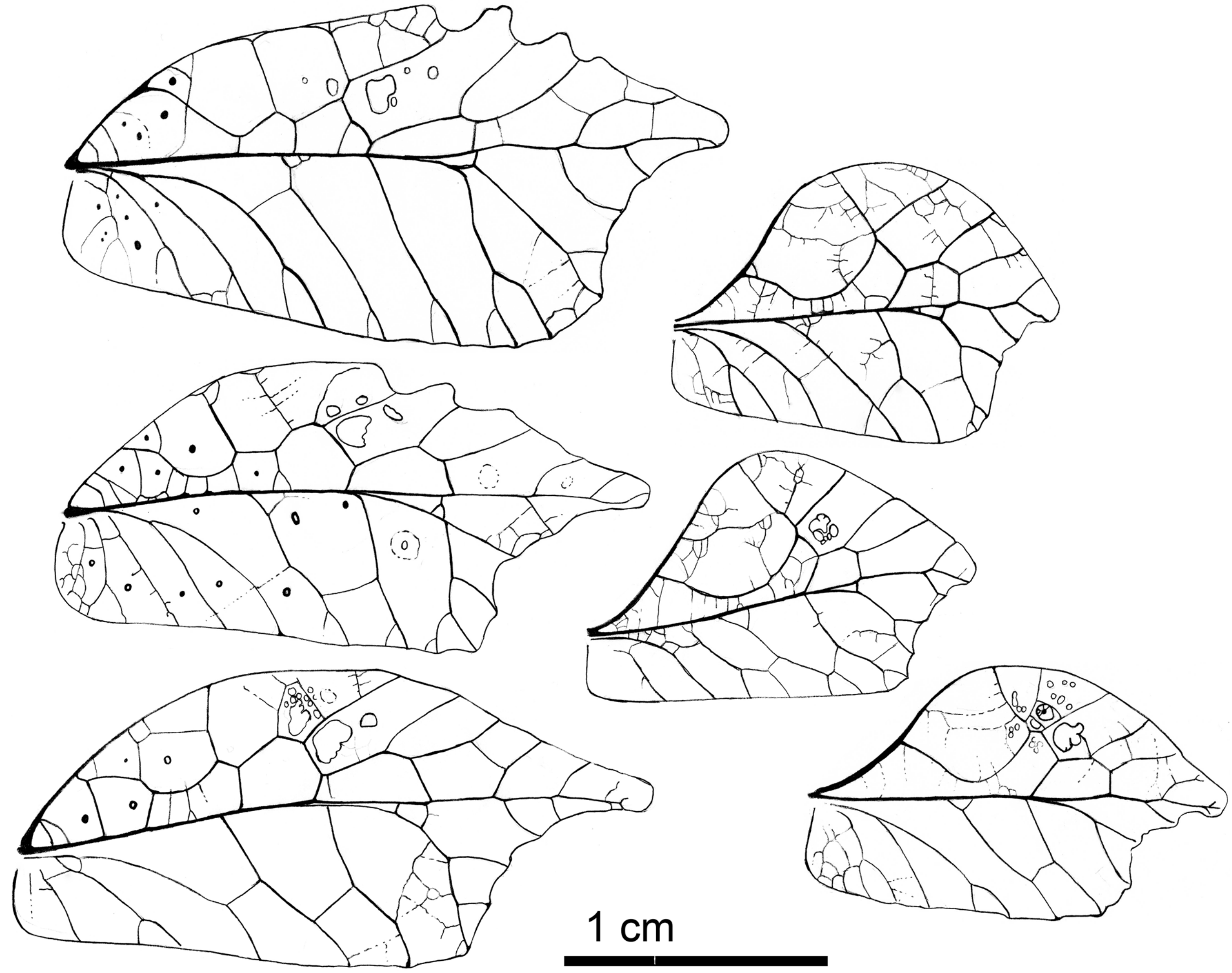

FIGURE 3. *Typophyllum egregium*: left tegmina of females (left column) and males (right), note variation in shape and venation (female specimens: cbt002s10, -s14, -s11, males: cbt002s02, -s15, -s06).

Typophyllum morrisi sp. nov.
(Figs. 5, 6, 7)

http://lsid.speciesfile.org/urn:lsid:Orthoptera.speciesfile.org:TaxonName:470144
Braun 2002: 66 (*Typophyllum* sp. 3, "Bombuscaro-Spaziergehblättlein"), Braun 2008: 220 (*Typophyllum* sp. 3).

Etymology. Dedicated to Glenn K. Morris, the pioneer of bioacoustics of neotropical tettigoniids, who documented for the first time songs of some *Typophyllum* and *Mimetica* species.

Examined specimens. Male holotype cbt003s04 (sound recording), Río Bombuscaro valley, 1100 m, 19 June 1999; female paratype cbt003s21, Alto Nangaritza, 1260–1350 m, 6–12 April 2009 both leg. H. Braun and deposited in the Museo de La Plata; 18 additional specimens from three sites are currently in the collection of the author: Bombuscaro 1000–1180 m, 13–19 November 1998: male cbt003s01 (recording) and male cbt003s02 (raised from nymph), 19 June 1999: male cbt003s03 (recording) and male cbt003s04 (recording), 20 July 2002: female cbt003s05 and male nymph cbt003s06 (leg. H. Braun); Maralí 860–980 m, 12 January 2009: female cbt003s07, and male cbt003s09 (leg. H. Braun); Alto Nangaritza 1260–1450 m, 6–17 April 2009: female cbt003s10, female cbt003s11, female cbt003s12, male cbt003s13, male cbt003s 14, male cbt003s15, male cbt003s16, male cbt003s17, female cbt003s18, male cbt003s19 (damaged spider victim), and male cbt003s20 (leg. Elicio Tapia & H. Braun). [male cbt003s08 turned out to be a different species, see below *Typophyllum* sp.]

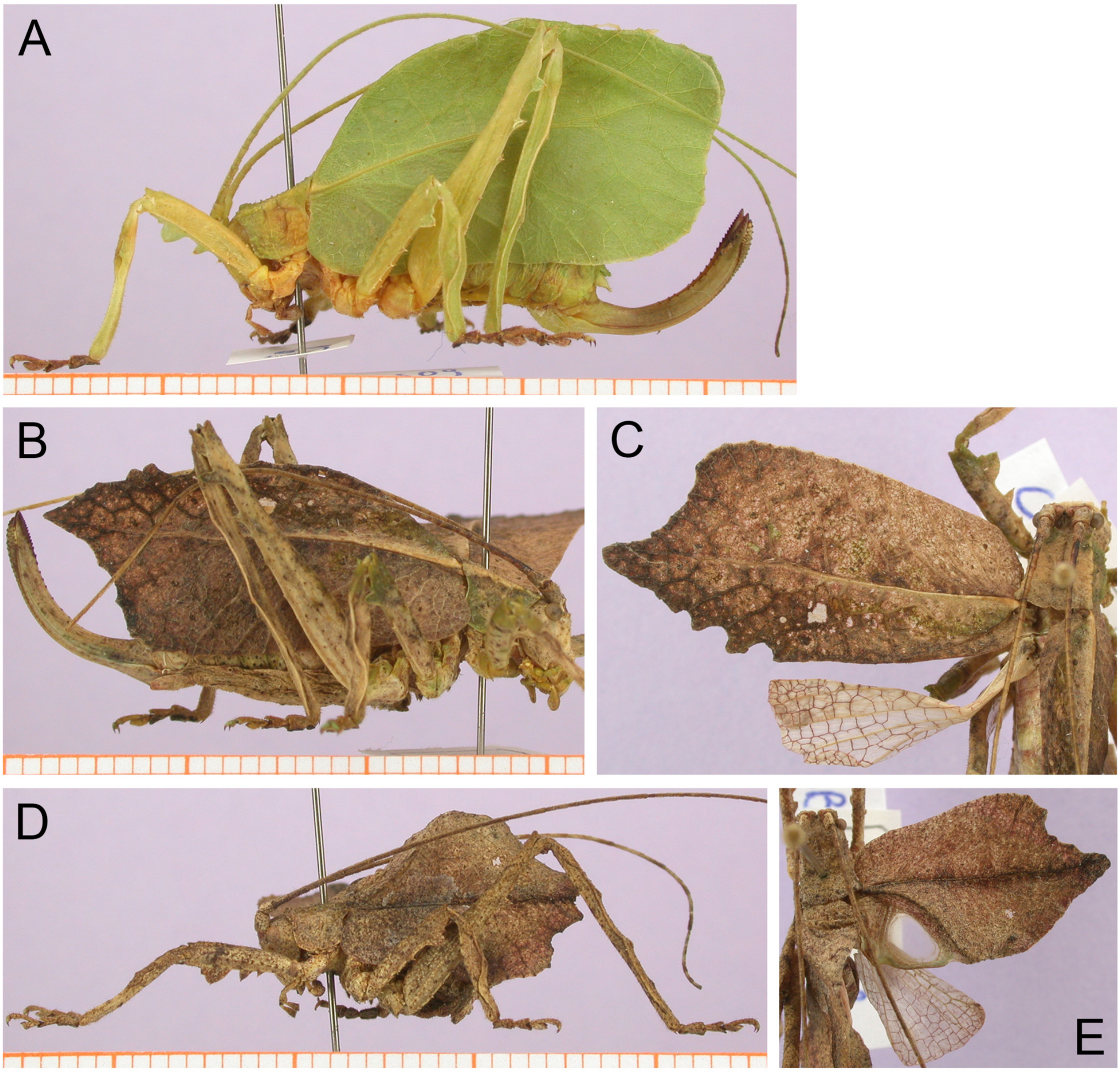

FIGURE 4. *Typophyllum egregium*: **A.** green female (specimen cbt002s09), **B**,**C.** brown female (-s10), **D**,**E.** brown male (-s03); in live females ovipositor usually concealed by tegmina; note transparent mirror in right tegmen of male (all photos to same scale).

Notes. There are 8 males and 2 females in the collection of G.K. Morris (inspected 2004/2005) from the Amazon region of Ecuador in Napo Province. According to morphology they could belong to this species as well, but the male calling song is different. Probably they are the same as *Typophyllum* sp. nr. *trapeziforme* Morris *et al.* 1989, whose song is compared below to the one of *T. morrisi*. Another male from this area belongs to the collection of the University of Michigan Museum of Zoology, Ann Arbor (UMMZ): Napo Province, about 8 km south-east of Tena and 2 km south of Ongota, 12 May 1963 leg. T.H. Hubbell & L.E. Peña. This site is at about 500 m and around 300 km north of the type locality of *T. morrisi*.

Description. As in *T. egregium* the internal tympanal chamber walls are not expanded beyond the dorsal surface of the fore tibia, but are developed like the external ones. Also, the bases of the hind tibia are not expanded, placing this species like the preceding one into the first group according to Vignon (1925a). Tegmen shapes (Fig. 5C) do not correspond sufficiently well to any described males or females. And in males there is a unique modification of the stridulatory area at the base of the left tegmen: the proximal end of the fairly bulky stridulatory vein is dorsally developed as a knob, and directly behind it is a second knob of about the same diameter and as

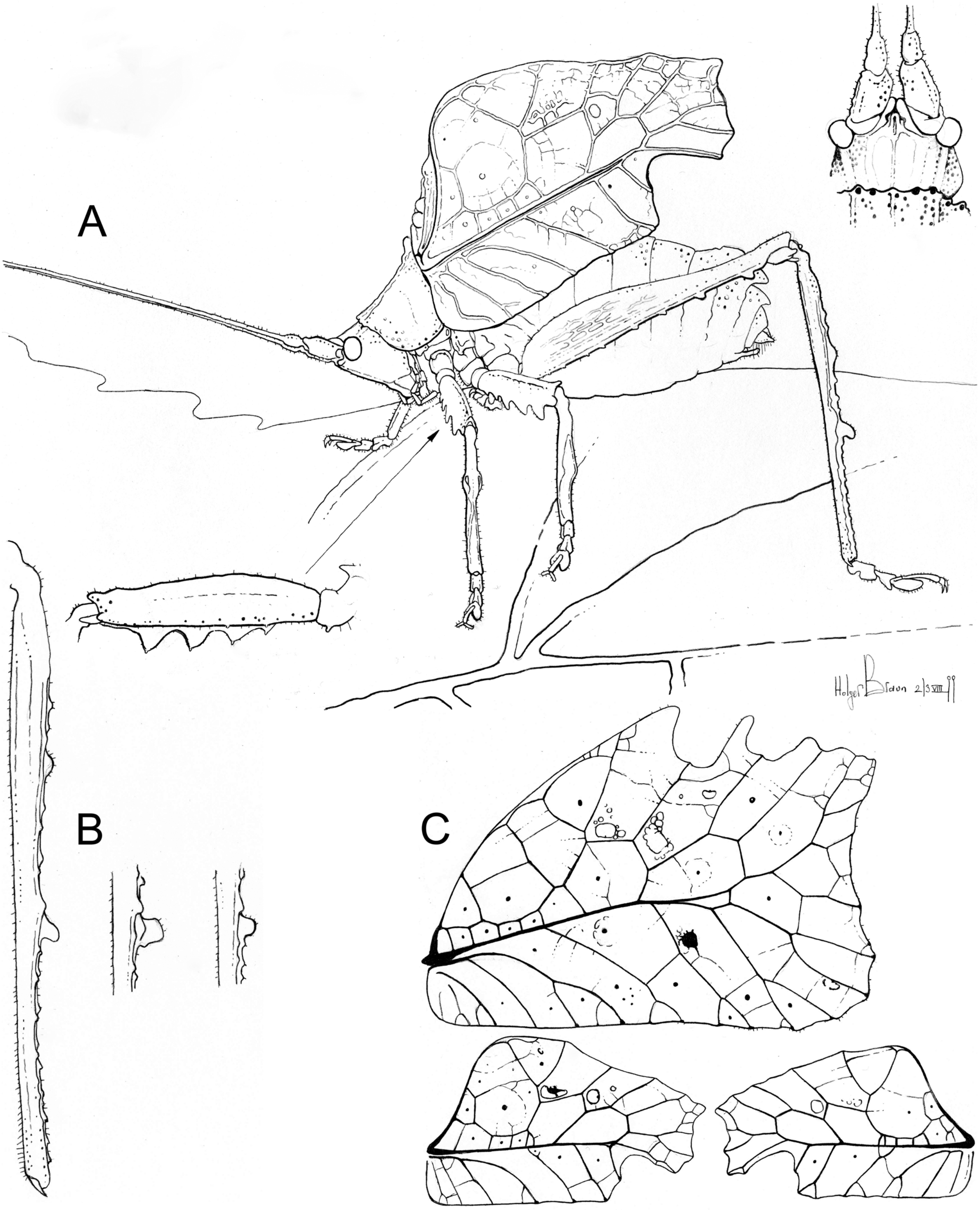

FIGURE 5. *Typophyllum morrisi* **sp. nov.**: **A.** male habitus, left fore femur in lateral view, and head in dorsal view (body length 18 mm including tegmina, slightly obese after longer time in cage feeding on cucumber, after specimens cbt003s03 and –s04); **B.** left hind femur with typical medial process (males cbt003s02, -s04, -s03); **C** left tegmen of female (25 mm, cbt003s05), left and right tegmina of two males (13-14 mm, cbt003s03, -s04).

