Vibrational signalling in a Gondwanan relict insect (Hemiptera: Coleorrhyncha: Peloridiidae)

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Ancient, long-extinct floras and faunas can be reassembled through fossils and phylogenetics, and even palaeo-environments can be reconstructed with the aid of palaeoclimatology. However, very little is known about the sound-scape of the past. Of what kind were the first biologically meaningful sounds and vibrations ever emitted and perceived? The earliest signals in the history of life were probably produced by arthropods making use of the mechanical properties of their exoskeleton. Here, we report an observation of vibrational signalling in the coleorrhynchan *Hackeriella veitchi*, a representative of a Gondwanan relict insect lineage which is still extant in the Queensland rainforest. Our finding suggests that vibrational signalling by tymbal organs is ancestral for the Hemiptera (exclusive of Sternorrhyncha)—the song of the Coleorrhyncha was a likely element of the acoustic environment in the Permian moss forests and had possibly changed little since.

1. INTRODUCTION

The Coleorrhyncha are survivors of an ancient evolutionary lineage which split off from Heteroptera (true bugs) in the late Palaeozoic. The taxon comprises 25 extant species (13 genera in a single family: Peloridiidae) from the Southern Hemisphere (Australia, Tasmania, Lord Howe Island, New Zealand, New Caledonia, Argentina, Chile). All the Peloridiidae species are flightless, except one. The present distribution of the Peloridiidae suggests that they 'must have been in existence before the break up of Gondwanaland' (Evans 1981) and, as the sister-group of the Heteroptera (true bugs), dates back to at least the upper Permian, more than 230 Myr ago (Hennig 1981; Shcherbakov & Popov 2002).

The extant Coleorrhyncha live in wet moss and leaf litter in temperate *Nothofagus* forests (figure 1*a*), usually at high altitudes, a habitat type which may have been prevalent on the southern continent. Their conservative morphology and habitat preferences suggest Coleorrhyncha may have retained their general behaviour as well.

Intraspecific communication by air-borne (sound) or substrate-borne (vibrational) signals is widespread and diverse in Hemiptera (Čokl & Virant-Doberlet 2003; Cocroft & Rodriguez 2005)—ranging from cicada songs close to the pain threshold of the human ear to the silent vibrational signals of obligate cavernicolous planthoppers in the Hawaiian lava tubes (Hoch & Howarth 1993). The signal-producing structure prevalent in the Hemiptera is the tymbal—an organ which is essentially composed of a specialized area of the abdominal cuticle and an attached muscle. Tymbal muscle activity deforms the cuticle, eventually resulting in the production of 'clicks' upon contraction and release. Hitherto, however, only the signals of 'modern', i.e. phylogenetically derived hemipteran taxa have been investigated. The presence of a tymbal had long been considered an autapomorphy for the 'Auchenorrhyncha' (Fulgoromorpha + Cicadomorpha, including cicadas; Hennig 1981), a view which has been challenged by recent cladistic analyses combining morphological and molecular data (Bourgoin & Campbell 2002; figure 1*d*). To better understand the origin and evolution of acoustic communication in the Hemiptera, information on the ancestral behaviour of the Heteroptera + Coleorrhyncha clade is needed. Here, we report an observation of vibrational signalling in the coleorrhynchan *Hackeriella veitchi*, which partly fills this gap.

2. MATERIAL AND METHODS

(a) *Recording*

Adult specimens of the Peloridiid *H. veitchi* (Hacker: 1932; total body length: 3 mm; figure 1*a*, inset) from Australia (South Queensland) were tested for their ability to produce vibrational signals. Individuals were placed on living moss tissue as a substrate. Vibrational signals were received with a magneto-dynamic induction converter system ('MD-system' *sensu* Strübing & Rollenhagen 1988) in an anechoic room (Museum für Naturkunde, Bioacoustics laboratory) and tape-recorded with a Philips D 6920 MK2 on a Sony UX Position Chrome 60 tape (IEC II/Type II, High Bias 70 μs EQ). In the process, the vibrational signals are amplified approximately 1000 times and thus made audible to the human ear.

(b) *Sound analysis*

The signals were digitized with a SoundMax Digital Audio 5.0 sound card (Analog Devices, Inc.), sampling frequency 96 000 Hz, 16 bits. Time pattern analyses were conducted with Avisoft-SAS Lab Pro, v. 3.72 (software by R. Specht (1991–2005), Germany, distributed by www.avisoft.de) at the Bioacoustics laboratory (Museum für Naturkunde, Berlin). Spectrographic analyses were performed with Praat, v. 4.3.14 (software by Boersma, P. & Weenink, D. (2001–2005), The Netherlands, distributed by www.praat.org) at the Tembrock laboratory (Institute of Biology, Humboldt-Universität zu Berlin).

(c) *Depository*

Song voucher of *H. veitchi*: Museum für Naturkunde, Berlin.
Original tape: archive of Animal Sounds ('Tierstimmenarchiv'), Museum für Naturkunde, Humboldt-Universität zu Berlin, Archive-No. Hackeriella_veitchi_1_1. http://www.biologie.hu-berlin.de/~tsarchiv (database).

