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Full title

Reviving the sound of a 150-year-old insect: the bioacoustics of

Prophalangopsis obscura (Ensifera: Hagloidea)

Short title:

Sound production in a 150-year-old insect

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Abbreviations: f_c , carrier frequency; f_o , resonant frequency; LW, left wing; RW, right wing

24 **Abstract**

25 Determining the acoustic ecology of extinct or rare species is challenging due to the
26 inability to record their acoustic signals or hearing thresholds. Katydid and their
27 relatives (Orthoptera: Ensifera) offer a model for inferring acoustic ecology of extinct
28 and rare species, due to allometric parameters of their sound production organs. Here,
29 the bioacoustics of the orthopteran *Prophalangopsis obscura* are investigated. This
30 species is one of only eight remaining members of an ancient family with over 90
31 extinct species that dominated the acoustic landscape of the Jurassic. The species is
32 known from only a single confirmed specimen – the 150-year-old holotype material
33 housed at the London Natural History Museum. Using Laser-Doppler Vibrometry, 3D
34 surface scanning microscopy, and known scaling relationships, it is shown that *P.*
35 *obscura* produces a pure-tone song at a frequency of ~4.7 kHz. This frequency range
36 is distinct but comparable to the calls of Jurassic relatives, suggesting a limitation of
37 early acoustic signals in insects to sonic frequencies (<20 kHz). The acoustic ecology
38 and importance of this species in understanding ensiferan evolution, is discussed.

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46 Introduction

47 Acoustic communication systems have long been a popular model for understanding
48 ecological and evolutionary relationships within and between species. In insects,
49 acoustic systems for both signal generation and recognition have evolved a substantial
50 variety of forms, to facilitate a range of communication functions [1,2], offering many
51 routes to studying the evolution of acoustic communication. However, for extinct and
52 rare insect species, we are often limited in our abilities to infer details of specific
53 communication systems, as we are unable to record the sounds such species
54 generate or measure their hearing capabilities.

55 In katydids (or bush-crickets; Orthoptera: Ensifera) and their allies, pure-tone and
56 broadband sound production has evolved as a key mechanism for mate attraction and
57 conspecific recognition [3–6]. These sounds are produced by tegminal stridulation –
58 the process of moving a hardened scraper on one forewing, against a row of teeth (the
59 file) on the other, producing vibrations on the wing which are then amplified by
60 specialized wing cells (namely the harp and mirror) [4,5] to radiate sound. This
61 mechanism of sound production is evolutionarily conserved across a majority of the
62 Ensifera, and its characteristics have been understood since the early 1900s [7,8]. The
63 retention of this mechanism across a diverse range of taxa, and the increasing ability
64 of state-of-the-art imaging and acoustic technologies, is rapidly allowing researchers
65 to re-visit once inaccessible specimens with novel methodologies to advance our
66 understanding of Ensiferan acoustic communication.

67 Here we investigate the bioacoustics of *Prophalangopsis obscura* (Walker, 1869)
68 (Ensifera: Prophalangopsidae), an insect belonging to an ancient katydid family of over
69 90 known species dominant during the Jurassic, with only eight extant members [9].

70 The genus *Prophalangopsis*, formerly *Tarraga*, has remained monotypic ever since
71 the discovery of *P. obscura*, and thus received considerable interest in relation to the
72 evolutionary history of the Ensifera [10–12]. The enigmatic nature of the type specimen
73 has been compounded by no further male specimens being discovered in over 150
74 years, and only 2 potential female specimens ever found [13]. In addition, no works
75 have explored the ecology of this species due to their uncertain geographic distribution
76 [13,14]. Therefore, a thorough study of their acoustic capabilities could improve our
77 understanding of the communication systems and acoustic ecology of *P. obscura* and
78 its long extinct relatives [15–17], and aid in future rediscovery of the species.

79 Using micro-scanning Laser-Doppler Vibrometry (LDV), we reconstruct the vibration
80 patterns and resonances of the sound production organs (forewings) of the *P. obscura*
81 type specimen. Furthermore, we investigate the morphology of the stridulatory
82 apparatus and tegmina in detail to compliment LDV experiments and infer the likely
83 carrier frequency (f_c) of this species' song over 150 years after specimen preservation.
84 Employing existing validated models, and novel measurements from LDV, we obtain
85 f_c for the acoustic signal of *P. obscura* and use morphological data to calculate acoustic
86 signal structure. Using knowledge of the wing biomechanics of other extant members
87 of this ancient family, we reconstruct the calling song of *P. obscura*, and discuss the
88 importance of this species in understanding the evolution of ensiferan acoustic
89 communication.