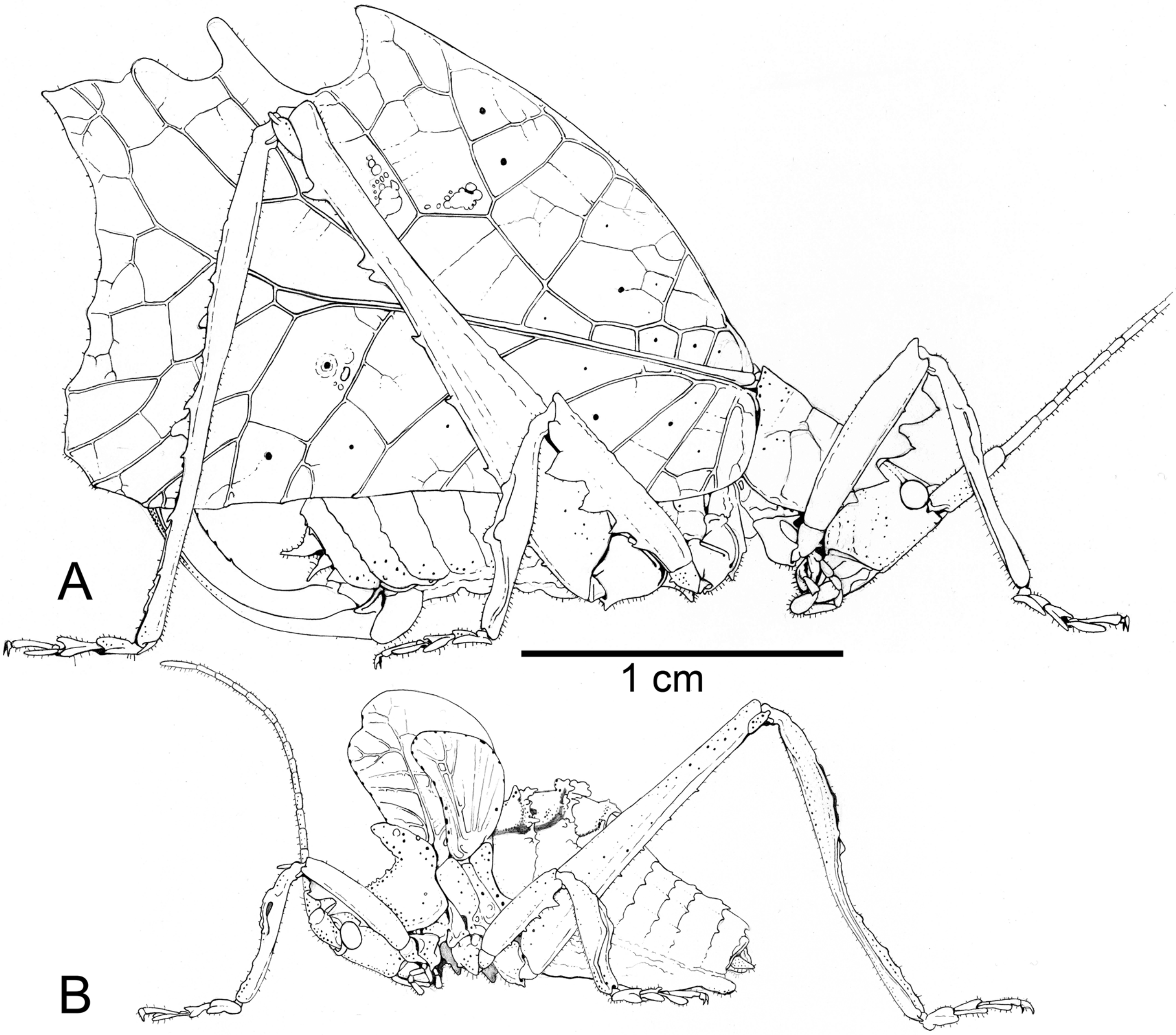

FIGURE 6. *Typophyllum morrisi* **sp. nov.**: **A.** female (cbt003s05): **B.** female nymph (-s06).

isolated structure being a little bit more conspicuous. The speculum of the right tegmen seems to be fairly stiff and is translucent but not transparent (Fig. 7B). In females the tegmina are mostly emarginated in a characteristic fashion at the distal anal margin (Figs. 6A, 7D), and only rarely the margin is uniform (Fig. 7E). One distinctive trait is shared by both sexes: the hind tibia sports a little below the middle, on the dorsal internal edge, a rounded, often downward-directed and drop-shaped process, of about the same diameter as the tibia (Fig. 5B). The prosternum has no spines; mesosterum and metasternum are laterally pointed, but not terminating as distinct spines.

Coloration. Little variation; various shades of brown; most individuals are dark brown (Fig. 7).

Measurementes. Tegmen length in males 13–16 mm and in females 25–28 mm, hind femora in males 12–13.5 mm and in females 18–20 mm, antennae in females at least 50 mm.

Acoustic behaviour. The two males that were recorded produced calls consisting of 3–6 (mostly 4 or 5) pulses (Fig. 19C). One individual pulse lasts about 30 ms and they are repeated every 120–130 ms. A five-pulse call lasts 500 ms at 23°C. Mostly two or three calls were produced together, separated by intervals of 400–500 ms. The pulses consist of a sustained and almost pure sine wave. The spectrogram shows a very narrow peak at 20.5 kHz and a faint harmonic at 41 kHz. The males seem to call only sporadically and the unique and easily recognizable song was never heard in the natural habitat while listening with a bat detector at night. The two knobs on the dorsal portion of the left tegmen of males might serve to dampen vibration of this tegmen, which otherwise could cancel out by negative interference the sound radiated by the speculum of the right tegmen, in case both tegmina vibrate out of phase.

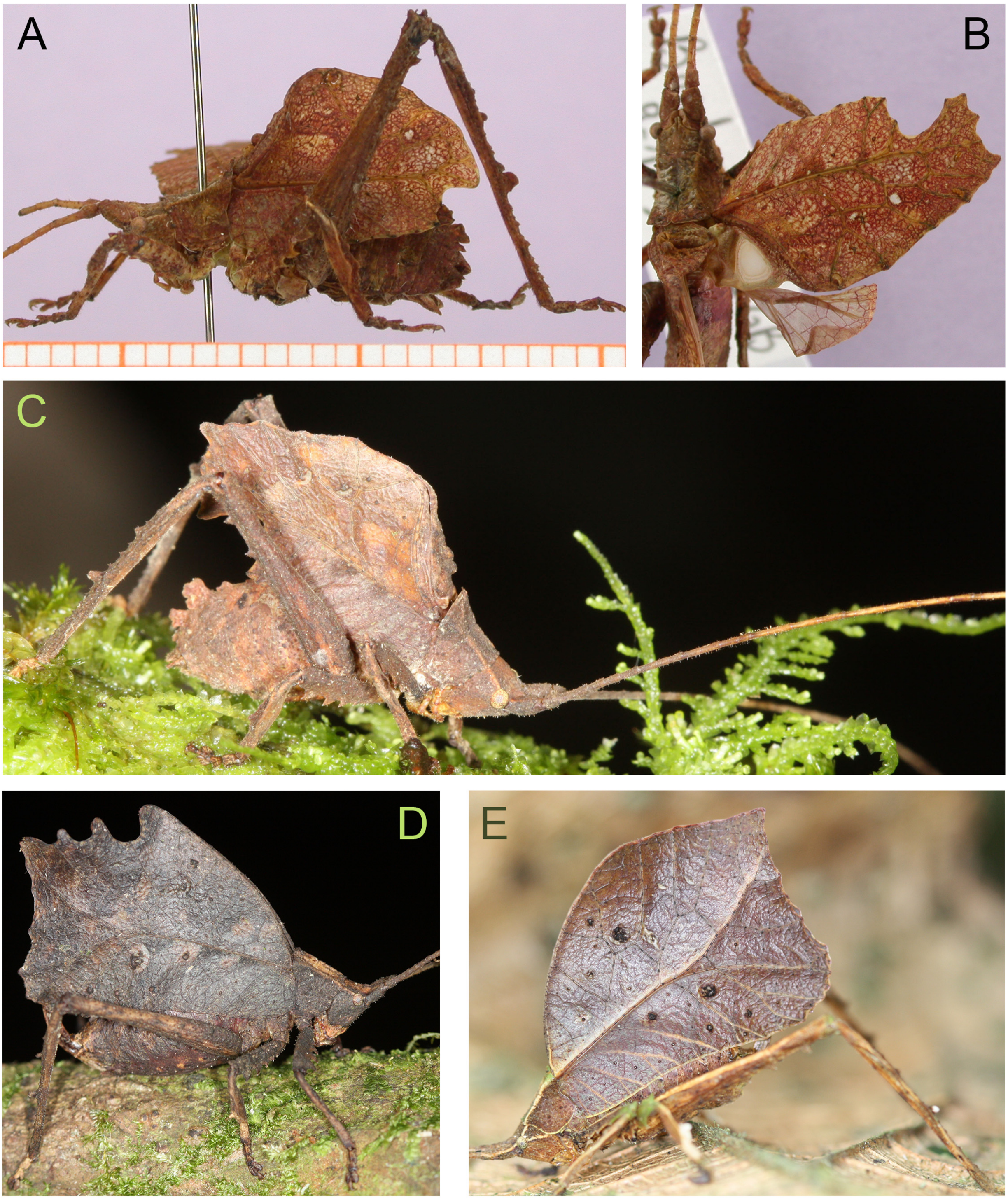

FIGURE 7. *Typophyllum morrisi* **sp. nov.**: **A,B.** male holotype, lateral and dorsal view (cbt003s04); **C.** male (cbt003s14); **D.** female (cbt003s10); **E.** atypical female with uniform anal margin of tegmina (cbt003s12) (see Fig. 5C for size difference between tiny male and large female).

For the above-mentioned *Typophyllum* sp. nr. *trapeziforme* (Morris *et al.* 1989) are described trills of 47–132 pulses with a total duration of 2.5–7.0 s. The principal carrier frequency is 23.2 kHz. The high duty cycle might be due to captivity (see above *T. egregium*; extremely elevated calling activity compared to duty cycles of freshly caught males, and males in natural habitat, also occur in other Ecuadorian katydids—pers. obs.). However, the carrier frequency is slightly higher than described for *T. morrisi*. So it is currently uncertain whether the lowland population from the Ecuadorian Amazon is truly conspecific.

Mating behaviour. In a cage with three females and one male, was once at night observed the male riding on a female, but this female was found moribund the next day and no copulation occurred.

Distribution. Eastern foothills of eastern Andean cordillera at 850–1450 m in south Ecuador, probably extending down into Amazon region of Ecuador and northern Peru.

Typophyllum onkiosternum **sp. nov.**

(Figs. 8, 9, 10, 11A–C)

http://lsid.speciesfile.org/urn:lsid:Orthoptera.speciesfile.org:TaxonName:463836

Braun 2002: 67 (male as *Typophyllum* sp. 4, "Schwarzgetüpfeltes Spaziergehblättlein", female as *Typophyllum* sp. 5, "Schmetterlings-Spaziergehblättlein", nymphs as *T. egregium*), Braun 2008: 220 (*Typophyllum* sp. 4).

Etymology. Referring to the hook-like sternal spines, from Greek *onkos* (hook, barb of an arrow).

