

1 **Wing resonances in a new dead-leaf-mimic katydid**
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3 **(Tettigoniidae: Pterochrozinae) from the Andean cloud forests**
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25 11 Running title: Wing resonances in a leaf-mimic katydid
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Abstract

Day-camouflaged leaf-mimic katydids *Typophyllum* spp. have a remarkable way of evading predators as male and female forewings appear as bite-damaged leaves complete with necrotic spots. As in all other katydids, males produce sound signals to attract females by rubbing their forewings together. The biophysical properties of these special leaf-like forewings remain obscure. Here we study the wing mechanics and resonances of *Typophyllum spurioculis*, a new species of leaf-mimic katydid with a broad distribution in the Andes from Western Ecuador to the middle Central Cordillera in Colombia. This species performs an unusual laterally directed aposematic display, showing orange spots that simulate eyes at the leg base. At night, males are conspicuous by their loud, audible calling songs, which exhibit two spectral peaks at ca. 7 and 12 kHz. Using micro-scanning laser Doppler vibrometry we find the effective sound radiators of the wings (speculae) vibrate with three modes of vibration, two of which include the frequencies observed in the calling song. Remarkably, this resonance is preserved in the parts of the wings mimicking necrotic leaves, which are in theory not specialised for sound production. The eyespot function is discussed.

Keywords: Katydid, Bush-cricket, Mimetism, Stridulation, Resonance

31 **Introduction**

32 Katydid species of the genus *Typophyllum* are masters of camouflage and mimicry. Both
33 sexes exhibit remarkable forewing adaptations, resembling chewed leaves living and dead,
34 with necrotic spots, marginal feeding ‘bites’ or even skeletonized ocellata (Braun, 2015b;
35 Nickle and Castner, 1995). During the daytime, males and females rest on trees and bushes
36 overlooked by diurnal predators. Individuals adopt postures making them almost
37 indistinguishable from the surrounding foliage: the head is applied to a plant branch and the
38 insect’s long antennae projected forward and down along the axis of the same branch (Fig. 1).
39 All known species are nocturnally active, when the males produce loud calling songs to
40 attract females. (Braun, 2015a; Braun, 2015b; Montealegre-Z and Morris, 1999). Females are
41 larger than males and their tegmina are not only comparatively larger, they also differ in
42 venation pattern and shape from the male wings (Braun 2002; Nickle, 1992).
43 During a collecting expedition in 1996 in Ucumarí (Colombian Andean cloud forests, see
44 methods), GKM and FM-Z discovered a male of a curious *Typophyllum* species, which they
45 later briefly mentioned (without description) (Morris and Montealegre-Z, 2001). In the same
46 article they also figure an analysis of its calling song: a spectrum with two maximum
47 harmonically-related peaks at around 7 and 13 kHz. More than 20 years later, FS, AB, and
48 FMZ discovered the same species in the montane forest of Santa Lucía, a cloud forest reserve
49 located in the Pichincha province of Ecuador. The species is very abundant in this locality,
50 with males dominating the audible acoustic space in the nights.
51 Male katydids produce calling songs to attract potential mates by rubbing their forewings, a
52 mechanism known as stridulation (Gwynne, 2001; Robinson and Hall, 2002). A sharp lobe on
53 the right wing (the scraper) is swept upon a vein lined with precisely arranged cuticular teeth
54 on the left wing. A large specular wing cell (adjacent to the scraper) on the right wing, the so-
55 called mirror, subsequently couples the low amplitude vibrations, produced by this initial file-

56 scraper interaction (Bailey and Broughton, 1970; Broughton, 1964; Morris, 1999; Morris and
57 Pipher, 1967; Robinson, 1990) to the air.

58 A particular characteristic of the acoustic signals in the genus *Typophyllum* is that the calls of
59 the males exhibit a very sharp spectrum with high Q and that most species known so far
60 communicate at about 20 kHz (Braun 2002; Braun, 2015a; Braun, 2015b; Montealegre-Z and
61 Morris, 1999; Morris et al., 1989) (Q =quality factor, which describes the properties of a
62 damped resonator or oscillatory system (Bennet-Clark, 1999b). Would the presence of two
63 harmonically related peaks in the call of our new species *Typophyllum spurioculis* (here
64 described) involve two independent resonators in the wings, or could not the same speculum
65 or another wing area vibrate to produce harmonics?

66 In katydids, the stridulatory fields of left and right tegmina are asymmetric. The stridulatory
67 area of the left forewing where the file resides, is usually damped to sound vibration, while
68 that of the right wing is heavily involved in sound radiation (Chivers et al., 2017;
69 Montealegre-Z and Postles, 2010; Sarria-S et al., 2016; Sarria-S et al., 2014). In contrast to
70 katydids, in crickets and grigs (with morphologically symmetric or nearly symmetric wings)
71 both left and right wings contribute more or less equally to sound radiation (Chivers et al.,
72 2016). In theory, the observed wing asymmetry in katydids will affect the radiating sound
73 field, having a negative effect on the output power. In other words, a sound radiator involving
74 symmetric wings is analogous to having two synchronised speakers. Therefore, katydids,
75 having only one functional sound radiator, sacrifice one speaker for sound radiation. Katydid
76 have resolved this problem by developing additional morphological adaptations to amplify
77 their signal (Bennet-Clark, 1998). For example, special wing positions that favour signal
78 broadcasting (Stumpner et al., 2013), wing inflations (Hemp et al., 2013), and exaggerated
79 pronotal extensions that work as resonators (Jonsson et al., 2017; Morris and Mason, 1995).
80 However the wings of male *Typophyllum*, seem not to have special adaptations for resonance

81 (Braun, 2015a; Montealegre-Z and Mason, 2005; Morris et al., 1989). While the effective
82 stridulatory area in the right wing, the mirror, is only a small oval portion of the entire large
83 leaf-like wing (Braun 2002; Braun, 2015a; Montealegre-Z and Morris, 1999), the calls of the
84 male are very loud, suggesting that these insects might use a combination of resonance and
85 subalar space to enhance the call output. The biophysical properties of the wing structure used
86 for camouflage and not involved in sound radiation remains elusive.

87 In this paper we use micro-scanning laser Doppler vibrometry to investigate the wing
88 resonances associated with the production of the species' acoustic signals, and the resonances
89 associated with the wing regions involved in camouflage. We also describe a new species of
90 *Typophyllum*, and document the variation of wing morphology and venation across
91 individuals.

93 **Materials and methods**

94 **Field sampling**

95 Fieldwork was conducted in Colombia, at Parque Regional Natural Ucumarí (5° N, 76° W).
96 This is located in the eastern slope of the Central Cordillera, above the tiny hamlet El Cedral,
97 22 km east from Pereira in the Department of Risaralda. A narrow glaciated valley rises into
98 the montane rainforest over elevations of 1850-2600 m, and high waterfalls enter along the
99 sides. Rainfall is 2000-4000 mm/year and the average temperature 12-18 °C. Insects were
100 collected in 1996 within a few kilometres from el Refugio Turístico La Pastora, some 6 km
101 from El Cedral.

102 We also conducted fieldwork in 2015 in Ecuador, at Santa Lucía cloud forest reserve, located
103 in the heart of the cloud forest on a mountain peak at 1900 metres. Santa Lucía conserves over
104 1800 acres of montane cloud forest in the Chocó Andean Bioregion, a biodiversity 'hotspot'.
105 Santa Lucía is located in the northwest of the Pichincha province, 80 km north-west of Quito

106 (00° 07' 05.9398" N, 078° 36' 37.1403" W). Specimens were localized by their calling song,
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2 107 mostly from trees and bushes along the main trail a few kilometres from the lodge.

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7 109 **Depositories**

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9 110 MEUV = Museo de Entomología, Universidad del Valle, Cali, Colombia.

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11 111 MEUCE = Museo de Entomología, Pontificia Universidad Católica del Ecuador, Quito,
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14 112 Ecuador.

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19 114 **Morphological measurements**

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21 115 Body measurements were obtained with a digital calliper (Fowler, Newton, Massachusetts,
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24 116 USA). All measurements presented are in mm, following the measuring protocols used by
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26 117 Montealegre-Z and Morris (1999). Digital photographs of preserved stridulatory files were
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29 118 taken on a scanning electron microscope (Inspect S50, FEI, Eindhoven, Holland).
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31 119 Measurements of inter-tooth spacing were obtained using CorelDraw X4 (Corel Inc. 2005)
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34 120 using the appropriate dimension tool, for details see Montealegre-Z & Mason (Montealegre-Z
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36 121 and Mason, 2005).

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41 123 **Song recordings**

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43 124 *Field recordings:* In Santa Lucía, Ecuador, four specimens were recorded in the field using a
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45 125 Tascam DR-5 V2, at a sampling rate of 96 kHz. The recorder was placed at 30 cm dorsal to
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48 126 the singing insect. Insects were captured and taken to the lab facility at the lounge, placed in
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50 127 cylindrical cages of metallic mesh (15 cm high x 8 cm diameter), and recorded again using
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53 128 the same recording device, positioned at 30 cm from the dorsum of the singing specimen.