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94 **Materials and Methods**

95 **The holotype material**

96 *Prophalangopsis obscura* (Walker 1869) is a large orthopteran (~10 cm; tegmina
97 wingspan) represented by a single specimen housed at the London Natural History
98 Museum, South Kensington, UK (specimen NHMUK 013806185). Collection details
99 are scarce, with the location information listed only as 'India'. The specimen was
100 originally set in a resting position following collection, but sometime between 1898 and
101 1939, the specimen was re-mounted with both wings spread [10], a position which
102 remains to this day (Fig. 1). At an unknown time after 1939, the left foretibia was lost.
103 The right foretibia, which contains the tympanic ear, remains intact (Fig. 1C). Both
104 forewings are present, with the stridulatory (sound producing) organs intact, however
105 the left wing is torn along the apical axis (Fig. 1A). In 2005, two female specimens
106 identified as *P. obscura* were located in China, later published by Liu et al [13]. While
107 male specimens were not identified to confirm the identity of these specimens, they
108 minimally belong to a close relative of *P. obscura*. No permits were required for the
109 described study, which complied with all relevant regulations.

110

111 **Fig 1. The holotype of *Prophalangopsis obscura* (collected in India, Walker**
112 **1869). A, dorsal habitus; B, lateral habitus; C, tympanal organ.**

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117 **Tegmina and stridulatory file anatomy**

118 *P. obscura* possesses a stridulatory file on each forewing. The morphology of each file
119 was imaged using an Alicona InfiniteFocus microscope (Bruker Alicona Imaging, Graz,
120 Austria) at 20x objective magnification, resulting in one composite 3D-image of each
121 file with a vertical and horizontal resolution of 0.7 and 7.8 μm , respectively. Using the
122 built-in Alicona software, the length of the stridulatory file was measured, as well as
123 the spacing between stridulatory teeth (inter-tooth distances), and length of each tooth.
124 The inter-tooth distance was measured as the distance between the central tip (cusp)
125 of adjacent teeth.

126

127 **Forewing resonance and deflection pattern**

128 The resonant frequency (f_0) and deflection patterns of the forewings was measured in
129 the holotype of *P. obscura* using micro-scanning LDV (PSV-500, Polytec GmbH,
130 Waldbronn, Germany), with approximately 1000 measuring points at a sampling
131 frequency of 256 kHz. Acoustic signals for wing excitation were generated by the LDV
132 internal data acquisition board (PCI-4451; National Instruments, Austin, TX, USA), and
133 consisted of broadband periodic chirps ranging from 1 to 60 kHz at 60 dB SPL (re 20
134 μPa). The signal was amplified by a Pioneer A-400 amplifier (Pioneer, Kawasaki,
135 Japan) and transmitted to a loudspeaker (Vifa, Avisoft Bioacoustics, Glienicke,
136 Germany; flattened frequency response across the whole range) positioned 20 cm in
137 front of the specimen. A reference signal to calculate the transfer function between the
138 wing vibration and the stimulus was recorded using a 1/8" condenser microphone

139 positioned horizontally at the wing plane between the wings (Model 4138-A015, Brüel
140 & Kjaer, Nærum, Denmark). For further details of method, see [18].

141

142 **Reconstruction of the sound**

143 To reconstruct the sound of *P. obscura*, several characteristics of the acoustic signal
144 are required. These are (1) the song carrier frequency (f_c), (2) the decay of a single
145 stridulatory tooth strike, (3) the number of oscillations produced during each
146 stridulatory file strike (one full sound pulse), and (4) the timing between stridulatory file
147 strikes. Previous investigations into the morphological parameters of katydid
148 stridulatory apparatus have shown that the best predictors of the f_c are the regions of
149 mechanical displacement of the tegmina (the acoustically active wing cells), and the
150 length of the stridulatory file [7]. In hagnoids (Hagnidae and Prophalangopsidae), which
151 lack a specialised mirror area, it has been suggested that measurements of file length
152 and LDV resonance, or the entire vibrating area, will be better predictors of f_c [7,8]. To
153 predict f_c , we used existing models [7] to compare the frequency derived from the file
154 length, right tegmen vibrational area, left tegmen vibrational area, and resonance from
155 vibrometry.