Examined specimens. Male holotype cbt004s01 (sound recording), Cordillera del Consuelo 2150 m, 9 May 1999, leg. H. Braun, deposited in the Museo de La Plata; same site and collector and in collection of author: female paratype cbt005s01, 2110 m, 13 September 1998; two female nymphs: cbt002s12, 2150 m, 13 December 1997; cbt002s16, above 2100 m, May 1999 [erroneously assigned to three different species codes: cbt002, -004, -005].

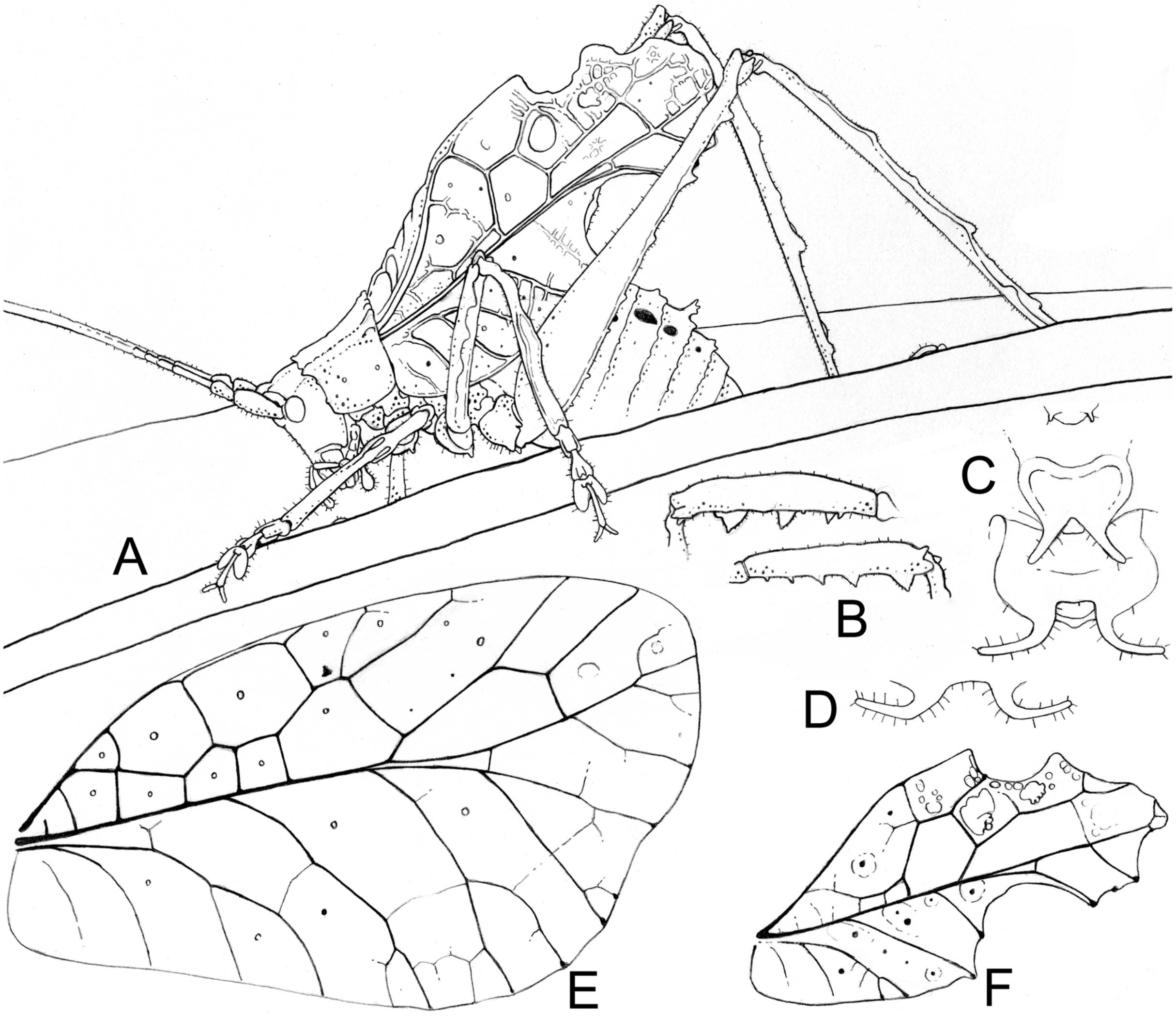

FIGURE 8. *Typophyllum onkiosternum* **sp. nov.**: **A.** male habitus; **B.** left fore and middle femora, external view; **C.** spines on pro-, meso- and metasternum, frontal view, slightly from below; all spines black, distance between tips of metasternal spines almost 2 mm (A,B,C after holotype cbt004s01); **D.** metasternal spines of female paratype, frontal view; distance between tips almost 3 mm (cbt005s01); **E** left tegmen of female paratype (24 mm); **F.** left tegmen of male holotype (14.5 mm, more schematic than in A).

Description. As in the two preceding species the internal tympanal chamber walls are not extending beyond the dorsal surface of the fore tibia, and the hind tibiae are developed normally, so this species also belongs to Vignon's first group. As in the other species the tegmina shapes of male and female are very different (Figs. 8, 10). The speculum of the right tegmen in males is fairly small and transparent. This species has unique black hooklike spines on the meso- and especially the metasterum, described for no other *Typophyllum* species (Fig. 8C,D). The prosternum has very small, short and obtuse processes. On the margins of the mesosternum sit delicate, almost straight and obtuse spines that diverge laterally about 45 degrees. The metasternum is equipped with curved and strongly laterally diverging spines that are longer and reach 1 mm in the male. Upon this character was established the conspecificity of the single male, the very dissimilar female, as well as the two nymphs.

Coloration. The only known male is light brown with greyish and yellowish hues (Figs. 10A,D and 11B). Its abdominal tergites have black lateral spots and the sternum is blackened. The only female is light green with dark brown legs and reddish brown ovipositor (Figs. 10B,C and 11A).

Measurements. Tegmen length in male 15 mm and in female 23 mm, hind femora in males 14 mm and in females 18 mm.

Acoustic behaviour. The single recorded male produced series of pulse pairs (Fig. 19B). At 18ºC the pulse length is 20–30 ms (without the soft hemisyllables corresponding to the opening strokes), and the interval about 50 ms. On a field recording of an untraceable male at 13ºC pulse length is 40 ms and interval 70 ms. These series can consist of 10–15 such pulse pairs, separated by 2–5 seconds respectively. The pulses are broken up into not completely fused impulses, and the spectrogram shows a fairly narrow peak between 20 and 22 kHz.

Distribution. Only known from the type locality: northern slope of Cordillera del Consuelo, 2100–2200 m. All four individuals as well as the only acoustic record are from a small area at the origin of a small creek. The male was sitting on a terrestrial bromeliad.

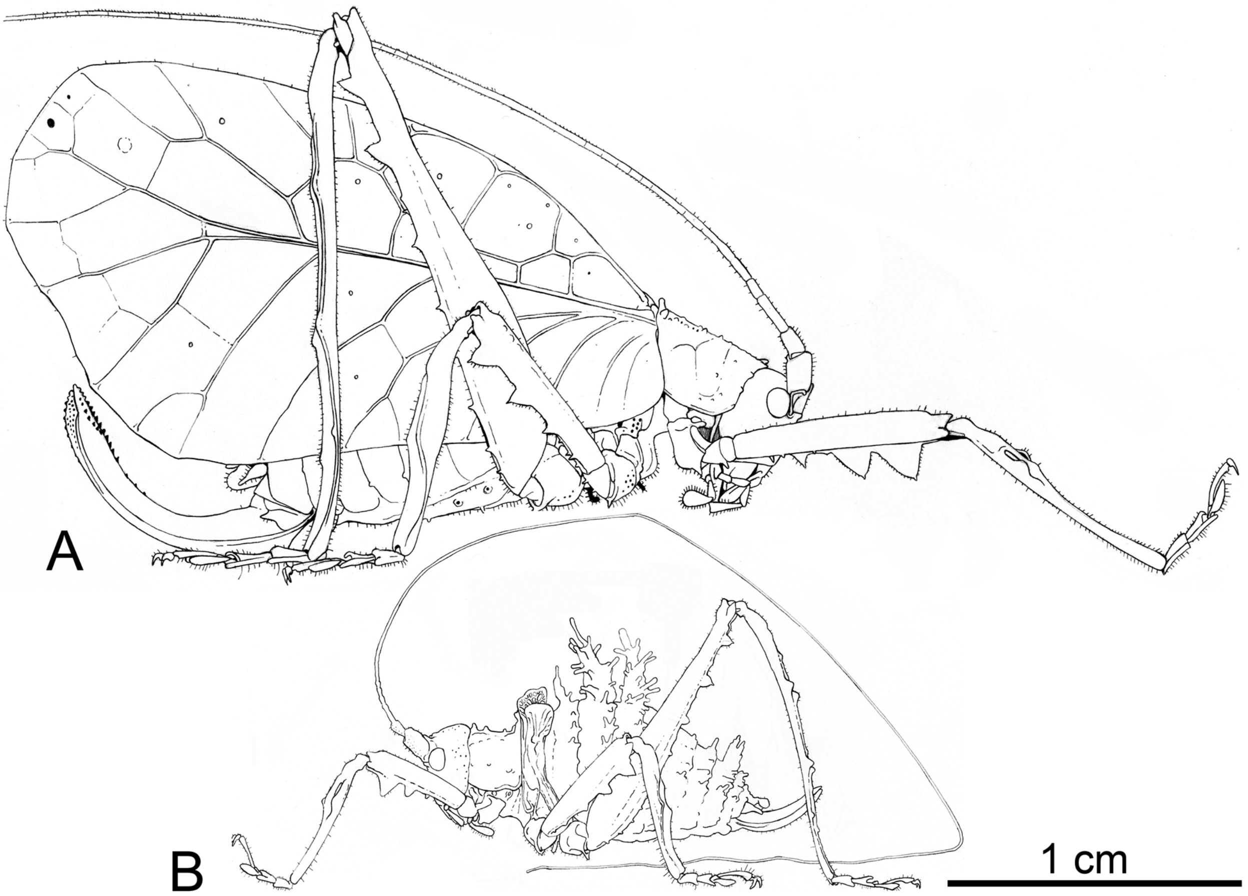

FIGURE 9. *Typophyllum onkiosternum* **sp. nov.**: **A.** female (paratype, cbt005s01); **B.** female nymph (cbt002s16).

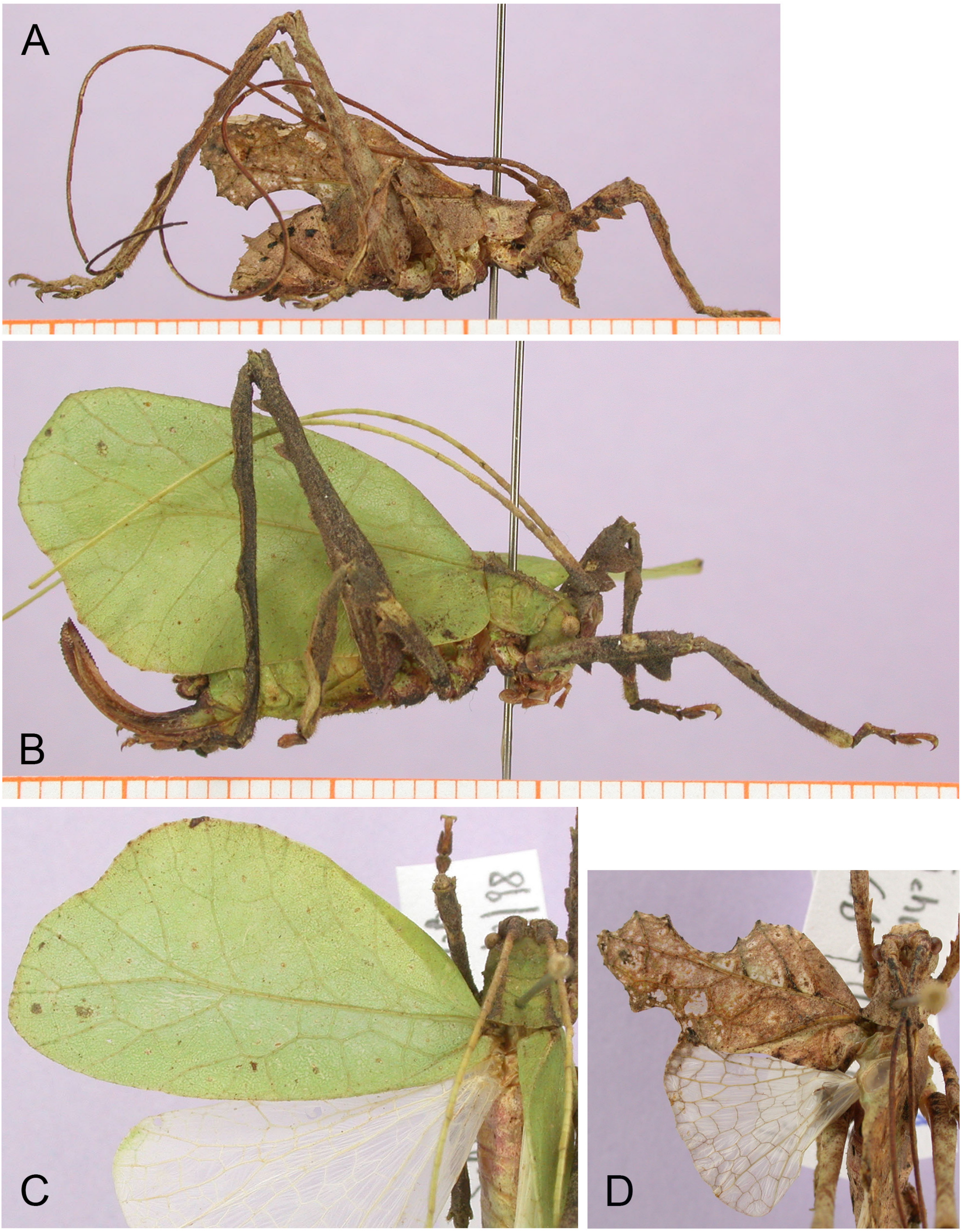

FIGURE 10. *Typophyllum onkiosternum* **sp. nov.**: **A**,**D.** male holotype (grey-brown morph); **B**,**C.** female paratype (green morph) in lateral and dorsal view (cbt004s01, cbt005s01, photos to scale).