3. RESULTS

An adult male of *H. veitchi* was observed emitting a series of signals immediately after being placed into the test arena. The signal shows a repetitive structure of several syllables, each consisting of a series of homogenous pulse trains (3–12 pulses per syllable; figure 1*b*). Pulses consisted of forced substrate vibrations with an average of 82 Hz (mean period length: 12.2 ms; s.d.=0.86). Single pulses varied between one and six oscillation periods in length,
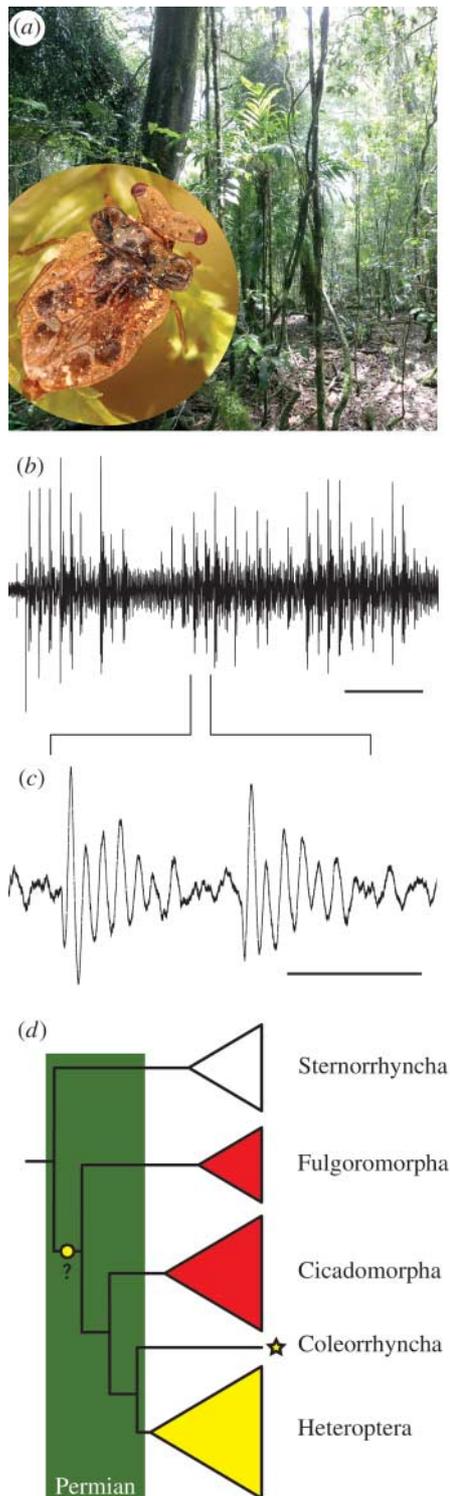
with duration ranging from 11 to 80 ms (s.d. = 20.7 ms; figure 1c). Amplitude modulation is observed and may be an integral part of the signal. The distinct signal pattern observed in *H. veitchi* suggests that the signal is not produced randomly by scratching or some other stereotypic movement, but does encode information.

4. DISCUSSION

Due to the physical constraints posed by their small body size (Claridge 1985) peloridiids were likely candidates to produce vibrational signals. Given the low frequency of the signals and the consistency of the host substrate (soft moss tissue), we assume the signal emitted to be effective specifically at short range, and hypothesize its function either as a disturbance call or spontaneous call in the context of initiating courtship, as has been observed in other hemipterans (e.g. Drosopoulos 1985).

It is still unknown how the signal is generated, however, the nature of the signal points to a tymbal-like organ without a resonator. Forced pulse frequencies observed in *Hackeriella* resemble those of cicadas and Heteropterans (true bugs) which result from the operating frequency of the modulator muscle in the tymbal organs or homologous structures (Tembrock 1959; Gogala 2006). The assumption of a tymbal as the signal generating mechanism is supported by the presence of large apodemes at the posterior margin of the first and second abdominal dorsal sclerites (Sweet 1996). Although behavioural observations were still missing, Sweet (1996) hypothesized their function as a tymbal. This assumption is corroborated by sexual dimorphism of the apodemes: they are apparently larger and more elaborate in the male than in the female, implying a function in intraspecific communication (Sweet 1996). The presence of a simple tymbal in the Coleorrhyncha is consistent with the hypothesis that the ancestral species of at least four Hemipteran subgroups (figure 1d) may have already used tymbal-like structures to produce vibrational signals. This early 'musical instrument' independently underwent refinement in other Hemipteran lineages and provided the morphological basis for the evolution of complex courtship patterns—a fact which may have attributed to the species-richness of the largest non-holometabolous insect order which today comprises approximately 80 000 species. Long before the evolution of birds and mammals, the acoustic environment of a Gondwanan moss forest in the Permian must have been mainly shaped by the sounds and vibrations of insects. Besides the Coleorrhyncha, there were Plecoptera (stoneflies) and ensiferan Orthoptera (crickets) (Grimaldi & Engel 2005) which were presumably already communicating acoustically in similar ways as extant species: stoneflies by tapping the substrate with the abdomen (Stewart 1997) and crickets by stridulation (Desutter-Grandcolas 2003). Our discovery of vibrational signalling in the Coleorrhyncha infers the presence of a simple tymbal in the ancestral species of four subgroups of the Hemiptera and thus provides the first evidence that 230 Myr ago the three major mechanisms of signal production in

Figure 1. (*a*) *Nothofagus* forest, south Queensland, Springbrook National Park, collecting site of *Hackeriella veitchi* (inset: adult male). (*b*) Oscillogram of time–amplitude pattern of vibrational signal. Scale line: 1 s. (*c*) Two single pulses. Scale line: 0.1 s. (*d*) Hypothesized origin of the tymbal organ. Size of triangles equal relative species richness of Hemipteran subgroups, comprising a total of 80 000+ described species (cladogram after Bourgoin & Campbell (2002), modified). Colours code for (vibrational) signal production by tymbal (yellow) as found in the Coleorrhyncha and the Heteroptera, and specialized tymbals (red) as found in the Fulgoromorpha and Cicadomorpha (formerly 'Auchenorrhyncha'). The existence of a tymbal in the Coleorrhyncha points to its presence in the ancestral species of all four taxa.

insects had already evolved: percussion, stridulation and tymbal vibration.

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