156 Following calculation of the mean f_c predicted by these four techniques, an artificial
157 impulse of a single tooth strike of *P. obscura* was produced at this frequency, including
158 a decay caused by damping. Oscillations of the tegmina mirror cells usually exhibit a
159 free decay of 3-4 ms in species communicating at the determined f_c [3,11,19], thus a
160 4 ms exponential decay was used.

161 Members of the Prophalangopsidae have a high stridulatory tooth density and short
162 functional file length, which permits the generation of uniquely pure-tone calls
163 [15,20,21], and as pure-tone singing katydids display a 1 : 1 relation between tooth
164 strikes and the number of oscillations in the song pulse [7], we used f_c , the number of
165 functional stridulatory teeth, and the spacing of the teeth, to infer the pulse structure
166 of the song of *P. obscura*. This was performed using a custom written Matlab code
167 [15] which calculates the instantaneous period for each tooth impact based on the
168 inter-tooth distance measurements. The resulting representative waveform of the
169 acoustic signal of *P. obscura* was further analysed using the Signal Processing
170 Toolbox in Matlab (R2021a, The MathWorks Inc., Natick, USA) with the following
171 spectrogram parameters: FFT size 512, Hamming window, 50% overlap; frequency
172 resolution: 512 Hz, temporal resolution: 0.15 ms.

173

174 **Results**

175 **Tegmina and stridulatory file anatomy**

176 The anatomy of the tegmina (forewings) of *P. obscura* is similar to those observed in
177 both extant and extinct relatives of the Prophalangopsidae. The left wing (LW) and
178 right wing (RW) display stridulatory files that are similar enough to be considered
179 functionally symmetrical. The pattern of tooth distribution is slightly gaussian (Fig. 2),
180 suggesting the file could be adapted for sound production during the opening or
181 closing phase of the wings. File length and number of teeth of LW and RW file were
182 9.60 and 9.99 mm and 134 and 137 teeth, respectively. The inter-tooth distances,

183 tooth lengths, and plectra are symmetrical, suggesting both might have been capable
184 of producing sound pulses (S1 Table).

185

186 **Fig 2. Stridulatory file anatomy and inter-tooth distances in *Prophalangopsis***
187 ***obscura*.** Orientation of both files is along the anal (left) to basal (right) axis.

188

189 **Forewing resonance and deflection pattern**

190 Despite over 150 years of preservation, it was possible to obtain the deflection
191 (vibratory) pattern of the forewings and f_o in *P. obscura*. An assessment of the regions
192 of the wings theoretically involved in resonant sound production and the displacement
193 of the wings in response to an acoustic stimulus (Fig. 3A,D) confirmed that the mirror
194 and pre-mirror are the most likely regions for sound production in this species, as with
195 all extant members of this family [21]. Displacement was highest within the mirror area
196 for both the LW (Fig. 3B) and RW (Fig. 3E). The normalised displacement amplitudes
197 of the mirror area of the LW displayed a peak frequency at 6.3 kHz (Fig. 3C). However,
198 despite morphological symmetry of the wings, the RW displayed a peak of 4.8 kHz
199 (Fig. 3F).

200

201 **Fig 3. Forewing resonance in *Prophalangopsis obscura*.** (A) Displacement map of
202 the LW; (B) Deflection pattern of the white profile line in A; (C) Frequency spectrum of
203 the left mirror; (D) Displacement map of the RW; (E) Deflection pattern of the profile
204 line in D; (F) Frequency spectrum of the right mirror; (G) Angled view of the left
205 forewing displacement pattern at 4.8 kHz.

206 **Reconstruction of the sound**

207 Using f_0 , stridulatory file length, and vibrational areas of the tegmina resulting from
208 LDV deflection measurements, f_c was calculated (Table 1). Based on phylogenetically
209 controlled linear models of several measurement parameters [7], we believe the f_c to
210 be $\sim 4.7 \pm 0.05$ kHz (Table 1). The measurements of inter-tooth distances and f_c
211 allowed the calculation of a time vector of a single sound pulse of the species' acoustic
212 signal (For more details of the song reconstruction method, see [15]).