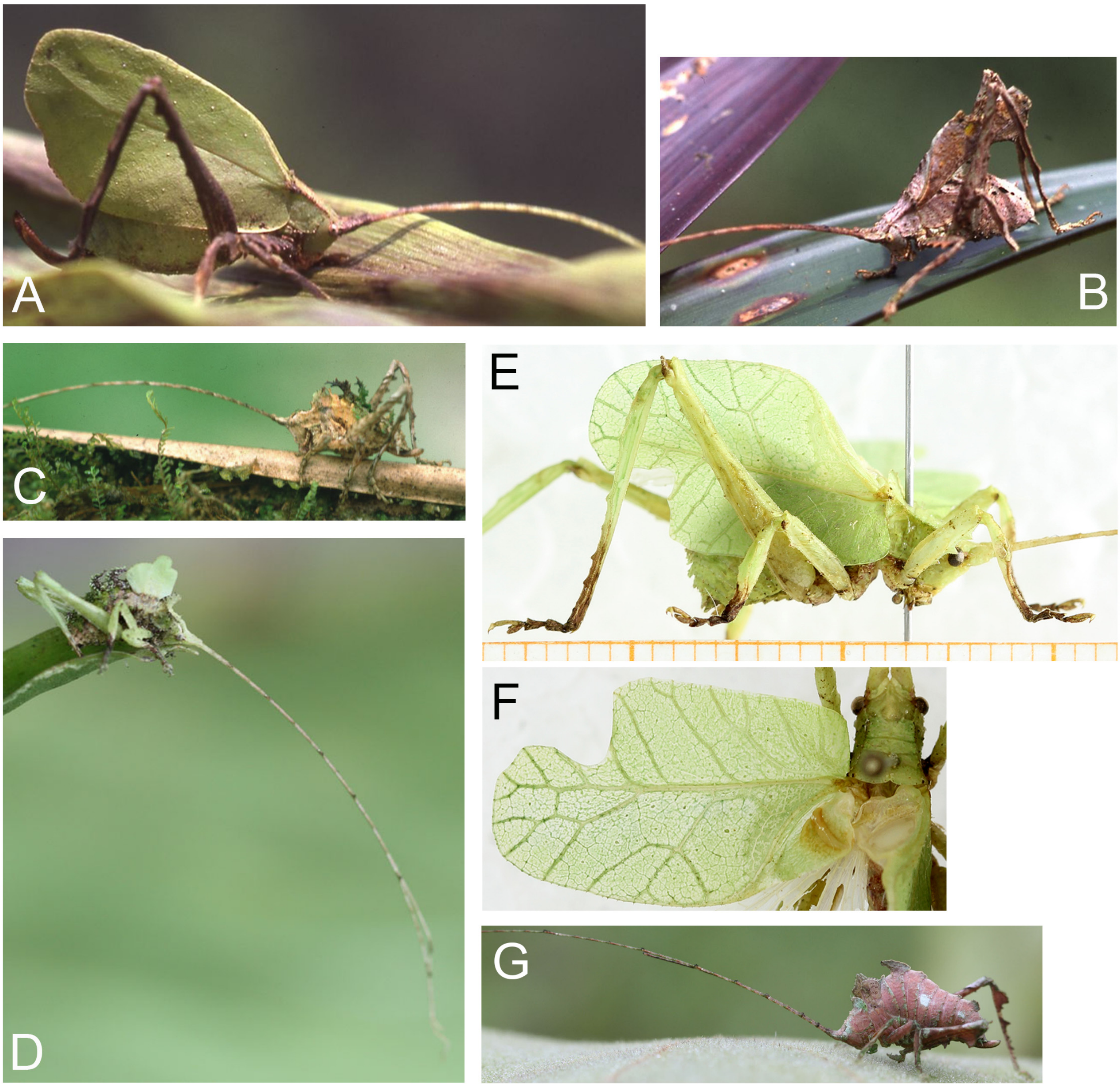

FIGURE 11. *Typophyllum onkiosternum* **sp. nov.** (A–C): **A.** female (paratype, tegmen length 24 mm), **B.** male (holotype, tegmen length 14.5 mm), **C.** female nymph (cbt002s12); *Typophyllum* sp., unknown male of species described from females only or new species (D–F, cbt003s08): **D.** nymph, **E**,**F.** adult; **G.** *Typophyllum bolivari*, nymph; photos of live individuals staged during day and approximately to scale.

Typophyllum sp.

(Fig. 11D–F)

Examined specimen. Male cbt003s08, Maralí 980 m, 12 January 2009, leg, H. Braun, found as nymph and raised to adult [originally identified as *T. morrisi* **sp. nov.**, species code cbt003].

Notes. Belonging like the previous three species to the first section of Vignon (1925). The only specimen, a male raised from a tiny nymph (Fig. 11D,E,F), is very different from all known males in this group, and the shape of the tegmina does not correspond to any known *Typophyllum* male. However, there will be left nine valid species of *Typophyllum* from Colombia, Peru, Venezuela, French Guiana, Brazil and Bolivia in this first section, which are known only from females. Since this single male could be conspecific with any of those, it is not described as new species at this point.

Coloration. Only specimen light green with brown tarsi.

Measurements. Male: tegmen length 15 mm, hind femora 13 mm.

Typophyllum bolivari Vignon 1925

(Fig. 11G)

http://lsid.speciesfile.org/urn:lsid:Orthoptera.speciesfile.org:TaxonName:5486

Vignon 1925a: 273, Vignon 1931: 137, Beier 1960: 367, Morris *et al.* 1989, Castner & Nickle 1995a,b,c, and some other references.

Examined specimens. Not collected, photos of a female nymph (2 January 2009, H. Braun) and one adult male (May 2012, A. González), both Maralí.

Description. This species has conspicuously enlarged hind tibiae, the characteristic of Vignon's (1925a) second group. A reddish brown nymph with a few whitish spots and mossy green coloration was found (Fig. 11G). It shows the lateral contour of the dorsal margin of the hind tibiae which is diagnostic for this species: a large lamelliform process just below the knee, and a small pointed one above the middle. Subsequently an adult male (light brown morph with light green palps) was photographed at the same locality, with the tegmina constricted on both margins, another diagnostic feature of this species.

Coloration. Very variable: individuals can be green (sometimes yellowish in museum specimens), or greyish, or light or dark brown, often with several shades mixed (Castner & Nickle 1995b, photos R. Oelman). This is one of the few *Typophyllum* species with dark brown fringes on the transversal veins of the yellowish hind wings.

Acoustic behaviour. The song of one male from Limoncocha (Napo, Ecuador) was analyzed (Morris *et al.* 1989): It made brief high-audio chirps, consisting of mostly four, sometimes three double pulses, lasting about 500 ms at 22.5°C. The spectrum shows a narrow peak at 14.9 kHz. Within a series of chirps they were repeated every 20–45 s. The male from Maralí made chirps consisting of three pulses, repeated every 5–21 s (recordings in MP3 format by A. González).

Mating behaviour. For this species is also documented the precopulatory riding of the small male on the large female (Nickle & Castner 1995a, photo R. Oelman).

Distribution. Amazon region of southern Colombia, Ecuador, and northeastern Peru (Vignon 1925a, Morris *et al.* 1989, Castner & Nickle 1995c, specimens in collection of University of Michigan Museum of Zoology, and photos by R. Oelman).

Typophyllum erosifolium Walker 1870

(Figs. 12, 13, 14, 15)

Typophyllum peruvianum Pictet 1888 **syn. nov.**

http://lsid.speciesfile.org/urn:lsid:Orthoptera.speciesfile.org:TaxonName:5481

T. erosifolium: Walker 1870: 464 (*T. erosifolia*), Kirby 1906: 350 (*Mimetica erosifolia*), Vignon 1925a: 275, Vignon 1931: 140, Beier 1960: 368, Braun 2002: 67, Braun 2008: 220; *T. peruvianum*: Pictet 1888: 29, and some other references; *Typophyllum* sp. 1: Braun 2002: 65 ("Pfeifendes Spaziergehblättlein"), Braun 2008: 220.

Examined specimens. Reserva Biológica San Francisco/Río San Francisco valley: male cbt001s01 (with sound recording), 1850 m, 30 September 1997; female cbt001s02, 1830 m, leg. H. Braun 14 July 1998; female cbt001s03, 2010 m, 26 July 1998; male cbt001s04 found riding on female cbt001s05, 1830 m, leg. F. Matt 12 August 1998; male cbt001s06 (sound recording) 1830 m, 4 June 1999; male cbt001s07 (sound recording), 1850 m, 8 June 1999; male cbt001s10, leg F. Matt 2002; Río Sabanilla valley 1640 m: male cbt001s08 (sound recording) and female cbt001s09, 5 September 1999; Bombuscaro 1200 m: female cbt007s01, captured as nymph and raised to adult, 8 January 2008; female cbt007s03; Alto Nangaritza, 1280 m, 8 April 2009; leg. H. Braun where no collector mentioned, all in collection of author.

Notes. *T. erosifolium* was described from a single female from the upper Amazon in northeastern Peru. The locality, Nauta ("Nanta" in original description, but corrected in Vignon's and Beier's revisions), is a small town in the Loreto Department with road and river access, at about 100 m, and might not be the actual collection site. No further records seem to be published. The type specimen's tegmina tips are damaged (photos in OSF), but it is visible that the distal anal margin is undulated or "deeply notched" (Walker 1870), from which the species name is derived. *T. peruvianum* was also described from a unique female from Peru, without further locality specifics. This specimen (photos in OSF) shows the same tegmen shape as *T. erosifolium*, only without emarginations, and also the venation is very similar. There is a female specimen from Yarinacocha in the UMMZ collection (photos in OSF). This locality is in eastern Peru in the Ucayali Department at about 150 m. Apparently there are also records from Ecuador (Beier 1960). Since the development of the anal margin is intraspecifically variable in females (found in this species, *T. egregium* and *T. morrisi* **sp. nov.**), *T. erosifolium* and *T. peruvianum* are considered to represent the same species.

FIGURE 12. *Typophyllum erosifolium*: male habitus, left fore femur, ear openings of left tibia, and abdomen tip in ventral view (cbt001s06); female habitus and left fore leg (cbt007s01).

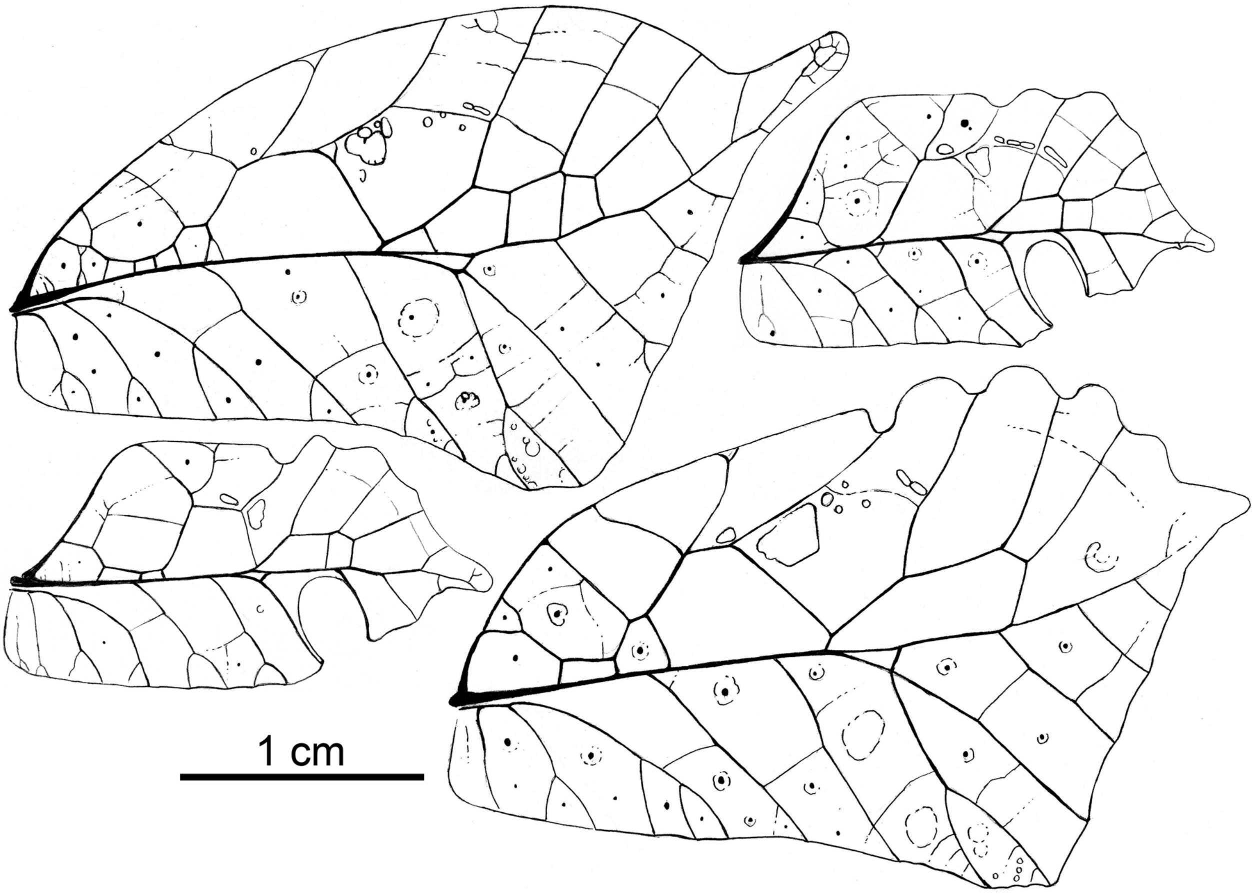

FIGURE 13. *Typophyllum erosifolium*: left tegmina of large females and small males (female cbt001s03, male -s10, female -s09, male -s07).