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58 130 *Lab recordings (Ecuadorean males):* In the lab, recordings were performed in a sound-
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60 131 attenuated booth at the University of Lincoln, at a temperature of 19 °C. The specimens were
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132 placed in metallic cages at 10 cm (dorsal aspect) from a G.R.A.S type 40DD 1/8" condenser
133 microphone (G.R.A.S. Sound and Vibration, Holte, Denmark). The microphone was
134 connected to a GRAS type 12AA preamplifier, which was, in turned, connected to a
135 soundboard (USB-6259, National Instruments, Austin, TX), and then to the controlling
136 computer. The microphone was calibrated at 94 dB SPL (re 20 μ Pa), using a Brüel & Kjaer
137 sound level calibrator (Type 4231, Brüel & Kjaer, Nærum, Denmark). Data was stored on a
138 computer hard disk at a sampling rate of 512 kHz. Sound was analysed using Matlab
139 (R2015a, The MathWorks, Inc., Natick, MA, USA).

140
141 *Lab recordings (Colombian male):* Laboratory analysis employed Brüel & Kjaer equipment.
142 A 1/4" (4135) or 1/8" (4138) condenser microphone was connected to a 2606 measuring
143 amplifier or to a 2204 B&K sound level meter. Output from either of these amplifiers was
144 recorded on a Racal instrumentation tape recorder running at 30" /s (Racal Electronics plc,
145 Weybridge, UK). Subsequently, the signals were digitized using either a Keithley DAS50
146 digitizing board (Tektronix U.K. Ltd, Bracknell, Berkshire, UK) or Tucker Davis system II
147 (Tucker-Davis Technologies, Alachua, FL, USA) and then analysed with DADISP software
148 (DSP Development Corporation, Newton, MA, USA). Energy in spectra was only considered
149 significant if it was no more than 20 dB below the most intense peak frequency. Readings
150 were taken on Fast or Impulse/Hold, usually with a distance of 10 cm from the microphone
151 tip to the dorsum of the singer. The long axis of the microphone was normal to the
152 longitudinal axis of the insect and the microphone cover was always on. Temperatures were
153 taken with an Omega HH23 digital thermometer (Omega, Northbank, Manchester).

154 155 **Forewing resonance**

156 Wing resonance was measured in five male specimens using micro-scanning laser Doppler
157 vibrometry (LDV; PSV-500, Polytec GmbH, Waldbronn, Germany). For the experiments, the
158 insect was mounted on a brass platform following the procedure described by Sarria-S et al.
159 (2016). The wings were laterally extended by fixing the axillary sclerites with a 50% mixture
160 of beeswax (Fisher Scientific, Loughborough, UK) and colophonium (Sigma-Aldrich
161 Company Ltd., Dorset, UK). This procedure only tests the natural resonance of the wings in
162 response to sound; it eliminates the effect of the subalar space, and leverage effects of scraper
163 motion upon right tegmen radiators during effective stridulation. The stridulatory area of both
164 tegmina were excited via sympathetic sound stimulation, and scanned with the LDV using
165 800 grid points.

166 In addition, the entire tegminal surface was also scanned to explore potential resonances
167 outside the stridulatory field. Acoustic stimulation consisted of broadband periodic chirps in
168 the range of 2-100 kHz. The spectrum of the stimulus was corrected to be flat (± 1.5 dB) at 60
169 dB SPL at all frequencies. The acoustic signals were generated by the PSV-500 internal data
170 acquisition board (PCI-4451; National Instruments, Austin, TX, USA), amplified (A-400,
171 Pioneer, Kawasaki, Japan) and passed to a loudspeaker (Ultrasonic Dynamic Speaker Vifa,
172 Avisoft Bioacoustics, Glienicke, Germany) positioned 30 cm from the specimen. The
173 reference signal was recorded using a 1/8" condenser microphone positioned horizontally at a
174 distance of 2-3 mm from the wings (Brüel & Kjaer, 4138-A-015 and preamplifier model
175 2670, Brüel & Kjaer, Nærum, Denmark). Laser and sound recordings were all obtained in a
176 sound-attenuated booth (1.8 x 1.8 x 2 m) at approximately mid-day in the animals' light
177 cycle). Laser experiments were done in five males collected in 2015.

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179 **Analysis**

180 For laser measurements of wing vibrations we use FFT (Fast Fourier Transform) with a
 181 rectangular window, resulting in a frequency spectrum for the laser and the microphone signal
 182 with a resolution of 7.5 Hz. The laser and microphone signals were then used to calculate the
 183 gain and phase responses. We integrated the results from all the points scanned across the
 184 wing surfaces (see details above), oscillation profiles and animations of membrane deflections
 185 were generated for the frequencies of interest. For the final analysis we calculated the transfer
 186 function (H1) of the membrane displacement D (nm) to reference sound level (Pa), to produce
 187 the amplitude gain and the phase response of the system at different frequencies. Therefore,

$$H1 = \frac{G_{ab}(f)}{G_{aa}(f)},$$

189 where, $G_{ab}(f)$ is the cross-spectrum of the displacement signal and reference signal, and $G_{aa}(f)$
 190 is the auto-spectrum of the reference signal.

192 Results

193 Taxonomy

194 *Typophyllum spurioculis* sp. nov.

195 See Figs. 1-3

197 *Holotype*: MEUCE 1♂, Ecuador, Pichincha, Nanegal, Reserva Santa Lucía. Collector: F.
 198 Montealegre-Z., July 14-20, 2017. *Allotype*: MEUCE 1♀, Ecuador, Pichincha, Nanegal,
 199 Reserva Santa Lucía. Collector: C. Soulsbury, F. Montealegre-Z., July 14-20, 2017 (see
 200 supplementary figure Fig. S1)

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 202 *Paratypes*: MEUV 1♂, Colombia, Risaralda, PRN Ucumarí, Collectors: G. K. Morris & F.
 203 Montealegre-Z., 25 May, 1996. MEUCE 3 ♂♂ Ecuador, Pichincha, Nanegal, Reserva Santa
 204 Lucía. Collectors: F. Sarria-S & F. Montealegre-Z., Sep, 2014. MEUV 2 ♂♂ Ecuador,

205 Pichincha, Nanegal, Reserva Santa Lucía. Collector: F. Montealegre-Z., July 1-12, 2015.

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2 206 MEUCE 1♂, Ecuador, Pichincha, Nanegal, Reserva Santa Lucía. Collector: F. Montealegre-

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4 207 Z., July 1-12, 2015. MEUCE 1♀, Ecuador, Pichincha, Nanegal, Reserva Santa Lucía.

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7 208 Collector: F. Montealegre-Z., July 1-12, 2015.

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12 210 *Etymology*: The species is named *Typophyllum spurioculis* in token of the pairs of vivid

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14 211 orange maculae on the coxotrochanteral area of pro- and mesothoracic legs on both sides (Fig.

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16 212 1, inset). ‘Spurioculis’ can be translated as ‘with/of false eyes’, i.e., the ‘leaf-mimic with false

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18 213 eyes’ or the ‘False-eyed *Typophyllum*’. It is a combination of *spurius*, meaning false in Latin

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20 214 and *oculus*, meaning eyes in Latin.

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24 216 *Diagnosis*: This species exhibits an orange vivid coloration in the coxal membranes of the

25
26 217 fore and middle legs. The extension of femur and trochanter relative to the coxa exposes this

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28 218 membrane (crescent-shaped) giving the appearance of a pair of "eyes" (Fig. 1A, yellow

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30 219 arrows in inset). In all individuals a small black, blunt protrusion lies on the right and left

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32 220 anterior corners of the coxal spine (Fig. 1A, white arrows in inset).

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36 222 *Description: Head*: Frons extense, considerably flat, occupying half of the head area as

37
38 223 viewed frontal. The other half of the head dominated by clypeus and labrum. *Pronotum*:

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40 224 Pronotal disk campaniform, granulose, with small tubercles abundant in the lateral portions.

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42 225 Posterior margin of the disk bilobulated, about 2x wider than anterior margin; lobes clearly

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44 226 depicted by a medial notch. Disk with a large tubercle in each corner of the distal margin, and

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46 227 two more tubercles (usually smaller than the corner ones) subequally distributed on the sides

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48 228 of the notch.