213

214 **Table 1. Model measurement parameters for calculation of the likely carrier**
215 **frequency (f_c) of *Prophalangopsis obscura*.**

Measurement parameter	Measurement (x)	Slope (m)	Intercept (c)	f_c (kHz)
File length (mm)	9.6	-0.97	3.74	4.693
RW vibrating area (mm ²)	45.31	-0.62	3.91	4.691
LW vibrating area (mm ²)	39.05	-0.54	3.53	4.716
LDV resonance (kHz)				4.800
Average				4.725

216 For all estimates of f_c : $\ln(f_c) = m * \ln(x) + c$, where \ln = natural logarithm.

217

218 The Matlab script for sound pulse reconstruction [15] revealed that the structure of a
219 single call pulse (Fig. 4) is similar to that of fossil relatives of the same family [15], but
220 differs in frequency and duration (Fig. 4). The duration of a single pulse was found to
221 be 42 ms (Fig. 4), which is very close to the predicted pulse duration from functional
222 file length using an existing model (40.78 ms; Montealegre-Z et al. 2017). Surprisingly,
223 a slight frequency modulation in each chirp of the call was observed (Fig. 4). Extant

224 species display similar modulations as a result of changing velocity over the course of
225 each wing stroke. The first predictions of how crickets produced their sounds looked
226 at tooth distribution to infer whether sounds are produced during opening or closing of
227 the wings [22]. As the frequency of the sound is a function of tooth strikes per time
228 period, any changes to wing velocity over the course of one wing stroke will cause
229 frequency modulation in the sound. Looking at the almost gaussian distribution of
230 seemingly functional teeth in *P. obscura*, we cannot confirm whether this species is
231 able to stridulate during the opening or closing of the wings, or both. The final
232 reconstruction of the sound (Fig. 4; S1 Audio File) therefore consists of a putative
233 diplo-syllable containing two pulses with every other chirp artificially reversed, to leave
234 this element of the reconstruction open for future interpretations.

235

236 **Fig 4. Reconstruction and spectral analysis of a diplo-syllable containing two**
237 **pulses of the sound of *Prophalangopsis obscura*.** Waveform of two chirps (top),
238 with spectrogram below and frequency spectrum on the left marginal axis. The 2nd
239 chirp is an artificial reversal of the 1st chirp, to demonstrate that frequency modulation
240 (FM) will differ depending on whether sound is produced during the opening or closing
241 wing stroke.

242

243 **Discussion**

244 Using LDV techniques, we were able to obtain the deflection pattern of the tegmina of
245 *P. obscura* and use information on tegmina and stridulatory file anatomy to reconstruct
246 the song of the 150-year-old preserved museum specimen. The anatomy of the

247 tegmina and stridulatory file display similarities to both fossil and extant
248 prophalangopsids [15,16,21], and this similarity is also represented in the frequency
249 and structure of the song (Fig. 4), although f_c here is lower than that of related fossil
250 species [15]. The resonant frequency (f_0) of the tegmina provided by the LDV
251 recordings matched the expected frequency from the models, and we were able to
252 obtain the area of deflection, which was also used to calculate the potential calling
253 song frequency (Table 1). Despite the matching frequency information provided by the
254 right tegmen, the left tegmen did not predict a similar f_c . We believe this discrepancy
255 is due to a tear down the apical axis of the LW, given the similarities of the frequency
256 predicted by the models to the resonance of the right tegmen (Table 1). In many
257 singing ensiferans, the LW is found to be a better predictor of f_c [7], however in the
258 prophalangopsidae, it is known that the wings are functionally symmetrical [7], so we
259 can be confident that the RW resonance is representative of the LW resonance. The
260 retention of resonance in the RW may seem surprising, as insect cuticles become
261 stiffer as they desiccate over time [23], and thus we may expect such stiffening to
262 result in changes to resonance. However, in this case, we believe that the topology of
263 the wings plays more of an important role in f_0 , and due to the size of the tegmina, the
264 effect of drying is not so pronounced. The thickness and area of the tegmina dictate
265 the resonant properties of the musical areas of the wing, and larger musical areas
266 display less variation in frequency response with changes to thickness [24]. For
267 example, in the gryllid *Tarbinskiellus portentosus* with a harp size of $\sim 25 \text{ mm}^2$, tegmina
268 thickness would need to decrease by more than 30% before thickness would begin to
269 greatly modify resonance [24]. Thus, for a large species like *P. obscura* which has a
270 harp size of $\sim 50 \text{ mm}^2$, even a significant change in tegmina thickness from desiccation
271 would be unlikely to result in large changes to resonance, explaining why the

272 resonance is here maintained. Nonetheless, further studies into the effects of wing
273 thickness and tissue desiccation on tegmina resonance across orthopterans would
274 offer a rich dataset for future works to calculate taxon-specific frequency changes over
275 time, increasing the information we can obtain from dry museum specimens.