FIGURE 14. *Typophyllum erosifolium*: female, ovipositor is usually concealed between the tegmina (cbt007s03).

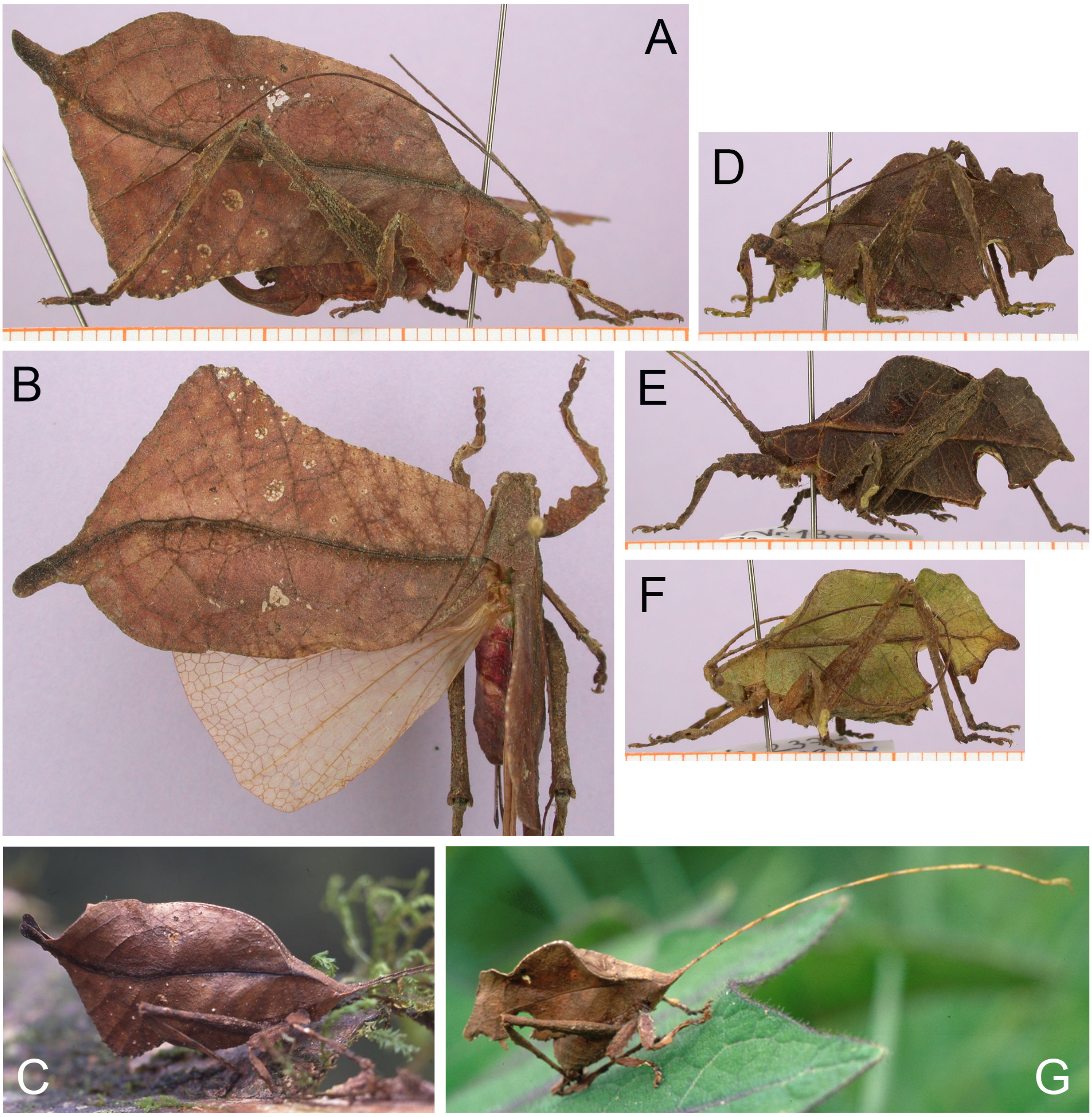

FIGURE 15. *Typophyllum erosifolium*:.**A**,**B**,**C.** female, lateral and dorsal view, and alive (cbt001s03); **D**,**E**,**F.** males with different coloration in lateral view (-s08, -s04, -s07); **G.** live male with complete antennae (-s01); photos of pinned specimens to scale, photos of live individuals staged during day.

Description. The internal tympanal chamber walls are expanded, extending well beyond the dorsal surface of the fore tibia, placing this species in the third group according to Vignon (1925a). Apart from the general shape of the sexually dimorphic tegmina (Fig. 13) there are no really disctinctive characters. Of the six females found in the area, five have tegmina with uniform anal margin, whereas in one the distal portion is undulated. In males the anal margin is undulated to varying degrees, and there is a deep distal emargination of the costal margin which almost reaches the radial vein. In the male holotypes of *T. curtum* and *T. mutilatum*, the only remaining species in the third group, this emargination is fairly far separated from the radial vein (photos in OSF). In females the pronotum has two elongated tubercles at the anterior margin, each located about one forth of pronotum diameter from the lateral edge, and in the middle of the posterior margin there is sometimes a small, basally fused two-tipped process. The speculum of the right tegmen in males is fairly stiff, whitish, and barely translucent. The prosternum has no spines, the lateral tips of the mesosternm are developed as delicate spines (almost twice as long as distal width of maxillary palp), and the metasternum has more robust spines of about the same length.

Coloration. Variable, light of dark brown, sometimes greenish or almost completely green (Fig. 15). The dorsal surface of the middle tibiae can be white in the lower half. One female had small white tubercles on the tegmina (Fig. 15C), which became dark after death. Another female had extensive whitish spots (Fig. 14). Especially the tegmina are distinguished by numerous tiny accessories that perfect the resemblance to a real decaying leaf, like transparent parts imitating holes, microscopic dark and whitish tubercles resembling small fungi, bright lichenous marks, or greenish parts as if there grew moss.

Measurements. Tegmen length in males 15–19 mm and in females 28–36 mm, hind femora in males 12–13 mm and in females 15–17 mm (in *T. peruvianum* 21 mm according to the description and missing in the holotype, tegmina 32 mm).

Acoustic behaviour. This species calls unwearily, sometimes many minutes without interruption. The pulse length usually is about 55 ms (ranging from 50 to 70 ms depending on the individual) and the intervals between the pulses last alternately 160 and 400 ms at 19°C, or 230 and 670 ms at 16°C in the natural habitat. The frequency spectrogram shows a very narrow peak at 18–19 kHz and very small peaks of the harmonics at 37 kHz and 55–56 kHz (Fig. 19D). While individuals can be heard over fairly long distances using a bat detector, with the unaided human ear the song is perceivable over only 1–2 m in the forest to a few meters in a quiet room, reminding of some very tiny machine in need of lubrication. Calling begins with the short equatorial dusk and the males mostly sit rather low in the vegetation, apparently up to 3–4 m. Within the range of this species in the well-investigated Reserva Biológica San Francisco, listening at night with a bat detector, very rarely more than one calling male was heard from a particular spot, and mostly none. This indicates a very low population density. At the sites Bombuscaro and Alto Nangaritza this species was never heard, despite extensive listening.

Mating behaviour. One male (cbt001s05) was found at night riding laterally on the wings of a female (cbt001s04), the whole ensemble sitting on the flower of a species of Solanaceae. This indicates that this little walking leaf shares the curious piggyback-behaviour typical of the genus *Typophyllum*, described above for *T. egregium*.

Distribution. Eastern slope and foothills of Andes in southern Ecuador and Amazon region of northern Peru. The conspicuous calling song of this little walking leaf allowed an assessment of its altitudinal distribution range in the San Francisco and Sabanilla river valleys (Fig. 20B). There it occurs up to 2100 m inside the forest, especially in vales and ravines, although never close to flowing water that would drown its song in broad-band ultrasound noise.

Typophyllum vignoni sp. nov.

(Fig. 16)

http://lsid.speciesfile.org/urn:lsid:Orthoptera.speciesfile.org:TaxonName:470367

Etymology. Dedicated to the French biologist Paul Vignon (1865–1943), specialist of “sauterelles-feuilles” and author of 50 species and varieties of “Ptérochrozées”. He is also renowned for his investigations on the Shroud of Turin.

Examined specimen. Male holotype cbt007s02, Alto Nangaritza, 1300–1350 m, 7 April 2009, leg. Elicio Tapia, deposited in the Museo de La Plata, Argentina [erroneous species code cbt007 refers to *T. erosifolium*].

Notes on two similar species: The male specimen resembles to a certain degree the unique male holotypes of the two remaining species in the third group (aside from the preceding *T. erosifolium*), *T. curtum* Vignon 1926 and *T. mutilatum* Walker 1870, which are mutually very similar (photos in OSF). In the *T. curtum* specimen the emargination of the costal margin of the tegmina is fairly narrow, U-shaped, with the contour distally almost parallel. In the *T. mutilatum* specimen this diagnostic emargination is much broader, with distally diverging contour. In addition, the costal margin of the tegmina is almost parallel to the main veins (Subcosta+Radius), whereas in the *T. curtum* male costal margin and radial vein are diverging (this is true despite that the costal area is basally slightly bent in the expanded left tegmen). So the two males described as *T. curtum* from “Cumbasi”, probably Distrito San Roque de Cumbaza in northern Peru, and *T. mutilatum* from Tefé (in description under old name Ega), some 1300 km to the east in northwestern Brazil, could in fact belong to two different species.

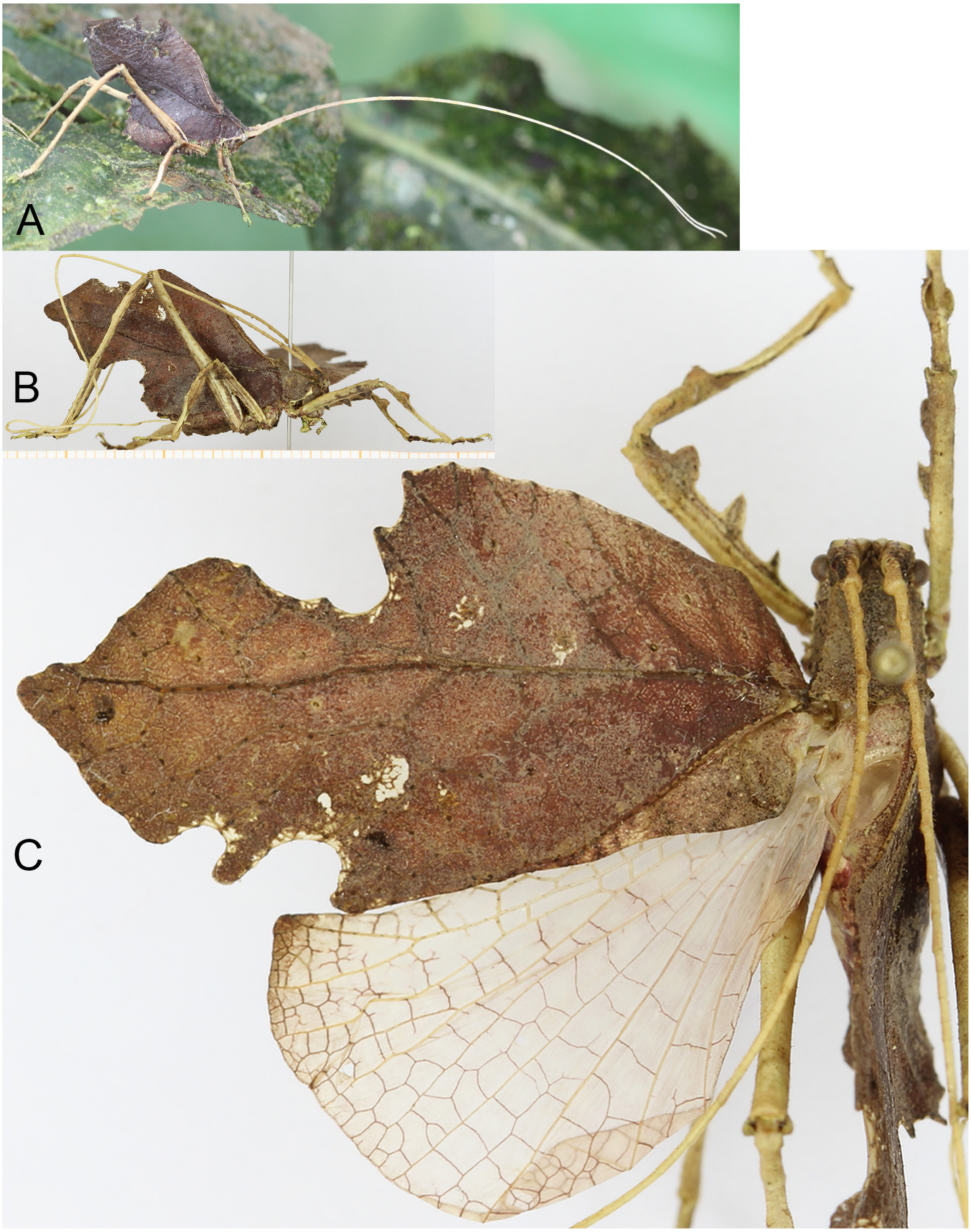

FIGURE 16. *Typophyllum vignoni* **sp. nov.**: male holotype (tegmen length 26 mm).