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229 *Legs:* Fore femora with four spines, forward facing and varying in size (Fig. 2C). Fore coxal
1 spine blunt, in the form of a black large tubercle (Fig. 1A, inset). Smaller spines located
2 230 proximal, larger spines distal, the two distal spines sometimes emerging from a broad cuticle
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4 231 protruding flap. The spines in males are usually very small except for the forelegs. Generally,
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6 232 forelegs and midlegs have 4 and hindlegs have 7-8 spines on the femur. Relatively evenly
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8 233 spaced, backwards facing spines on the dorsal interior edge of the femora.
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12 235 *Wings:* Tegmina of the female (measured from basal to distal) about 1.5x larger than those of
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14 236 the males (Fig. 1A, Table 1). Adult females' wing marks vary from necrotic spots in the
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16 237 wings (Fig. 1) to white large marks that resemble fungal patches (see supplementary figure
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18 238 Fig. S1). These are usually absent in males. Venation patterns in males are variable (Fig. 2A),
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20 239 but a common venation pattern becomes evident across specimens when the wings of several
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22 240 specimens are overlaid (Fig. 2B). Stridulatory file ca. 5 mm long, bearing 160-170 teeth (n=5
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24 241 males, Table 1, Fig. 3). The file shows a peculiar tooth distribution forming 8-10 clear groups
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26 242 of teeth with high density (or shorter inter-tooth distances) alternating with 8-10 groups of
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28 243 teeth with low density (larger inter-tooth distances, Fig. 3AB). This file morphology is neatly
29
30 244 associated with the size (length) of individual teeth. Groups with high density of teeth bear
31
32 245 larger teeth (Fig. 3B).
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34 246 *Abdomen:* Small short pale spines on side of female abdomen. Pale patch with dark border on
35
36 247 side of abdomen is common on several specimens, but not in all. Small medial lappets on
37
38 248 abdominal tergites (probably vestigial moss camouflage from earlier nymph stages).
39
40 249 *Genitalia:* Male subgenital plate small, distally with a shallow sinusoidal notch. Female
41
42 250 subgenital plate with a broad v-shaped notch, the depth of the notch is comparable to a 1/3 of
43
44 251 the plate length. Ovipositor up-curved, dorsal valve with 25-30 serrated distal teeth, ventral
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46 252 valve with 18-22 serrated distal teeth (see supplementary figure Fig. S2). These ovipositor
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48 253 serrations do not occur in nymphs (see supplementary figure Fig. S3).
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254 *Variation:* The right tegmen of the male has a translucent mirror.

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2 255 Small black spots all over body of the female (only a few of the males exhibit this). Spots and
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4 256 holes (transparent parts imitating holes on a leaf) are also highly variable. Small light or dark
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7 257 brown spots tend to appear [in-between](#) tegmen veins. A middle cell in the radial field of the
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10 258 tegmina is commonly affected by a spot or 'hole'.

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12 259 *Colouration:* Highly variable. Most individuals green, others brown/yellow, necrotic patches
13
14 260 highly variable. One individual had an orange/brown head and body along with green legs,
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17 261 antenna and tegmina. Some tegmina are brown with light or dark brown patches, others are
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19 262 green with light brown patches. It is unknown if these patches appear with age. Male hind
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22 263 wings are translucent white with green veins. The tips of the hind wings are tinted green. Legs
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24 264 are usually green but can be brown or a mixture of both (brown individuals can have small
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26 265 yellow patches). Antennae are usually various shades of green, but can also be brown with
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29 266 faint green patches. Dark line from the base of the antenna to the lower mandible, barely
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32 267 visible in some brown males.

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36 269 *Measurements:* see Table 1.

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41 271 *Remarks:* There are 34 species described in the genus *Typophyllum* (Cigliano et al., 2017).
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43 272 We described *T. spurioculis* as a species new to science based on morphological and acoustic
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45 273 evidence; however we suspect this species might be part of a species complex (within
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48 274 *Typophyllum*). We have observed other cloud forest species, which also exhibit the coxal
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51 275 orange eye-spots, and present variable morphology and different calls. But these are so far
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53 276 observations of a few random specimens for which we do not have the acoustic, and
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55 277 mechanical evidence presented here. [The eye-spots are also present in pre-adult nymphs.](#)
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58 278 [However, we do not have data for earlier nymphal stages.](#)

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280 **Bioacoustics**

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2 281 The description of the song is based on the recording of the call of a single male specimen
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5 282 collected in Ucumarí Colombia, and five males from Santa Lucía, Ecuador.
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7 283 *Colombian specimen*: One male was recorded indoors at a temperature of 23 °C, rather high
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10 284 relative to common field temperatures. This male produced three bouts of sibilant four-pulse
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12 285 calls, each comprised of two syllables. In *T. spurioculis*, each syllable consists of two pulses,
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14 286 one produced during the opening stroke of the wing and the other during the closing (Fig.
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17 287 4A). Here, syllables are therefore equivalent to what other authors term phonatomes, and a
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19 288 call of several phonatomes is in turn equivalent to a chirp or verse (compare e.g. Jatho et al.,
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21 289 1994; Stumpner and Meyer, 2001; Walker and Dew, 1972). Five to six calls were given in 3-6
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24 290 s with bouts separated by silence of 17-18 seconds. Mean call duration for this male was 95
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26 291 ms (n=13). There is a consistent pause before the concluding pulse, which usually begins
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29 292 more abruptly. Mean values for the duration of the four high-amplitude pulses in two calls
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31 293 were 23.3, 17.6, 12.3, and 34.3 ms respectively. The waveform (Fig. 4C) shows the
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34 294 characteristic pattern of two harmonically-related subequal carrier frequencies. The call is
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36 295 easily heard by a human ear, being almost entirely in the audio range (Fig 4E). There are two
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39 296 harmonically related spectral peaks of comparable intensity. The more intense is near 12.1
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41 297 kHz while its potential fundamental, 6.8 kHz, is slightly suppressed (mean values for n=13
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43 298 calls, FFT calculated over the whole of each song).
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46 299 *Ecuadorean specimens*: five males from Ecuador were recorded at 17 °C under field
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49 300 conditions using a portable recorder. From this group, two males were also recorded in
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51 301 laboratory conditions at 19 °C in Santa Lucía, Ecuador using the same device. Males of this
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53 302 population also produced groups of calls, each group consisting of four or five calls (each call
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56 303 containing two syllables), and groups are separated by silent intervals of 18.2 ± 4.2 s (Mean \pm
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58 304 SD, n=5, average measured from six random silent intervals of one recording of each male,
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305 for a total of 30 calls, Fig. 5A). From field recordings, specimens delivered 3 to 4 calls in 10
306 seconds; a similar pattern was maintained under lab conditions only when more than two
307 males interacted acoustically. Isolated singing males produced a more sporadic pattern,
308 sometimes producing one call per minute. The average duration of one call (two syllables) of
309 the Ecuadorian males was 117.6 ± 7.1 ms ($n = 5$, 7 calls randomly selected from each male,
310 and averaged, Figs. 4B, 5C). The mean pulse duration of the high amplitude pulse was $31.6 \pm$
311 3.6 ms (Fig. 4B, 5C). The waveform of the pulse also shows similar characteristics to that of
312 the Colombian male, with two dominant frequencies harmonically related (Fig. 4D). The
313 major syllable pulse contains 160-170 oscillations. As measured in the Colombian specimen,
314 the call of the Ecuadorean males also shows two consistent spectral peaks of comparable
315 intensity that are harmonically related. The most intense peak was measured at 13.9 ± 2.2 kHz
316 ($n=5$, 1 random call per male) and its fundamental occurs at 7.0 ± 1.2 kHz (Fig. 4F). Analysis
317 of frequency in time shows an unusual frequency modulation (FM) pattern of the two pulses
318 in each syllable. The FM occurs periodically between 6.3 and 7 kHz, and this is more
319 pronounced in the first syllable of the group (Fig. 5).

320 Sound Pressure Level (SPL) measured across males in lab conditions was 98.2 ± 2.9 dB (re
321 $20 \mu\text{Pa}$; root mean square over recorded songs with calibrated microphone at 10 cm dorsal
322 from the singing male).

324 Wing resonances

325 Five male specimens were used for LDV experiments. Both LW and RW were stimulated
326 with broadband sound and wing resonances obtained by scanning the wing surface using
327 LDV. These recordings show that only the right mirror plays a major role in sound radiation,
328 while the equivalent left sound-radiating field is highly damped to vibrations (Fig. 6A-F).
329 Within individuals the mirror shows three modes of vibration at around 6.8 ± 0.7 kHz, $13.5 \pm$

330 1.5 kHz, and 16.6 ± 1.9 (n=5 individual averages of 120-130 scanned points in each mirror).

331 Fig. 6G shows average FFT spectrum across the five males. The observed resonances of 11.3-

332 16.6 kHz are within the range of carrier frequencies measured across specimens.

333 During the same experiments we also studied the resonances of the entire wings using

334 broadband stimulation (Fig. 7). We divided the wings in broad regions, represented by

335 numbers in Fig. 7A. Region 1 in the middle of the costal field, region 2 radial/middle field,

336 region 3 wing apex, and region 4, the stridulatory field. Although regions 1-3 vibrate with

337 lower amplitude than the right stridulatory field, both wings show components of the

338 resonances observed in the mirror of region 4 (~7, and 10 kHz, ranges observed across five

339 individuals), as well as those frequencies observed in the calling song in these ranges. The

340 resonant peaks are variable within this range across individuals, but all of them show a

341 common resonant peak between at 10 and 11 kHz, as illustrated in Fig. 7E-H.

342

343 Discussion

344 Acoustics and wing resonances

345 Males of most *Typophyllum* spp. reported so far produce signals approaching acoustic purity

346 at around 20 kHz (Braun, 2015a; Montealegre-Z and Morris, 1999; Morris et al., 1989).

