

Historical use of substrate-borne acoustic production within the Hemiptera: first record for an Australian Lophopid (Hemiptera, Lophopidae)

Adeline Soulier-Perkins,^{1*} Jérôme Sueur² and Hannelore Hoch³

¹Muséum National d'Histoire Naturelle, Département Systématique et Évolution, USM 601 MNHN & UMR 5202 CNRS, Case Postale 50, 45, Rue Buffon, F-75005 Paris, France.

²NAMC-CNRS UMR 8620, Bât. 446, Université Paris XI, F-91405 Orsay Cedex, France.

³Museum für Naturkunde, Institut für Systematische Zoologie, Humboldt-Universität zu Berlin Invalidenstr. 43, D-10115 Berlin, Germany.

Abstract Here the first record of communication through substrate-borne vibrations for the Lophopidae family is reported. The signals from *Magia subocellata* that the authors recorded were short calls with a decreasing frequency modulation. Acoustic vibrations have been observed for other families within the Hemiptera and a scenario concerning the historical use of vibrational communication within the Hemiptera is tested using a phylogenetic inference. The most parsimonious hypothesis suggests that substrate-borne communication is ancestral for the hemipteran order and highlights the groups for which future acoustic research should be undertaken.

Key words Cicadomorpha, Coleorrhyncha, evolutionary scenario, Heteroptera, Sternorrhyncha, substrate vibration.

INTRODUCTION

Many animals have been recently recognised for their ability to communicate through substrate-borne vibrations (Hill 2001). While elephants produce vibrations transmitted by the soil to communicate over very large distances (O'Connell *et al.* 1997; O'Connell-Rodwell *et al.* 2001), tiny insect species may emit substrate-borne vibrations on their host plant to exchange information at short range (Henry 1994; Virant-Doberlet & Čokl 2004; Cocroft & Rodríguez 2005). Among insects, the Hemiptera and the Neuroptera are probably the best-investigated groups for the substrate-borne vibrations they produce during mating behaviour (Claridge & Vrijer De 1994; Henry 1997; Kanmiya & Sonobe 2002; Gogala 2006).

Communication by substrate-borne vibration has been reported from 29 Hemiptera families, and more precisely, in 40% of the Fulgoromorpha families (Delphacidae, Cixiidae, Meenoplidae, Dictyopharidae, Tropiduchidae, Acanaloniidae, Issidae, Flatidae) (Čokl & Virant-Doberlet 2003). The Lophopidae (Hemiptera, Fulgoromorpha) have been recently studied in an evolutionary and biogeographical context (Soulier-Perkins 2001). This small monophyletic group with around 130 described species is confined to the tropical regions. This group is hypothesised to have originated somewhere in South-East Asia 65 million years ago. From this origin, the distribution extended northward with some

Lophopidae migrating into America via the Bering land bridge. Some other ancestors of the extant groups moved onto newly emerging land in the Pacific, expanding their distribution as far east as the Samoan Islands, and as far south as Australia (Soulier-Perkins 2000).

While evolutionary and biogeographical information has been gathered for these insects, no ethological studies have been yet undertaken. Only some aspects of copulatory mechanisms were studied for the genera *Jugoda* Melichar, 1915 and *Pyrilla* Stål, 1859 (Soulier-Perkins & Bourgoïn 1998). *Magia* is a monospecific genus endemic to Australia. *Magia subocellata* Distant, 1907 can be found on *Archontophoenix alexandrae* (F. Muell.) H. Wendl. & Drude, an Arecaceae growing in the central to northern Queensland coastal rainforest. *Magia subocellata* specimens can occur in significant numbers in greenhouses with *A. alexandrae*.

We report here the substrate-borne vibrations produced by a male of *M. subocellata*. Given that Lophopids can produce substrate-borne vibrations, we mapped the evolution of substrate-borne communication onto the Hemiptera phylogeny.