Description. The internal tympanal chamber walls are conspicuously expanded (Fig. 16B,C), as is diagnostic for the third group according to Vignon (1925a), a character shared with the usually somewhat bigger species of *Mimetica*. In tegmina of *Typophyllum* the first big cubital cell at the base of the anal area borders on the big cell located at the Rs origin, while in *Mimetic*a these cells are separated (Vignon 1931, Beier 1960), or touch in a single point in males. In the male found in the Alto Nangaritza valley these cells share a common border along 2.5 mm. It is considerably bigger than the *T. curtum* and *T. mutilatum* specimens: tegmen length 26 mm vs. 14.5–17 mm (Vignon 1925a, Beier 1960—the "17 lines" in the original description of *mutilatum* must be wrong according to detailed measurements by Vignon, who apparently inspected this specimen). The most obvious difference to these two species and all other *Typophyllum* males are the two emarginations in the distal half of the anal margin of the tegmina (Fig. 16C). Only the male of the otherwise very different *T. bolivarí* has there also deep emarginations (photos of holotype and additional males in OSF). But the contour of this part of the tegmina as well as the development of its tip (pointed in contrast to *curtum* and *mutilatum*) could be variable, as is shown here for females of *T. egregium*, *T. morrisi* **sp. nov.** and *T. erosifolium*. However, no such variation was found in males. The legs are considerably longer and more slender as in other species, and the spines on fore and middle femora are much more separated. The speculum on the base of the right tegmen is fully transparent. Spines on prosternum are very small, much shorter than the width of the tip of the maxillary palp, meso- and metasternum bear spines that are slightly longer than this comparative measure.

Coloration. The only specimen is dark brown with light brown legs and antennae, a light spot behind each eye continues into a thin light anterio-ventral margin of the lateral lobe of the pronotum. The palps are light greenish.

Measurements. Tegmen length in male 26 mm, hind femora 18.5 mm.

Distribution. Only known from type locality on the Cordillera del Condor near the border with Peru, Alto Nangaritza, above Las Orquídeas.

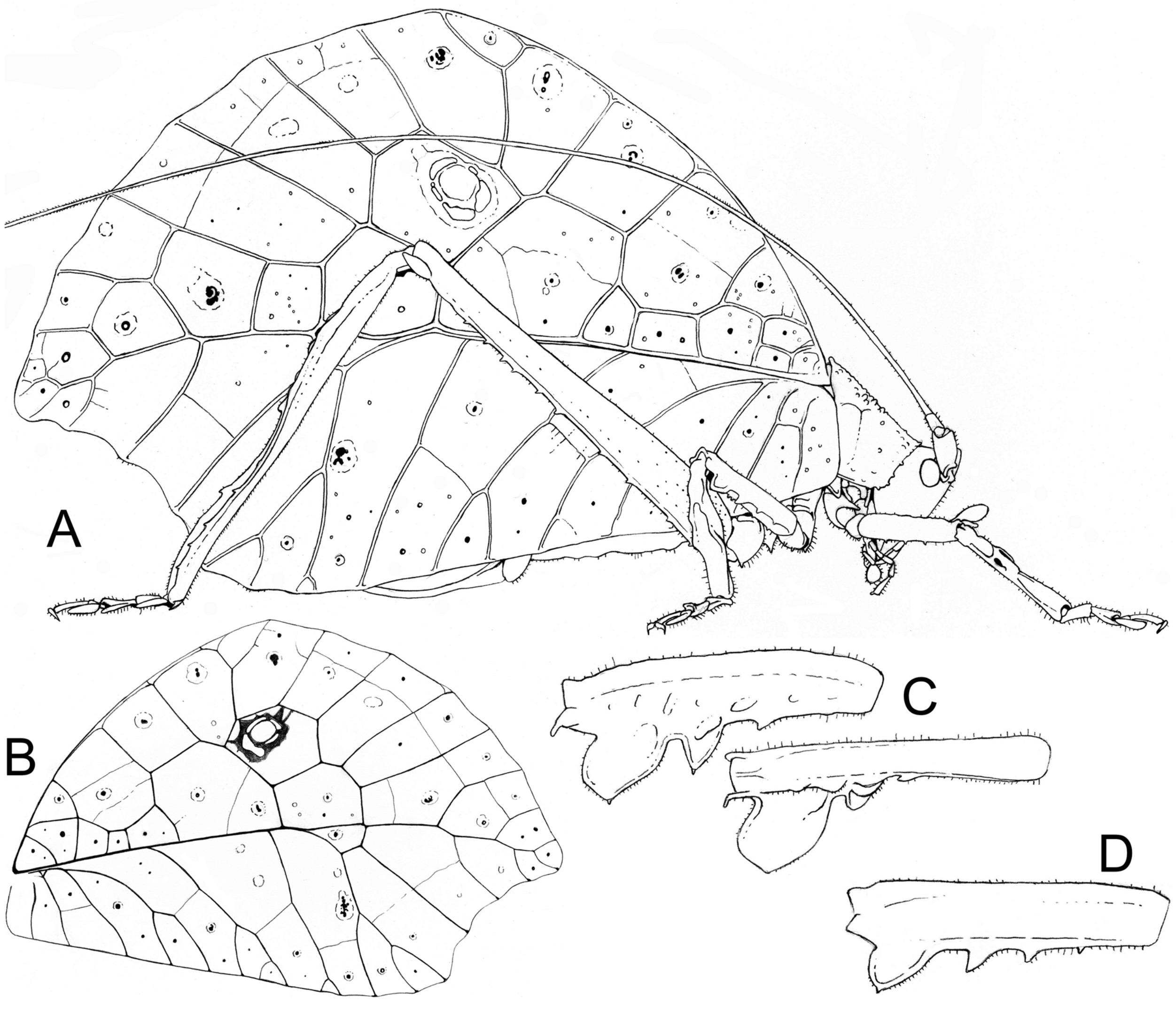

FIGURE 17. *Typophyllum mortuifolium*: female, **A.** habitus (tegmen length 36.5 mm); **B.** left tegmen; **C.** right fore femur in dorso-lateral and dorsal view; **D.** right middle femur, lateral view (cbt006s01).

***Typophyllum mortuifolium* Walker 1870**
(Figs. 17, 18)

Typophyllum lunatum Pictet 1888 (syn. in Xiberras & Ducaud 2014b)
http://lsid.speciesfile.org/urn:lsid:Orthoptera.speciesfile.org:TaxonName:5471
T. mortuifolium: Walker 1870: 466 (*T. mortuifolia*), Kirby 1906: 350 (*Mimetica mortuifolia*), Vignon 1925a: 277, Vignon 1931 (*T. mortuifolia*): 143, Beier 1960: 369, Leroy 1985: 1063 (*T. mortuifolia*), Morris *et al.* 1989: 233, Xiberras & Ducaud 2014b: 228; *T. lunatum*: Pictet 1888: 27, Vignon 1925a: 279, Braun 2008: 220, and other references.

FIGURE 18. *Typophyllum mortuifolium*: female, lateral view (cbt006s01).

Examined specimens: female cbt006s01, Reserva Biológica San Francisco, 1810 m, 8 May 1999 (sitting on a fern leaf); female cbt006s02, Alto Nangaritza, 1300–1430 m, 9 April 2009 (collected as subadult), both leg. H. Braun; photo of male from Maralí, 820 m (May 2012, A. González); three specimens borrowed from University of Michigan Museum of Zoology: male from Ecuadorian Amazon: Pompeya, island at Napo Jivino river junction (Provincia de Orellana), May 1925, leg. L.E. Peña; male and female from central Peru: Dept. Huánuco, Tinga María, 650 m, 7 April 1963, leg. T.H. Hubbell & L.E. Peña (photos of additional UMMZ specimens in OSF).

Description. The only remaining member of fourth group according to Vignon (1925a), characterized by radial vein of tegmina slightly curving downward from base to tip (or forward when spread). In both sexes the tegmina have a shallow distal emargination at the lower margin. Females often bear a ring of transparent patches in the costal area (Fig. 18). In the smaller males the dorsal (anal) margin is much more curved than in females (photos in OSF). The speculum is translucent. In the only female specimen found as adult in the investigation area, the large distal spine of the fore femur is lobiform and almost perpendicular (Fig. 17A,C), which seems to be an abnormal state. Usually it is more spiniform and directed ventrally like the other spines. The prosternum is spineless, meso- and metasterum bear small spines.

Coloration. Light green, legs sometimes light brown, tegminal margin at distal emargination as well as margin of transparent windows in tegmina brownish.

Measurements. Tegmen length in males 20–25 mm and in females 34–39 mm, hind femora in males 14–16 mm and in females 19–26 mm.

Acoustic behaviour. Producing squeaky chirps in the audio range, which can be repeated over several minutes without pause (Morris *et al.* 1989). Individual chirps consist of two sustained sinusoidal pulses, and the spectrum shows a very narrow peak at 9.4 kHz (op. cit.).

Mating behaviour. Also performing precopulatory riding of the smaller male on the female, sitting sidewise on one tegmen, as in the other species (Nickle & Castner 1995c, photo by R. Oelman).

Distribution. Andean foothills and Amazon region of Colombia, Ecuador, Peru, and northern Brazil. Based on acoustic records very common in the Ecuadorian Amazon (Morris *et al.* 1989).

Discussion

Delimitation difficulties of *Typophyllum* species and additional synonymies. The clandestine mode of life of the little walking leaves is reflected in their complicated recognisability in taxonomic literature. The only really diagnostic morphological feature of most *Typophyllum* species is the shape and the venation of the tegmina. However, due to the sexual size dimorphism, the small males have much less area for the venation network compared to the considerably larger females, so that branching plan and proportions of enclosed cells are totally different between sexes. Within both sexes of a particular species the venation bauplan shows some variability. Only the males usually show a distinct pre-apical emargination in the costal margin (the lower margin of the tegmina). The contour of this emargination underlies very little intraspecific variation and can be considered diagnostic for each species. In females the apical portion of the anal margin (upper margin in folded wings) can be either uniform or undulated. Among the six collected females of *T. erosifoilum* five have a uniform tegmen margin, whereas one has a series of emarginations near the tip. In females of *T. morrisi* **sp. nov.** undulated tegmina seem to be the common state: among the five collected females only one has a uniform margin. In both males and females of *T. trapeziforme* the anal margin can be either uniform or undulated (Xiberras & Ducaud 2014b). The length of the elongated tegmen tip in females is also variable (Xiberras & Ducaud 2014a). On top of all this intraspecific variation in shape comes the colour polymorphism, taken to extremes by *T. egregium* (Fig. 1). One early description of a species of Pterochrozinae mentions green and dark brown morphs among five females of *Mimetica pehlkei* (Enderlein 1917). Also for *M. mortuifolia* are mentioned specimens with different coloration (Vignon 1931, Beier 1960). Discontinuous colour variants were then explicitly described for *Typophyllum trigonum*, *T. bolivari*, *Roxelana crassicornis* and *Pterochroza ocellata* (Castner & Nickle 1995b). In particular the latter species exhibits a great spectrum of colour variants. This was demonstrated by breeding experiments (Xiberras & Ducaud 2004), evidencing the synonymy of the last five at that time valid species names of this now monospecific genus, described additionally under 12 synonym names (Eades *et al.*).

The most obvious problem is to bring together individually collected or photographed males and females of a particular species, which usually look completely different to each other. Vignon synonymized his species *Typophyllum deforme* Vignon 1925, based on a female holotype, under *T. mutilatum* Walker 1870, based on a male holotype, when he learned that both specimens were found in copula (Vignon 1926b, photos of both specimens in OSF). Likewise, by means of individuals found in “piggyback position” in the forest, as well as observed mating of individuals in captivity, could be confirmed the conspecificity of males and females in *T. erosifolium* and *T. egregium*. Two other species can be recognized by a distinctive character shared by males and females: *T. morrisi* **sp. nov.**, the only species of little walking leaf found in the Bombuscaro area (apart from a nymph of *T. erosifolium*), has a distinctive drop-shaped dorsal process in the middle of the hind tibia (Fig. 5B), whereas *T. onkiosternum* **sp. nov.** has long and curved spines on the metasternum, not known from any other *Typophyllum* species.