347 *Typophyllum spurioculis* is singing lower than most *Typophyllum* spp. This cloud forest

348 species became distinctive for the loud, audible call, easy to localise by humans. In most

349 acoustic Ensifera the calling song carrier frequency depends on, and closely matches, the

350 resonance of the sound generator (the right mirror and associated cells) (Bennet-Clark, 1999a;

351 Chivers et al., 2017; Montealegre-Z et al., 2011; Montealegre-Z and Postles, 2010). This is

352 because the tooth strike rate matches the resonance of the sound generator. For example, if the

353 resonant frequency of the radiating areas is 5 kHz, and the stridulum is excited at a rate of

354 5000 teeth per second the system is said to reach resonance and vibrate at maximum
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2 355 amplitude (Bennet-Clark, 1999a, 2003b; Fletcher, 1992, 2007).
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4 356 We showed here that the mirror vibrates with three modes, two of them within the frequencies
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7 357 observed in the calling song (~7 and 14 kHz, Fig. 6). These resonances were also observed in
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10 358 other wing regions not directly involved in stridulation (Fig. 7). The two observed peaks
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12 359 result from one sine wave superimposed on another, which is twice as fast and it gives a
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14 360 sinusoid with a recurring bump (Fig. 4CD). This phenomenon has been observed in other
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17 361 katydids. Morris, 1980 first realized this in *Copiphora rhinoceros* (see Fig. 3 in that paper),
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19 362 but it has been shown that other species show more than one peak of subequal amplitudes
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22 363 (e.g. *Panacanthus cuspidatus* in Montealegre-Z and Morris, 2004 and *Uchuca halticos* in
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24 364 Montealegre-Z and Morris, 2003). This is what we observe in *Typophyllum spurioculis* (Fig.
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26 365 4EF).
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29 366 Our findings suggest that the two harmonically-related peaks observed in the calling song at
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31 367 around 7 and 14 kHz result from stimulation of any of the two modes, as both resonances are
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34 368 present in the various parts of the wings. Since we do not have mechanical evidence of the
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36 369 wing motion during sound production we cannot assert which of the two modes is stimulated
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39 370 during the interaction of scraper and file. However, based on the duration of the major pulse
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41 371 in the syllable (~32 ms), and assuming that this pulse was produced by sweeping the entire
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44 372 file length (~5.3 mm, with some 160-170 teeth), an average velocity of file sweeping could be
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46 373 inferred to be ~165 mm/s. This velocity and the average inter-tooth distances (0.03 mm) could
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49 374 be used to predict the time used by the scraper to jump between two teeth, which will in
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51 375 theory correspond to the period (p) of the fundamental oscillation, in other words $p=0.03/165$,
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53 376 whose reciprocal gives an instantaneous frequency ($f=1/p$) \cong 5.5 kHz. This analysis suggests
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56 377 that the wings are stimulated with a tooth strike rate that closely matches the fundamental
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58 378 frequency of the call (ca 6k teeth/sec, average in Fig. 6). That excitation may cause the low
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379 frequency components across both wings, including the mirror) to release sounds at 6-7 kHz
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2 380 (see Fig. 7), but also excites the higher vibration mode of the mirror at ca ~12-14 kHz (Fig.
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4 381 6). Proof of this is that the number of file teeth matches the number of fundamental
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7 382 oscillations in the major pulse of the syllable (see call analysis and file description). In
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10 383 summary, the observed energy peaks in the spectrum of the calling song (Fig. 4EF) are the
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12 384 result of excitation of the first mode of vibration of the wings, and indirect excitation of the
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14 385 dominant mode of vibration of the mirror (Fig 6). This form of excitation is not uncommon in
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17 386 *Ensifera*, and it seems to be a strategy for energy conservation in high-frequency Eneopterinae
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19 387 crickets (Robillard et al., 2013)
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22 388 At the fundamental frequency, we also observed that both pulses in a syllable are sinusoidally
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24 389 frequency modulated (Fig. 5C, lower part). This seems to be the result of a default mechanical
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27 390 modulation already encoded in the file morphology. The tooth density (and in turn the
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29 391 produced frequency produced at constant speed) periodically alternates between small groups
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31 392 of high-density and small groups of low density of teeth (Fig. 3). We attribute the observed
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34 393 modulation of the pulses in the call to such tooth arrangement. The sweeping of the scraper
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36 394 over a group of teeth with high density will produce high frequencies, while low frequencies
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39 395 are produced in the segments with low-density of teeth. This is a case of mechanical
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41 396 frequency modulation, which [was first](#) documented in other leaf-mimic katydids singing at
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44 397 higher frequencies (Braun, 2015b; Montealegre-Z, 2005), but not studied in detail so far. [FM](#)
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46 398 [has been a widely reported phenomenon observed in the call of insects, mostly in crickets and](#)
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49 399 [katydids. It was originally reported by Leroy, 1966 in crickets, and subsequently followed by](#)
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51 400 [measurements of Morris and Pipher, 1967 in the katydid *Conocephalus nigropleurum*. In](#)
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53 401 [crickets and katydids, FM seems to be the result of the gradual decrease in wing speed during](#)
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56 402 [the closing stroke \(Montealegre-Z, 2005; Montealegre-Z et al., 2011; Montealegre-Z and](#)
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58 403 [Mason, 2005\). However, in field crickets, the envelope of the modulation is a ‘finger print’ of](#)
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404 each male individual (Montealegre-Z et al., 2011). This seems to be associated to the levels of
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2 405 asymmetry between left and right tegmina (Bennet-Clark, 2003a). Very little is known about
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4 406 the function of FM in the calling song of many species and the only existing neuro-
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7 407 ethological study in crickets suggests that females prefer non-modulated calls over modulated
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10 408 ones (Hirtenlehner et al., 2013).

14 410 **On the function of the eyespots in *Typophyllum spurioculis***

16 411 The function of the coxal eye spots of *Typophyllum spurioculis* are currently unknown.
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19 412 Antipredatory markings have been reported in other orthopteroid insects, for example in the
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21 413 hind wings of praying mantis (Maldonado, 1970), the wings of grasshoppers (Steiner, 1981)
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24 414 and in the wings of the katydids, *Pterochroza ocellata* (Castner, 1995). The eyespots, in *P.*
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26 415 *ocellata* (another leaf-mimicking katydid) are usually relatively large, brightly pigmented
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29 416 patches positioned on the lower tegminal surface and hindwings, away from more vital areas
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31 417 (e.g. the head) (Edmunds, 1974). In response to a physical disturbance, the wings are
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34 418 suddenly flicked open, startling the predator. It is believed that, when viewed from behind,
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36 419 the spots and abdomen resemble a bird's eyes and beak respectively (Castner, 1995; Nickle
37
38 420 and Castner, 1995). Eyespots reduce predation on conspicuous (non-camouflaged prey), but
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41 421 increase them on camouflaged prey (Stevens et al., 2008). This explains why *P. ocellata*
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43 422 eyespots are hidden under the resting tegmina and are only exposed when the insect feels
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46 423 threatened. There is also the benefit of surprise to gain time: fear/flight reaction evoked in a
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48 424 predator by sudden disconcerting change (Edmunds, 1974).

50 425 In *P. ocellata* and other Pterochrozini species (e.g., *T. spurioculis*) the general morphology is
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53 426 one of leaf mimicry: they have a general antipredator strategy of crypsis. Crypsis is their
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55 427 primary defense (Robinson, 1969) and only when this pose is breached by a foraging predator
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58 428 will the secondary defense be brought into play. For *P. ocellata* this secondary defense is the
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60 429 large wing eyespots. The secondary strategy of *T. spurioculis* is to employ its metathoracic
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430 legs and leap forcefully and quickly away in some unpredictable direction in the cluttered
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2 431 vegetation. The small coxal eyespots of *T. spurioculis* could have a function other than
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4 432 deterring predators. Larger markings, and more markings are more effective deterrents of
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7 433 predation than smaller or fewer ones. Eyespots that actually look like eyes work better to
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10 434 deter predators than equally conspicuous markings (De Bona et al., 2015). In *T. spurioculis*
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12 435 each spot has a melanised black border, which boosts the contrast between the spot and the
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14 436 body. These eyespots are localized in the anterior part of the thorax (fore and mid coxae), and
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17 437 close to the head (Fig. 1). Therefore, it seems reasonable to assume they have signal function
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19 438 between conspecifics. It is possible that the spots have a role in sexual selection. For example,
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22 439 salient spots on cryptic individuals usually increase predation (Stevens et al., 2008), therefore
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24 440 only the fittest individuals survive to reproduce. The brightness of the spot could be an honest
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27 441 signal of high fitness. However if the spots are adornments influencing female choice then
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29 442 presumably they should be absent from the female herself, which is not the case in *T.*
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31 443 *spurioculis* (Fig. 1A).

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34 444 The eye pairs of *T. spurioculis*, which appear on the right and left, are not common as
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36 445 defensive mechanisms. Eyespots for deterring predators occur usually symmetrically as one
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39 446 ‘eye’ on each side of the body (Hossie, 2014; Janzen et al., 2010). These small ‘paired eye’
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41 447 displays of *T. spurioculis* on the side must be effective laterally, but the **reduced** size might to
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44 448 be effective against predators approaching laterally. However, it is well documented that male
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46 449 leaf-mimicking katydids (at least *Typophyllum* spp.) position at 90 degree plane on the side of
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49 450 the much larger female during mating (Braun 2002; Braun, 2015a; Braun, 2015b;
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51 451 Montealegre-Z and Morris, 1999) and we observed this behavior in *T. spurioculis* in caged
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53 452 specimens). Perhaps the coupling posture is when these eye markings could be most useful,
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56 453 for example for mate recognition. But other *Typophyllum* species with similar mating
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58 454 behaviour do not have coxal eyespots. Very little is found in the literature on experimental
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455 data on the eyespot behavioural display in Orthoptera, and this topic deserves further
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2 456 attention.