276 Just like the other extant members of this family, and unlike modern katydids
277 (Tettigoniidae), *P. obscura* is likely capable of using both wings for singing, with both
278 tegmina possessing symmetrical stridulatory files, plectra, and acoustically functional
279 areas [15,16,21]. The mirror region of the tegmina displayed the greatest deflection,
280 and the pattern of deflection followed that of extant relatives [21]. However, as
281 suggested by Zeuner [10], the tegmina are not as specialised for sound production as
282 other closely related extant species such as the great Grig *Cyphoderris monstrosa*.
283 The size and function of the wings is one of the key features of *P. obscura* that
284 separates it from the other extant prophalangopsids and resembles the specimens of
285 the fossil record [10,15]. While all other extant prophalangopsids (e.g. *Cyphoderris*
286 spp.) are flightless and use their wings exclusively for sound production and mate
287 attraction/gifting [25], *P. obscura* has wings potentially large enough for short or
288 sustained flight, resembling both the extinct prophalangopsids and many tettigoniids.

289 Reduced flight is a well-established evolutionary mechanism to reduce or avoid
290 predation by aerial predators, and in particular, bats [26]. The other extant species in
291 this family, all of whom have lost the ability to fly, exhibit novel anti-predator defences,
292 namely ultrasonic sound production organs [27], which likely evolved to act as a
293 deterrent to a new host of predators they now face after switching to a terrestrial
294 lifestyle. Such anti-predator adaptations are not present in *P. obscura*, nor are any
295 other morphological adaptations associated with predation by bats such as enlarged
296 cuticular spines [26]. We may predict therefore that this species lives in a region with

297 reduced selection pressure from ultrasonic aerial predators, allowing it to retain the
298 Jurassic form even after the emergence of echolocating bats [28]. Similarly, low
299 frequency calling songs such as that of *P. obscura* are indicative of reduced pressures
300 from eavesdropping predators, as low frequency sounds travel larger distances and
301 could give away the location of the signaller [29]. Tettigoniids regularly predated by
302 bats benefit from the increased attenuation of ultrasonic conspecific signals by a
303 reduced detection range by eavesdropping predators [26]. However, it should be noted
304 that correlating call frequency to ecology in such a manner does not consider other
305 factors which will be driving call frequency evolution [26,29].

306 Unfortunately, further inferences on natural history remain challenging as the precise
307 origins of the type specimen remain obscure. Previous literature on the specimen
308 references a wide geographic area broadly synonymous with the extent of the former
309 British India at the time of collection (e.g. Hindustan, E. Indies). The combined
310 historical evidence suggests that the specimen was collected in northern India,
311 although it is at present not possible to give a more precise location. If the female
312 specimen described in Liu et al [13] are confirmed to be *P. obscura* and not a closely
313 related species, then the known range may be extended from northern India to include
314 Tibet, a region certainly too cold to support an abundance of echolocating bats. Further
315 collections from this area to confirm the association between males and females, and
316 to investigate the local composition of potential predators, would be very valuable.

317 Following this song reconstruction, it may be plausible to deploy autonomous
318 recording units (ARUs) into potential field sites and use signal detection algorithms to
319 aid in the rediscovery of this species [30,31]. We hope that in time, further specimens
320 of *Prophalangopsis obscura* are located, to record the true song of this elusive
321 species, and to validate the accuracy of the predictions presented here.

322 **Data accessibility**

323 No data beyond those presented in the main text or supplemental material is available.

324 Custom Matlab scripts are available from the authors upon request.

325

326 **Author contributions**

327 All authors contributed to the writing and editing of the manuscript. CW and FMZ
328 collected vibrometry data. CW completed the first draft, analysed data, reconstructed
329 the song, and produced the figures and illustrations. EB organised the specimen loan,
330 aided in handling of the specimen during vibrometry experiments and provided
331 information on specimen history. TJ conducted Alicona scans of the wings and aided
332 in song reconstruction. FMZ developed the custom Matlab codes and supervised the
333 study.

334

335 **Competing interests**

336 The authors declare no competing interests.

337

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441 **Supporting Information**

442 **S1 Table. Morphological characters of the tegmina stridulatory files of *P.***
443 ***obscura*.**

444 **S1 Audio File. The reconstructed calling song of *Prophalangopsis obscura*.**

445 **S1 Fig. Visual reconstruction of *Prophalangopsis obscura* on a tree branch in**
446 **a temperate montane habitat. Illustrated by CW.**

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