Based on these considerations four additional species names are synonymized here, so that the genus will include 34 valid species. Only 12 of them are known from both males and females, while 9 are known from males only, and 12 from females only. Certainly still more species have been described under different and currently valid names (e.g. *T. scissifolium* Walker 1870 and *T. flavifolium* Saussure & Pictet 1898 from Venezuela look indistinguishable). The focus of this study is restricted to western South America though, otherwise it might never get finished and its author would go insane.

Typophyllum inflatum **Vignon 1925**

T. gibbosum Vignon 1925 **syn. nov.**
http://lsid.speciesfile.org/urn:lsid:Orthoptera.speciesfile.org:TaxonName:5502

T. inflatum: Vignon 1925b: 446, Vignon 1931: 129, Beier 1960: 362; *T. gibbosum*: Vignon 1925b: 448, Vignon 1931: 130, Beier 1960: 262.

First group according to Vignon (1925a). *T. inflatum* is described from a female holotype, along with a male holotype as variation *minor*, that subsequently became syntype or allotype of *inflatum* (Vignon 1931). *T. gibbosum* is known from a unique female. All three specimens (photos in OSF) are from Chiquitos in eastern Bolivia (Departamento Santa Cruz). The only difference between the female types is the dimension of the postmedian dilatation of the costal margin of the tegmina. In *gibbosum* it is more pronounced. However, the degree to which the costal margin is dilated is variable, as shown by 12 female specimens from Iguazú National Park in northeast Argentina, where *T. inflatum* has recently been found (Braun in prep.). *T. abruptum* Brunner von Wattenwyl 1895, described from a slightly smaller female from Bolivia, is also very similar (photos in OSF). It has tegmina with a distally undulated anal margin, a condition not found among the Iguazú specimens. So it seems advisable to wait with a possible synonymization until more specimens from Bolivia become available.

Typophyllum trigonum **Vignon 1925**

T. quadriincisum Vignon 1925 **syn. nov.**

http://lsid.speciesfile.org/urn:lsid:Orthoptera.speciesfile.org:TaxonName:5516

T. trigonum: Vignon 1925a: 262, Vignon 1930: 427, Vignon 1931: 123, Beier 1960: 358; *T. quadriincisum*: Vignon 1925a: 265, Vignon 1930: 427, Vignon 1931: 124, Beier 1960: 358.

Also first group. The female holotype of *T. trigonum* from north-western Brazil (Amazonas) has tegmina with uniform margins (the paratype from the Loreto Region in northern Peru apparently as well). The female holotype of *T. quadriincisum* from northern Peru (also Loreto Region) shows identical tegmen shape and venation, except for the eponymous four emarginations near the tip (photos of both specimens in OSF).

Typophyllum lacinipenne **Enderlein 1917**

T. undulatum Caudell 1918 **syn. nov.**

T. acutum Vignon 1925 **syn. nov.**

http://lsid.speciesfile.org/urn:lsid:Orthoptera.speciesfile.org:TaxonName:5490

T. lacinipenne: Enderlein 1917 (*T. lacinipennis*): 19, Vignon 125a: 270 (*T. lacinipennis*), Vignon 1931 (*T. lacinipennis*): 135, Beier 1960: 365; *T. undulatum*: Caudell 1918: 53; Vignon 1925a: 269, Vignon 1930: 427, Vignon 1931: 134, Beier 1960: 365; *T. acutum*: Vignon 1925a: 270, Vignon 1931: 135, Beier 1960: 365.

Second group acording to Vignon (1925a), with basally broadened hind tibiae. All three described from unique females (photos in OSF). *T. lacinipenne* with mostly green tegmina is from central Bolivia (Provincia Sara). *T. undulatum* from central Peru is brown, slightly smaller, and has the anal margin of the tegmina distally undulated. The specimen of *T. acutum*, also from central Peru (Pozuzo), with distally slightly undulated tegmina, is yellowish brown and was perhaps greenish in life. Since there are only marginal differences, it does not seem very reasonable to maintain three different names. Hopefully the corresponding males will be discovered soon.

The songs. With the calling songs of four species added here, there are now documented the songs of eight or nine *Typophyllum* species: *T. bolivari*, *T. mortuifolium*, *T.* sp. nr. *trapeziforme* (Morris *et al.* 1989, the latter could be *T. morrisi* **sp. nov.**), *T. zingara* (Montealegre & Morris 1999), *T.* sp. (Morris & Montealegre 2001), *T. egregium*, *T. erosifolium*, *T. morrisi* **sp. nov.** and *T. onkiosternum* **sp. nov.** (this work, Fig. 19). From two other species of Pterochrozinae the songs are known as well: *Mimetica incisa* (Morris & Beier 1982) and *Cycloptera arcuata* (Braun 2002, recordings in OSF). In all species the spectrum of the carrier frequencies is extraordinarily narrow, in some species composed of almost pure sine waves. In the large *Cycloptera* male the peak is at 10 kHz, and in *M. incisa*, with the male about the size of the females of small *Typophyllum* species (27–29 mm tegmen length, Vignon 1931), 14 kHz. In the so far studied *Typophyllm* males the fequency ranges from 9.5 to 23 kHz, with the smallest species calling at around 20 kHz, which is slightly above the boundary to ultrasound. In these species only very close to a calling male a faint sound is audible to the unaided ear, possibly rather a suppressed fundamental frequency than low-energy components close to the real carrier frequency. With an ultrasound detector, calling males can be heard over fairly long distances. Provided that the females can hear equally well, these maximum broadcast distances probably cover more than the range a phonotactically approaching female can move in one night through understory vegetation.

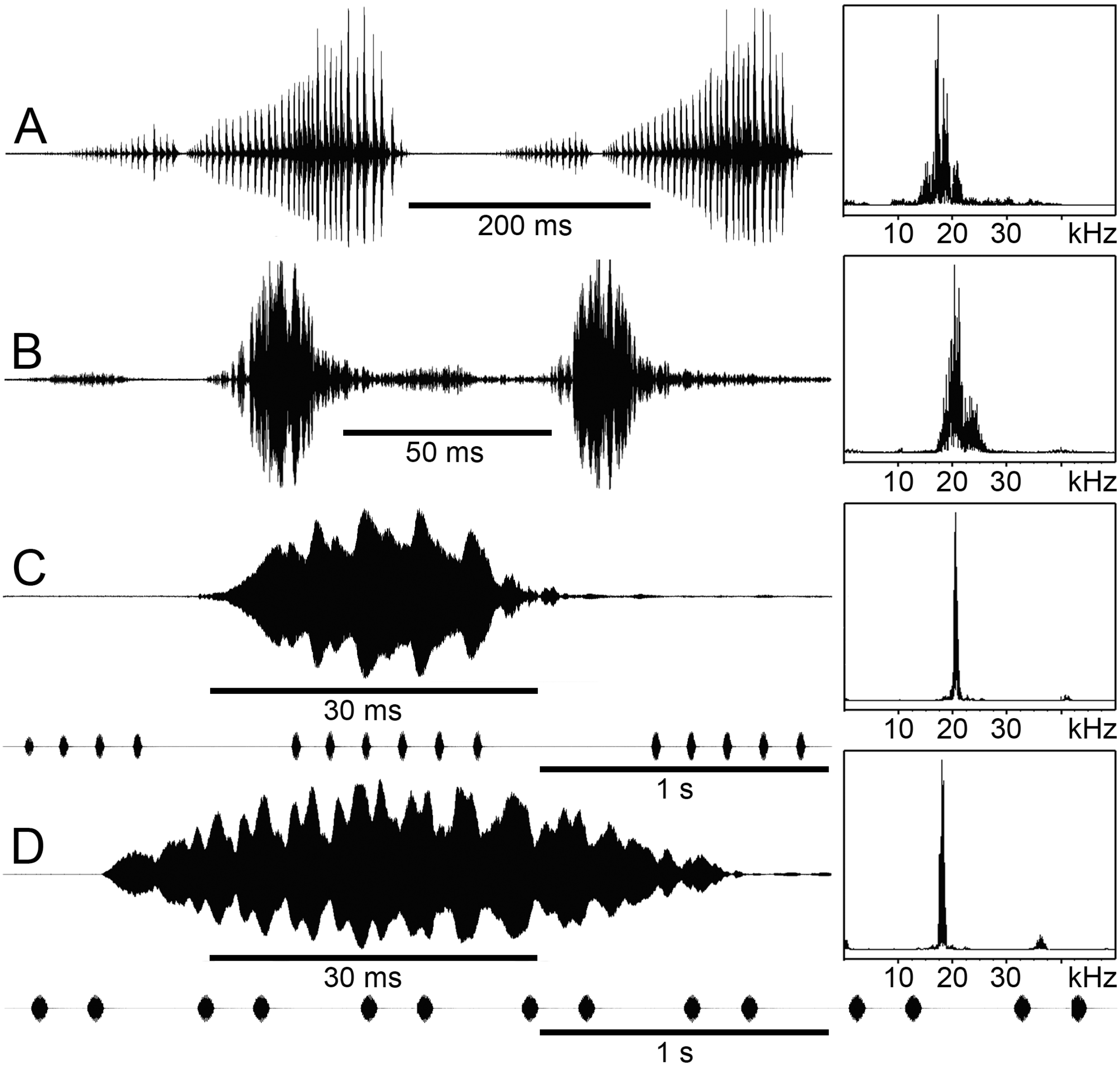

FIGURE 19. Oscillograms and linear spectrograms of calling songs of four *Typophyllum* species: **A.** *T. egregium*, complete call (field recording, 9.5°C, specimen cbt002s21); **B.** *T. onkiosternum* **sp. nov.**, one double pulse of longer sequence (cage, 18°C, cbt004s01); **C.** *T. morrisi* **sp. nov.**, one pulse and below complete call, here consisting of three pulse groups (cage, 23°C, cbt003s01); **D.** *T. erosifolium* one pulse and below seven double pulses from continuous calling (cage, 20°C, cbt001s01); all recordings made at night.

A somewhat broader carrier frequency spectrum show the partly audio-range *T. egregium* and the ultrasonic *T. onkiosternum* **sp. nov.** (Fig. 19A,B). The distribution of *T. egregium* reaches up to almost 3000 m (Fig. 20A), where it lives in patches of low elfin woodland (Fig. 21A). *T. onkiosternum* **sp. nov.** is known from very few indivudals that were found around 2150 m. The species that produce pure tone songs, like *T. erosifolium*, *T. bolivari* and *T. mortuifoium*, all occur in lower elevations, where the trees are high and the understory vegetation is relatively sparse. With increasing elevation, the density of the understory vegetation increases as well, whereas the size of the trees decreases. A similar correlation with habitat structure, that open-habitat species produce songs with a broader spectrum, is reported for birds (e.g. Bertelli & Tubaru 2002). Forest bird songs tend to be more pure tone, probably due to a comparatively stable atmosphere, which permits selection to favour mechanisms to increase the sound intensity (Morton 1975). By concentrating all the energy on a very narrow frequency band, the transmission range can be maximized (Wiley & Richards 1978). This may be also important for the sparsely distributed forest-dwelling katydids. Broad-band songs might evolve as an adaptation for distance ranging by differential degradation of higher versus lower frequencies in dense vegetation (Montealegre & Morris 2004). This could be particularly important for females of *T. egregium* in the upper range of the species, where its habitat comprises patches of elfin forest. These are fairly fragmented and separated by areas with low vegetation of a small bamboo species and terrestrial bromeliads, which provide little protection against the harsh weather conditions. So it could be hazardous to approach a male calling from too far away.

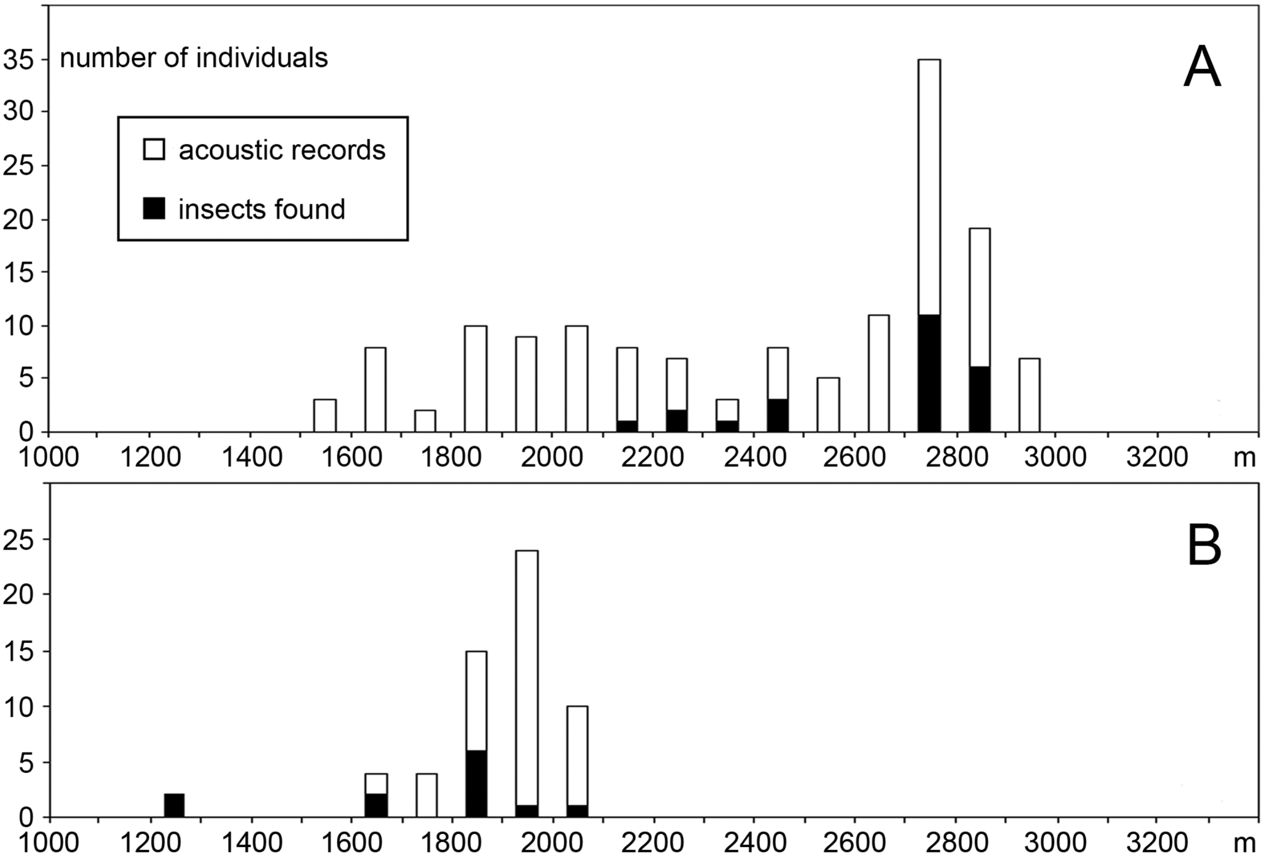

FIGURE 20. Altitudinal distribution of **A.** *Typophyllum egregium* and **B.** *T. erosifolium*; investigated gradient from 1000–3400 m divided in 100-m intervals, acoustic records based on one survey per locality, the two individuals of *T. erosifolium* between 1200 m and 1300 m were found at sites where no calling could be detected (Bombuscaro and Alto Nangaritza).