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23 24 25 465 **Competing interests**

26
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610 **Figure captions**

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Fig. 1 *Typophyllum spurioculis* sp. nov. A, habitus of male (lower specimen) and female (top specimen). Inset: close up view of the female showing the orange eye-spots in the coxotrochanter membrane (yellow arrows). B-D, pictures illustrating variation in wing morphology across individuals.

Fig. 2 Wing venation pattern. A, line drawings showing variation in wing venation in 10 male left wings. B, the enlarged inset shows all the wings overlaid to highlight the most common venation pattern. C, the left fore legs of a male and female in antero-posterior view.

Fig. 3 Stridulatory file and tooth distribution. A, SEM of the file of an Ecuadorean male. B, tooth distribution based on inter-tooth distances (filled, black circles) and tooth length variation (open, red circles) across the file. Note that the file clearly exhibits groups of large teeth with short inter-tooth distances and groups of smaller teeth with large inter-tooth distances.

Fig. 4 Description of the calling song based on individuals of two populations. A, B, a single call composed of two syllables. C, D, high resolution of small segment of the major pulse of the second syllable, showing the characteristic of two harmonically related carrier frequencies. E, F, spectral analysis of both calls, showing fundamental frequencies at 6.8 and 7.0 kHz, respectively, and a harmonically related peak in each case.

Fig. 5 Analysis of the song of an Ecuadorian male *T. spurioculis*. A, two minute-sequence of the song of one individual showing call groups. B, two consecutive calls extracted from the

635 segment selected by the dashed box. C, close up view of the first call (including only the
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2 636 closing stroke of the syllable 1, and opening and closing of syllable 2) in B (upper part) and
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4 637 analysis of fundamental frequency variation in time showing that the frequency of calls is
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7 638 periodically modulated (lower part).

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12 640 **Fig. 6** Right mirror resonances in two male *T. spurioculis*. A, B, close up dorsal view of the
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14 641 stridulatory fields of two mounted specimens with wings extended. C, D, vibration maps of
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16 642 the mirror of the males shown above. E, F, scanning lattice (dorso-anterior view) of the wings
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19 643 showing the mirror membrane deflection in 3D. G, right mirror resonance. Black outline:
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21 644 average resonance measured from five males. Shaded areas indicate one standard deviation.

24 645

26 646 **Fig. 7** Complete laser scan of both wings showing resonances at different locations. A, male
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29 647 specimen with the wings extended. Numbers indicate some of the areas of interest. B, same as
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31 648 A, showing the scanning mesh and density of scanning points over the wings. C, vibration
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33 649 map showing major areas of deflection. D, 3D view of the map in C to show that amplitude of
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36 650 vibration is dominant in the right mirror. E-H, wing resonances measured from the four areas
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39 651 indicated with numbers 1-4 for each wing in A.

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Table 1: Morphological measurements of *Typophyllum spurioculus*. F, fore; H, hind; L, left; M, mid; R, right; SD, standard deviation.

Character	Males (n=9)	SD	Females (n=2)	SD
Body (incl. tegmen)	36.46	2.23	60.59	4.84
Tegmen	30.35	1.52	50.25	8.48
Pronotum	5.21	0.42	7.25	0.86
F-Femur R&L	9.02	0.63	11.73	1.14
M-Femur R&L	8.89	0.39	11.74	0.03
H-Femur R&L	18.70	1.37	25.61	2.81
F-Tibia R&L	10.14	0.51	12.01	0.67
M-Tibia R&L	9.41	0.45	11.45	0.48
H-Tibia R&L	20.11	1.07	26.34	1.63
Subgenital plate	2.22	0.28	3.79	0.00
Stridulatory file	5.50	0.13	n/a	n/a

Fig. 1

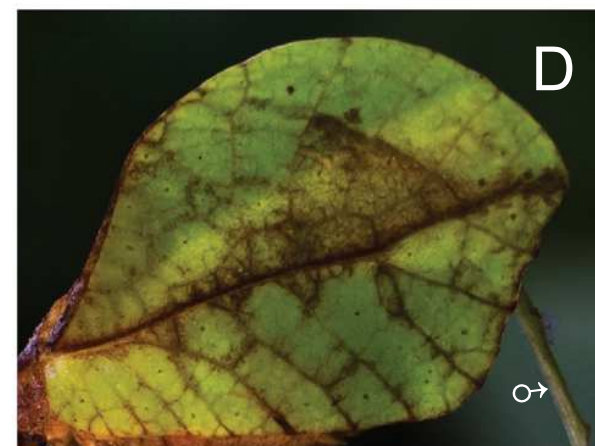
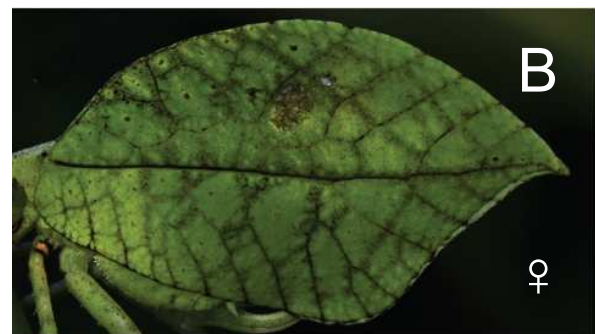
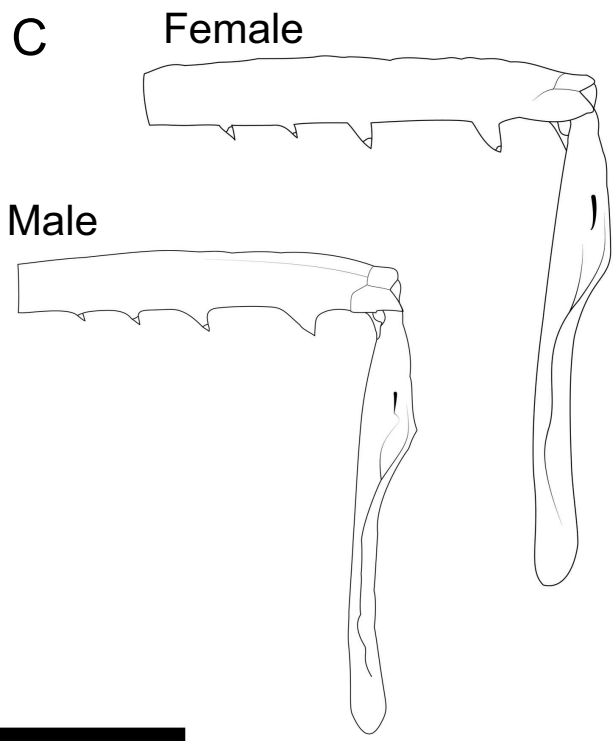
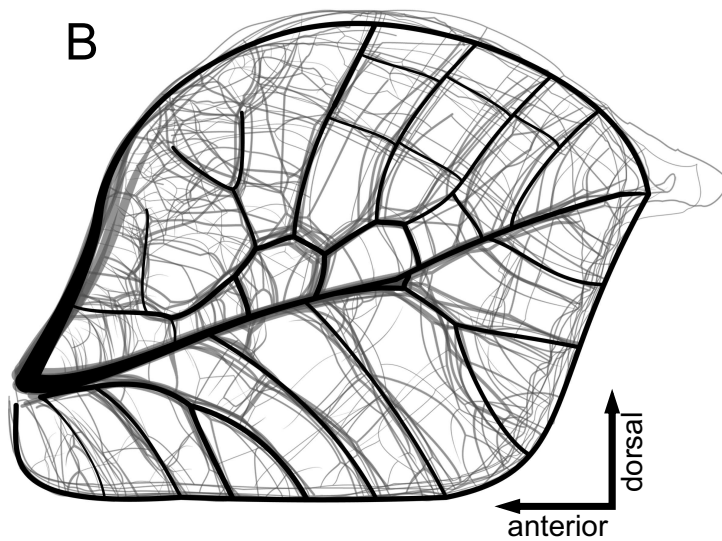
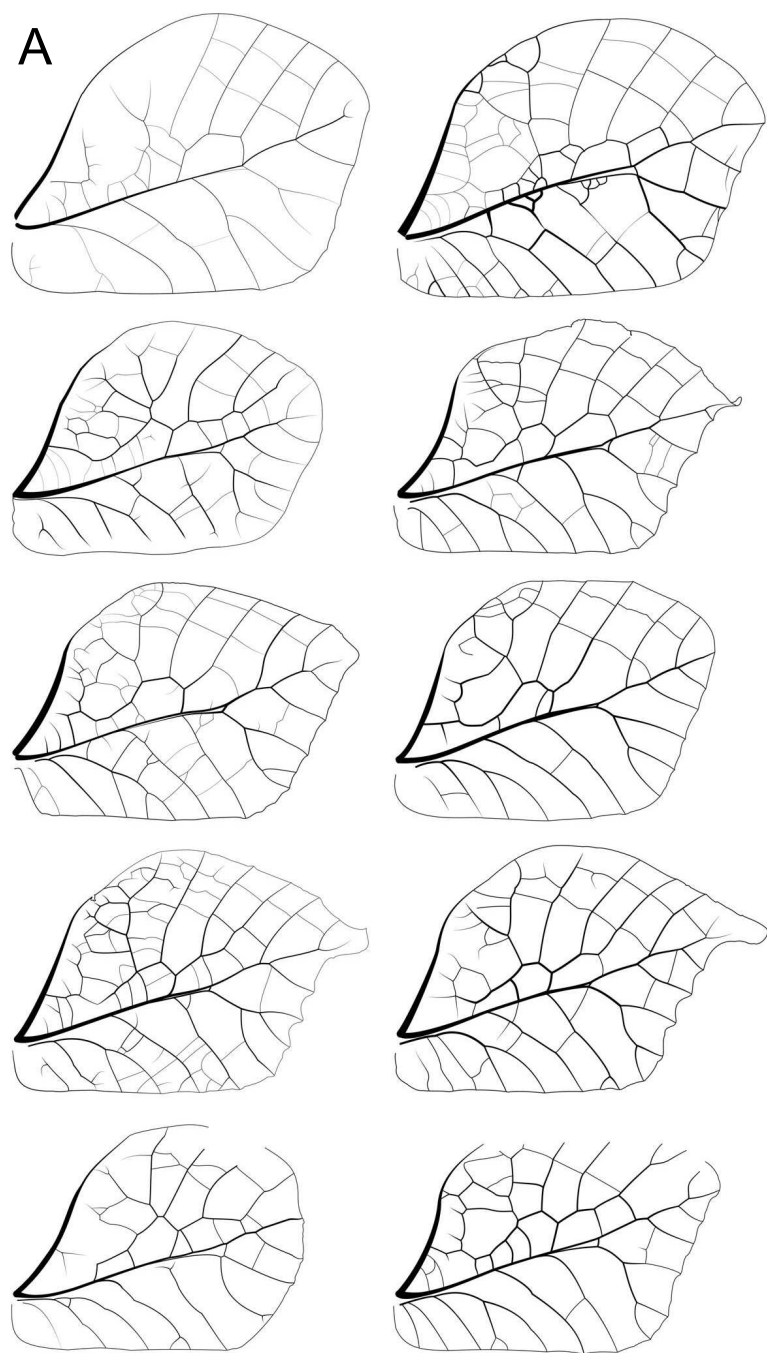


Fig. 2



5 mm

10 mm

Fig. 3

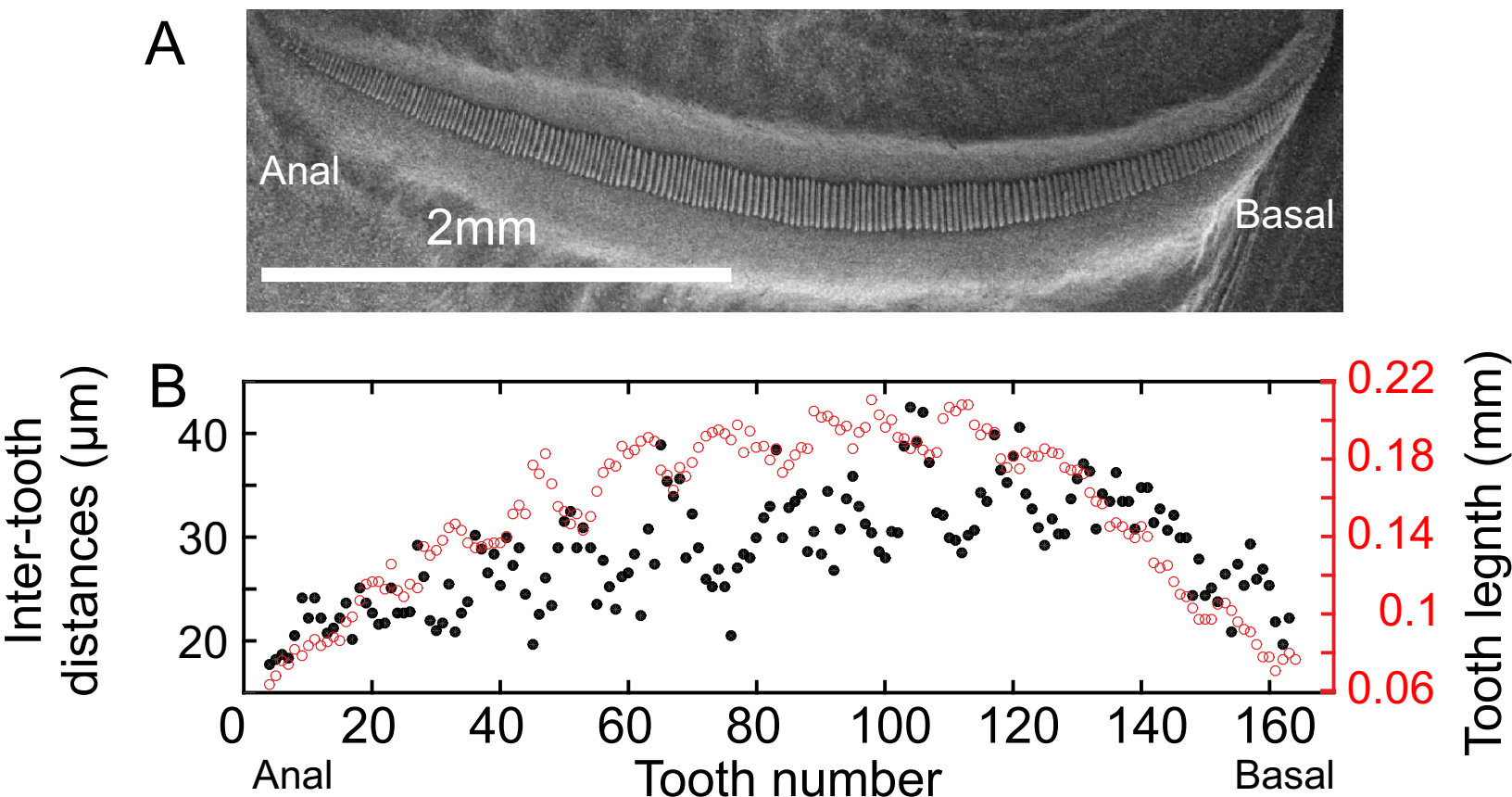


Fig. 4

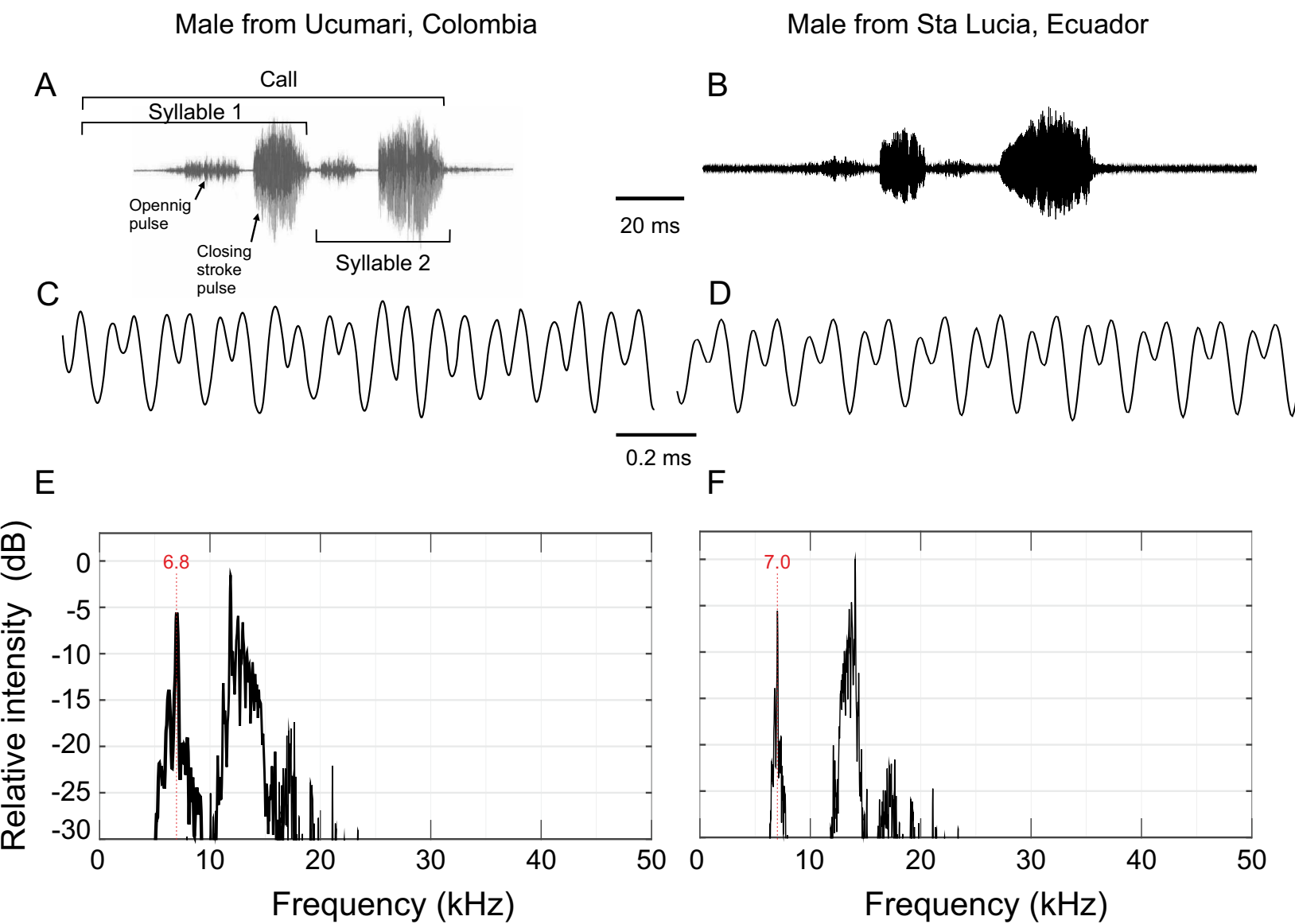


Fig. 5

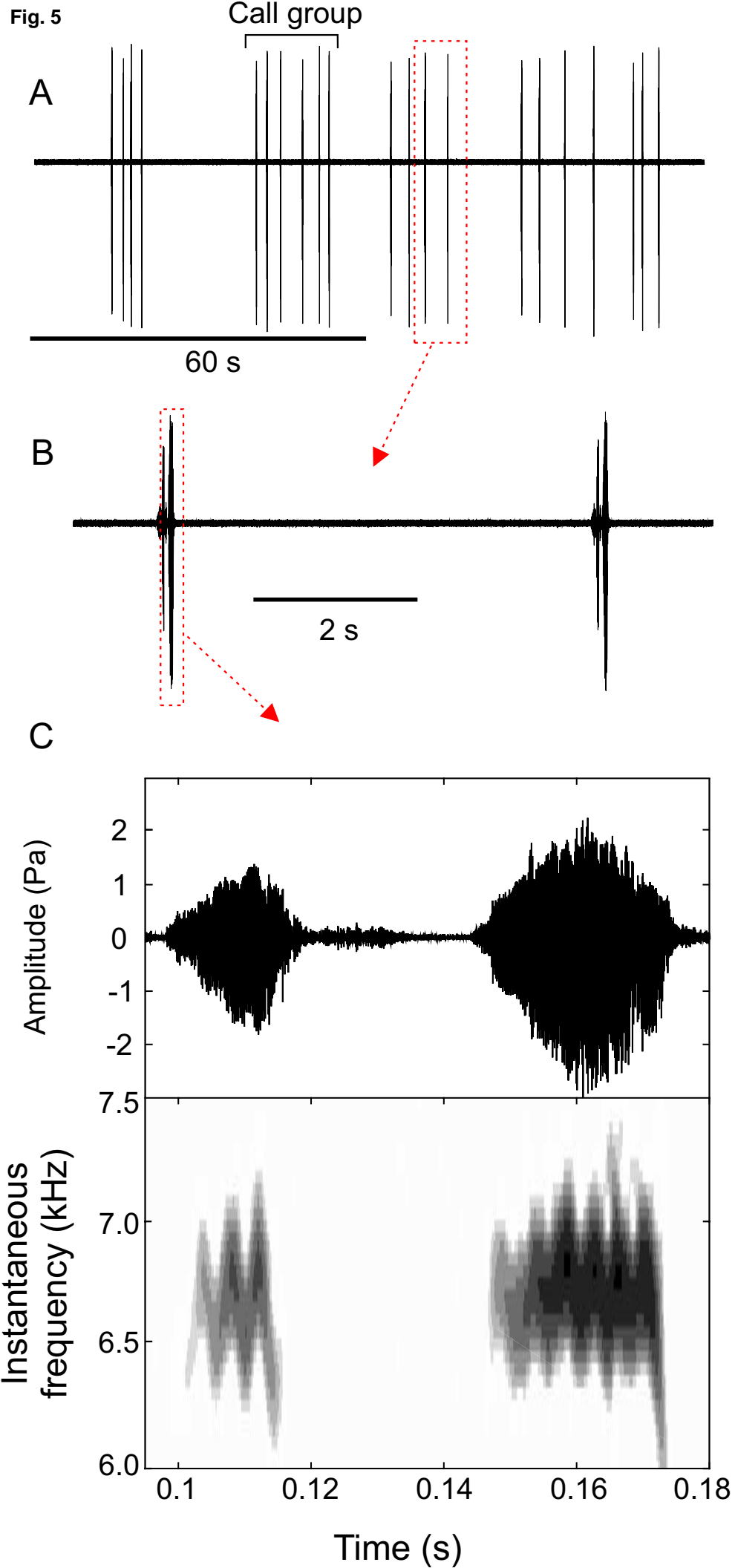


Fig. 6

Male 1

Male 2

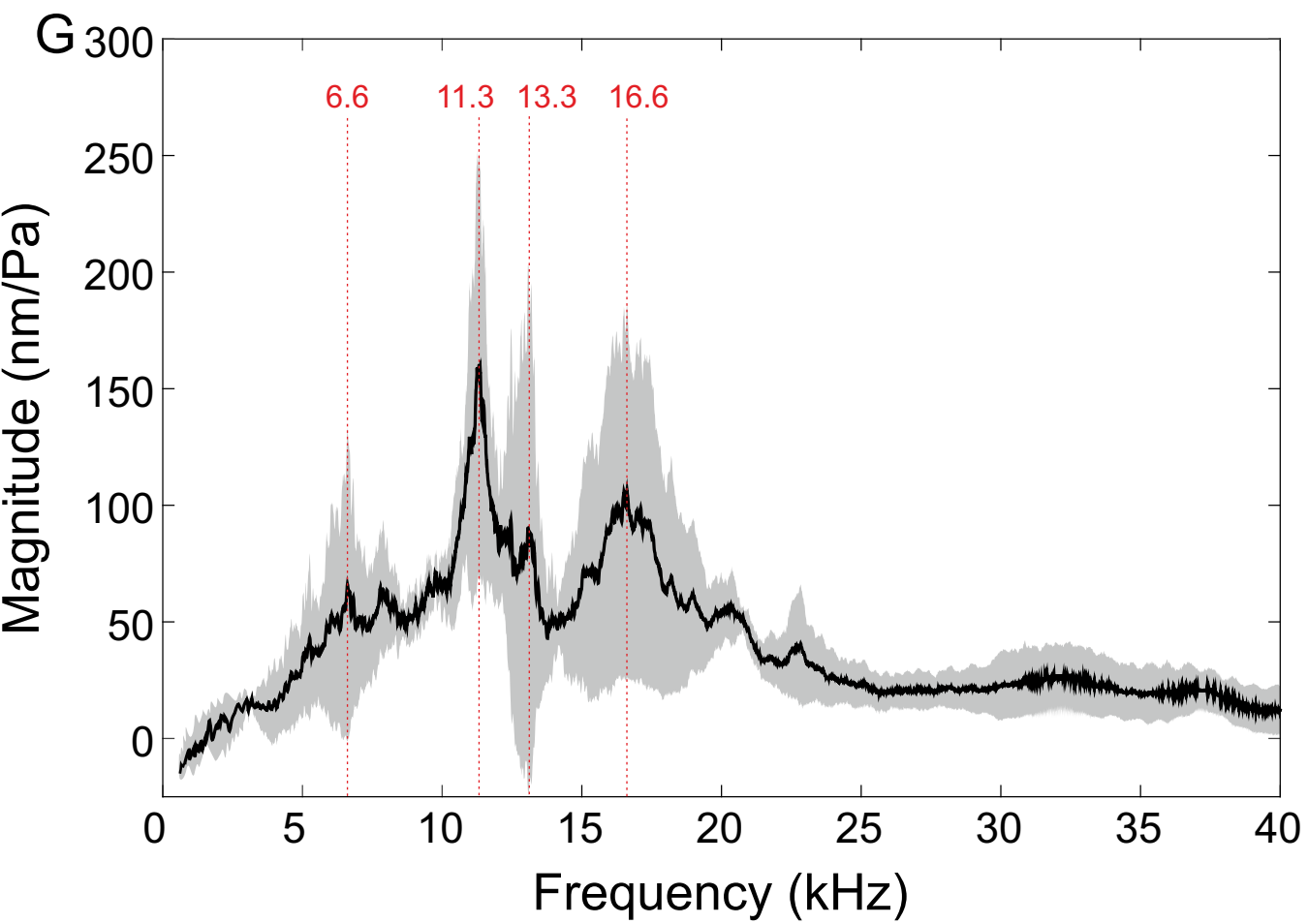
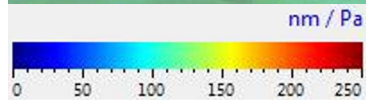
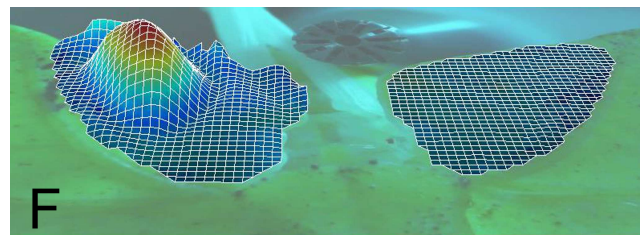
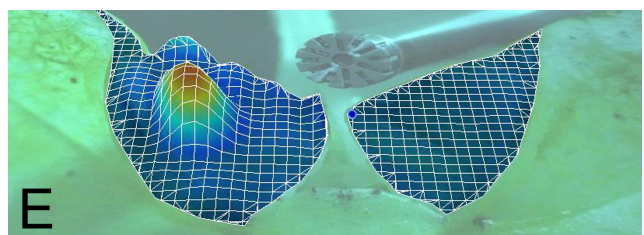
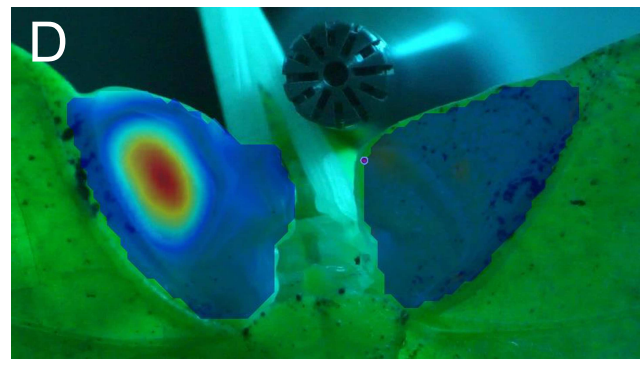