In males of the species that produce pure tones, the speculum on the base of the right tegmen, that serves to amplify and spread the sound, seems to be rather stiff and is merely translucent (Fig. 7B, photos of *T. morrisi* **sp. nov.** and *T. erosifolium* in OSF). Males of *T. egregium* and *T. onkiosternum* **sp. nov.**, whose songs have a broader spectrum, have a fully transparent speculum (Fig. 4E). This was also found in the neotropical katydid genus *Panacanthus*, with pure tone resonant songs as ancestral state, where in species with non-resonant songs the speculum membranes are glassy and thin (Montealegre & Morris 2004). Such a thin speculum could be more capable of vibrating in intrinsic modes as a result of successive transient tooth-scraper impacts, while the thicker and less transparent speculum of resonant singers is more suitable for a mechanism where the membrane is driven by tooth-contact rate (op. cit.). In males of *T. morrisi* **sp. nov.** and *T. erosifolium* the speculum membrane looks very homogenous and must oscillate uniformly and smoothly between the solid surround. The teeth on the stridulatory file of these two species are microscopically small and very densely packed, compared to the non-resonant *T. egregium*, where they are not so small and tooth density and number are lower. Whereas one male of *T. erosifolium* has almost 300 teeth on its file, a male of *T. egregium* has less than 150.

FIGURE 21. Habitat photos: **A.** at upper distribution limit of *Typophyllum egregium* in Cajanuma; **B**,**C.** understory vegetation and small creek in Alto Nangaritza, in this area were found *T. morrisi* sp. n., *T. erosifolium* and *T. mortuifolium*.

The curious mating behaviour. Pre-copulatory riding of the tiny male on one side of the female's tegmina, as observed in *Typophyllum egregium* and *T. erosifolium*, is also recorded for *T. trapeziforme* (Xiberras & Ducaud 2014b), *T. zingara* (Montealegre & Morris 1999), *T. bolivari*, *T. mortuifolium*, *T. trigonum*, as well as for *Roxelana crassicornis* and *Pterochroza ocellata* (Castner & Nickle 1995a; whereas this is doubtful for the latter species, where the male reaches almost the same size as the female, and which apparently shows a different behaviour— P. Ducaud pers. comm.). In *T. egregium* the riding of the male on the female's tegmina preceded mating, and the two always separated after having accomplished the protracted transfer of the spermatophore. Likewise proceeds *T. trapeziforme*, where the male also rides several days and always leaves the female after mating (P. Ducaud pers. comm.). However, Castner & Nickle (who unfortunately neither assign the behaviour to a certain species nor provide details of their nine field and more than 100 cage observations) report the male remounting the female after mating and resume riding for several hours to several days. This seems to conflict most of the speculations about the adaptiveness of this peculiar behaviour already discussed by the authors themselves (op. cit.).

One possible explanation for the pre-copulatory riding might be associated with the low probability for males and females to meet, due to the low population density, a widely acknowledged feature of arthropods in tropical forests (e.g. Elton 1973, Novotny & Basset 2000). Therefore, one or both partners might for some economical reason not always be disposed to mate immediately. But since the male does not feed while atop the female, he could only reallocate internal resources to produce a spermatophore. The female should not have any problems with receptivity, since adult female tettigoniids have a spermatheca to store sperm until use.

Another potential explanation discussed by Castner & Nickle (1995a), mate-guarding by the male, can probably also be excluded, as the peaceful contiguous riding and subsequent mating of three males with the same female in caged *T. egregium* showed. Furthermore, it does not seem to be necessary because of rarity in the natural habitat—'chance encounters' of male and female (op.cit.) are highly unlikely and the males have to rely on their calling song to bring about a rendezvous. However, if the male should actually resume the piggyback position after mating (op.cit.), it could be adaptive for the pair to stay together. It would save the female future toilsome and possibly dangerous phonotactic approaches, and the male the calling, which might attract predators or parasitoids. But if the probability for the male to attract another female before his previous mate uses up all his sperm is higher than to attract the interest of an eavesdropping bat, he should desert her (or perhaps resume calling atop).

According to another assumption (op.cit.) the female might evaluate the male by assessing his weight. But why should she venture a phonotactic approach at all (calling already can convey information on male quality, e.g. Gwynne 2001), and then carry him around for several days instead of retrieving on the spot a more or less nutritious spermathophore and get rid of him? An instance of a male *T. egregium*, who descended after five days of riding on the female without mating, rather suggests the possibility of the male assessing the female.

Possibly the piggyback behaviour of the little walking leaves is one facet of their sophisticated crypticity (see next section). Castner & Nickle (1995a) already presumed that a male sitting on the wings of a female might foil the search image of predators. But perhaps it is the female alone who obliges the male to ride on her. If the curious ensemble attracts the attention of a predator despite its camouflage, the small male 'sitting on a leaf' is spotted first, while the female can escape. For instance in stick insects survival of females can improve considerably with dorsally coupled males (Sivinski 1983). Probably the time the male can spend riding (up to five days in *T. egregium*) is limited by starvation, unless he descends from time to time to feed.

Likewise mysterious as the reason for this behaviour remains presently the question whether the sexual size dimorphism in *Typophyllum*, which is extraordinarily pronounced for a katydid, might be an adaptation to it. This seems to be the case in certain stick insects with prolonged mating, were the female carries around the smaller male. In those species the sexual size difference is especially distinctive (Sivinski 1978, 1983).

Why are the little walking leaves so leaf-like? Already early orthopterists were intrigued by the perfection of mimetism in which the Pterochrozinae excel. While the tegmina with their venation are predestined for the imitation of a leaf, as many other katydid species apparently use as simple camouflage, the little walking leaves additionally exhibit various details that mimic a real separate leaf in various stages of decay. These include tiny transparent windows, brownish patches and margins in otherwise green individuals, undulated or excised margins, light greyish spots, and minute whitish or dark tubercles—all even through a stereomicroscope looking like real holes caused by small herbivorous insects, necrotic spots, lichens, or fungi. In the larger females the dorsal edge of the tegmina is sometimes slightly twisted, so that in dorsal view the midline of the tegmina is s-shaped, just like a withered leaf. Brown body parts sometimes are partly green and "mossy". Nymphs, that cannot mimic a leaf due to the undeveloped tegmina, frequently have light green and ramified processes on the abdominal tergites, that look like real moss (Figs. 9B, 11C). The antenna tips are often curled (Figs. 11D, 15G, 16), reminiscent of a tiny vine, as in other camouflaged katydids, like the little lichen dragon *Lichenodraculus matti* (Phaneropterinae, Dysoniini), that was also found in the investigation area (Braun 2011).

Back in 1894, the eminent orthopterist Brunner von Wattenwyl considered these numerous details as exuberance and an effort far in excess of the necessary, which could not be attributed exclusively to natural selection. Vignon (1925a) concurred with this view and thought the luxury of accessories to be rather contrary to real mimetism. Still in his fine and beautifully illustrated monograph (1931) he came to the conclusion that the detailed resemblance to decayed leaves, or leaves apparently mined or eaten by caterpillars, was useless, his reason being that other species with the much simpler likeness to uninjured leaves are able to hold their own in the struggle with greater success, as shown by their comparative abundance. He considered the details as a decoration unnecessary in the life of the insects, a multiform comedy, mimetism and aesthetics being two aspects of a sole mystery. In contrast Karny (1914) already assumed that to deceive sharp-eyed insect-feeding birds it requires an imitation of the leaf in colour and shape up to the smallest detail. He still entertained some doubt that selection alone was sufficient for such crypticity and contemplated Lamarck's (1809) theory of active acquisition of useful traits.

The different birds of mixed species flocks in the investigation area actually searched very meticulously bark, foliage, bromeliads and other epiphytes, including all sorts of crevices and possible hiding places of arthropod prey (pers. obs.). Since the little walking leaves furthermore come in multifarious outfits (as shown particularly in *T. egregium*), it becomes even more difficult for birds as the main visual predators to develop a search image, a term introduced by Tinbergen (1960). Such polymorphism in colouration has been recorded in a variety of cryptic prey species (Bond & Kamil 2002 and references therein) and is shown to be the potential outcome of frequency dependent selection (op. cit.), since predators have to allocate their attention economically (Dukas 2004 and references therein). The underlying mechanisms are complicated and not fully understood (Gray & McKinnon 2007). Through the piggyback behaviour males and females stay together during day and can perceive colour, so even some sort of "assortative" mating is thinkable. The little walking leaves held in cages did not choose their daily roosting places according to their own colour, although differently coloured substrates were available, not confirming observations for *Mimetica mortuifolia* (Bellwood 1988), but consistent with other observations (Castner & Nickle 1995a). And why should a little leaf as an object of its own have the same colour as the background anyway?

In the investigation area the little walking leaves were quite rare. This fits into an additional line of reasoning (Hochkirch 2001): a high predation pressure combined with habitat stability might favour individuals that invest in high life expectancy (a *T. erosifolium* male caught as adult lived for nine more months, calling almost every night) and produce small clutches (one egg per site in unspecified Pterochrozinae, Caster & Nickle 1995a), therefore, do not have to feed and move much. The resulting low reproduction rate would explain the low population density, which in turn complicates prey specialization by predators. Low population densities also affect evolution. Speciation might be accelerated by rarity, small distribution areas and low dispersal abilities (Chown 1997). The underlying (and controversial, op.cit.) logic concerns gene flow, which tends to prevent speciation in abundant species with broad distribution areas (Mayr 1963, Stanley 1979). Similar predictions make the theory of shifting balance (Wright 1931, 1977, Eldredge 1985, Holt 1997). The potentially creative role of random genetic drift permits small populations to move between adaptive peaks, while in large populations adaptive evolution is less likely and they are in some measure evolutionary inert because of gene flow.

These merely indicated mechanisms might have contributed to the extraordinarily perfect imitation of tiny leaves, including all the microscopic accessories like factitious fungi cultures on the tegmina. If the tropical diversity is not already very old compared to temperate regions, then the speciation rate must be especially high (e.g. Chown & Gaston 2000). Additionally the predation pressure in the tropics is thought to be higher than in temperate ecosystems (Hawkins *et al.* 1997 and references therein), probably again as a result of rarity of potential prey species.

Where did the walking leaves originate in the tree of life? A recent molecular phylogeny of Tettigoniidae includes a remarkable result: a clade consisting of *Mimetica tuberata* from Costa Rica and *Typophyllum* sp. from Peru is found to be a sister group to all other katydids (Mugleston *et al.* 2013). Traditionally the group was mostly treated as tribe Pterochrozini within Pseudophyllinae (e.g. Beier 1960), sometimes as subfamily (e.g. Gorochov 2012, there under subfamily group Pseudophyllidae), and it was proposed to place it directly under Tettigoniidae (Braun 2015). One indication that the Pterochrozinae might be unrelated to Pseudophyllinae is the development of the non-functional stridulatory file on the right tegmen. It appears as an unsclerotized and inconspicuous vestigial copy of the functional one on the left tegmen, like in all other subfamilies investigated regarding this character, except for the true pseudophyllines, that typically have it completely reduced (Chamorro-Rengifo *et al.* 2014). However, another characteristic share *Typophyllum* species and Pseudophyllinae: The functional file is located all along a fairly massive cubital vein that projects basally beyond the lower tegmen surface. Another indication for an early phylogenetic origin is the pure-tone resonant stridulation, which is thought to represent an ancestral character state in katydids (Montealegre-Z. & Morris 2004, Montealegre-Z. 2009). Future studies on katydid phylogeny will hopefully substantiate how long ago these fascinating insects did branch off.

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