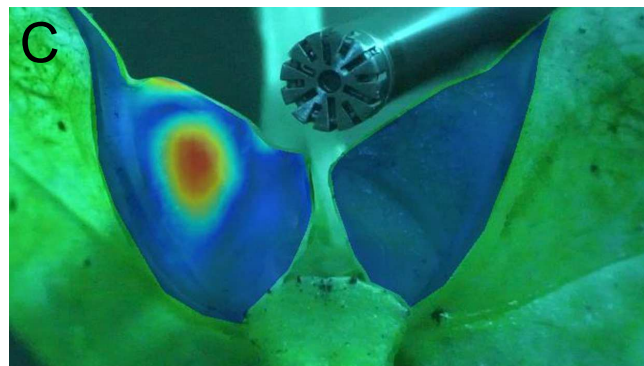
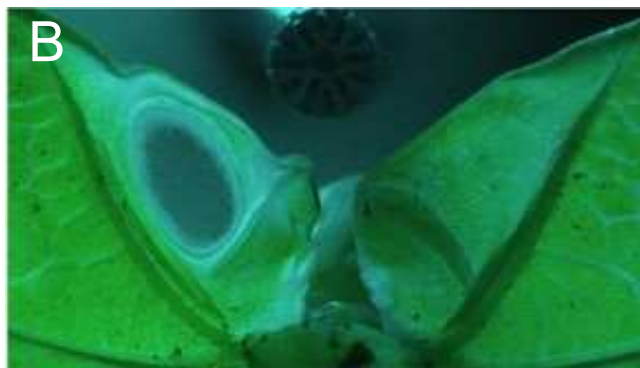
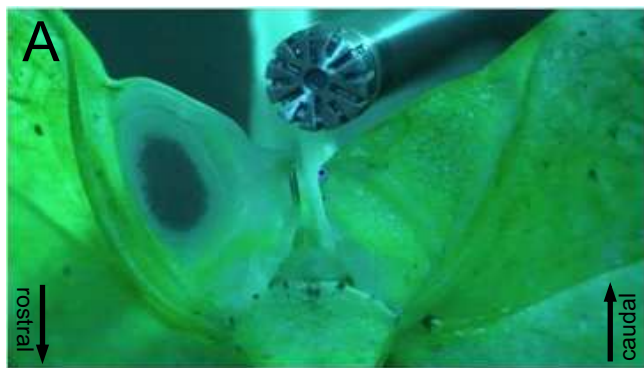
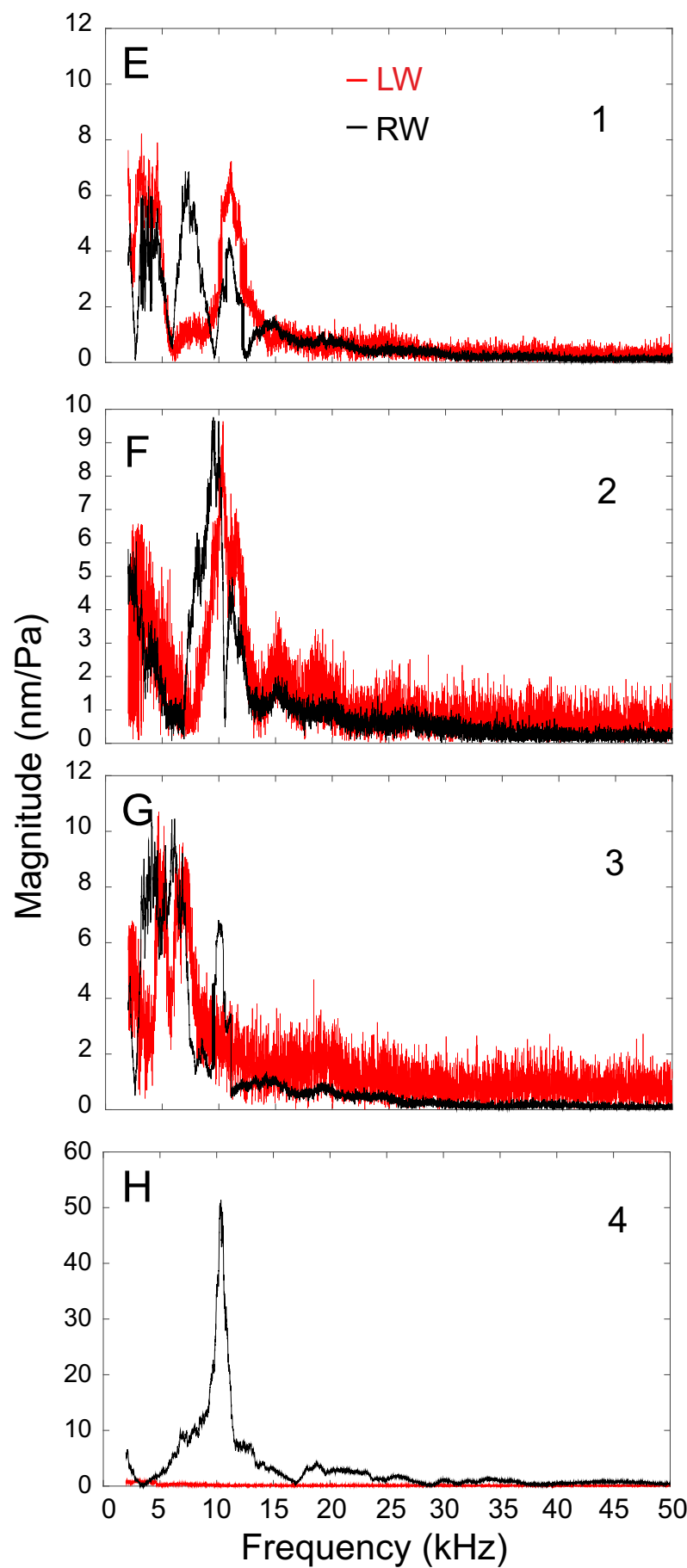
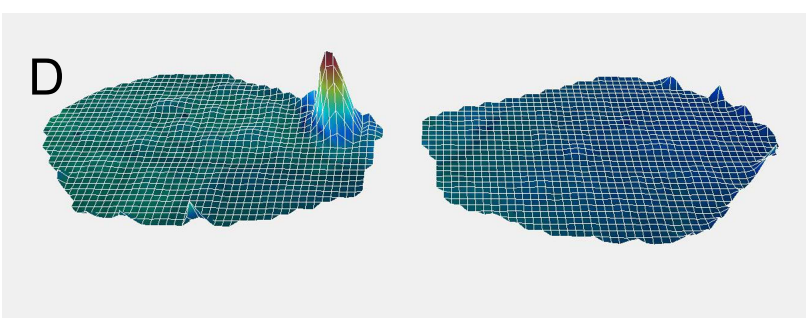
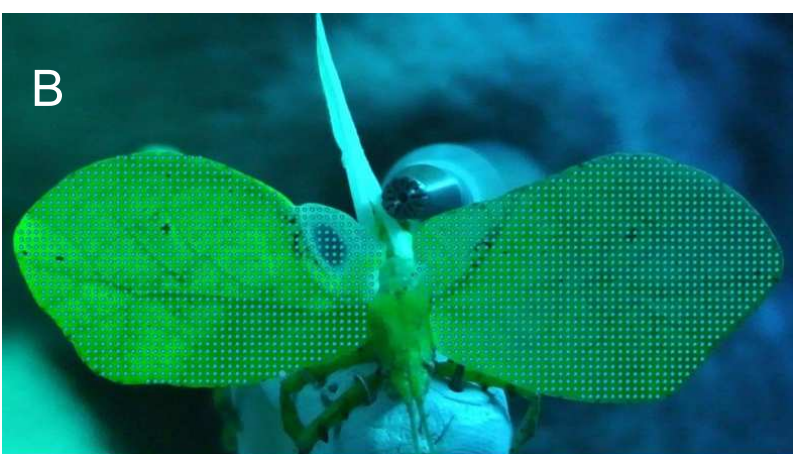


Fig. 7



Supplementary Material

[Click here to download Supplementary Material: Baker et al. Supplementary Materials.pdf](#)

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We, the authors, wish to confirm that there are no known conflicts of interest associated with this publication and there has been no significant financial support for this work that could have influenced its outcome.

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We further confirm that the order of authors listed in the manuscript has been approved by all of us.

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