MATERIALS AND METHODS

Recording

Magia subocellata males and females were collected in the Kuranda butterfly sanctuary in Queensland in March 1997.

*soulier@mnhn.fr

Individuals were kept with parts of their host plant and sufficient humidity in a cage while being transferred to a field laboratory near Malanda, Queensland where they were recorded in the evening following their capture. One male and one female were placed together into a chamber where substrate-borne vibrations were recorded with a Magneto-Dynamic System (Strübing & Rollenhagen 1988) and a SONY TCD-5M Professional audio tape recorder. The ambient temperature was 28°C with a relative humidity of *ca.* 80%.

Signal analysis

Signals were digitised from the audiotape to a PC computer at a rate of 44.1 kHz with a 16 bit precision. The signal was then under-sampled at 2 kHz to increase frequency resolution. The calls were analysed using Seewave (Sueur *et al.* 2006) and Avisoft 4.33b acoustic software (Specht 2004). To increase the signal to noise ratio, a frequency filter was applied to the signal. The spectrum of the filter was designed as the complement of a Fourier Transform calculated in a signal section where only noise occurred. This manipulation allowed removing selectively those frequency bands, which were caused by background noise while preserving the sounds of the insect call. Call duration and intercall duration were measured on the envelope of the signal. Main frequency parameters were assessed by generating Fourier transforms (Hamming window, frequency resolution = 1.95 Hz).

Optimisation of attributes

The use of substrate-borne vibration in the hemipteran order is only partially documented and the primary homology is difficult to define. For this vibrational communication system, the signal production and perception mechanisms may have undergone changes across all the taxa. As such, it seems inappropriate to include this ethological character in a phylogenetic analysis. However, such characters that cannot be used for building the phylogeny can be optimised on an already built phylogeny and is called an attribute (Mickey & Weller 1990; Desutter-Grandcolas 1997; Grandcolas *et al.* 2001). Two states are coded: presence of substrate-borne vibration and unknown. The unknown state of this attribute might correspond to a true absence of vibration production but more likely to a lack of observation. The program used for the optimisation is MacClade (Maddison & Maddison 2002). Attribute states were mapped onto a composite Hemiptera phylogenetic hypothesis provided by Bourgoin and Campbell (2002). The fossil taxa originally included in this phylogeny were excluded here. The optimisation presented is the most parsimonious hypothesis.

RESULTS AND DISCUSSION

The recorded male of *M. subocellata* produced vibrations made of four successive calls regularly spaced (Fig. 1a). The duration of calls was 3.03 ± 0.44 s and the gap in between

calls lasted 12.47 ± 1.81 s. All calls showed the same pattern. They were made of a series of harmonics modulated in amplitude with the fundamental frequency (F_0) slowly decreasing from around 47 Hz at the beginning to around 32 Hz at the end of the call. There was a relatively constant dominant band throughout the signal between 240 and 280 Hz. This constancy associated with the frequency modulation implies successive drops in the dominant frequency from the fifth ($=6 \cdot F_0$) to the eighth harmonic ($=9 \cdot F_0$).

Although very few recordings were obtained, and the biological context in which the calls were emitted is not entirely clear, our recording suggests that at least some Lophopidae are capable of producing substrate-borne vibrational signals. Whether this acoustic production acts as a signal for intraspecific communication as it has been previously shown for other Fulgoromorpha (see below) must await a more detailed behavioural study.

The Lophopidae can be now recognised as one of the nine families of Fulgoromorpha that produce substrate-borne vibrations. There is no information available yet for the remaining Fulgoromorpha families, and further investigation is urgently needed in these taxa. The optimisation suggests that the use of substrate-borne vibrations is ancestral for the Fulgoromorpha (Fig. 2). The most parsimonious hypothesis (seven steps) implies that substrate-borne vibrational communication is ancestral for the Hemiptera. Nine steps are needed when the acoustic production is not considered as ancestral. Vibrational communication is observed within the five monophyletic lineages (Sternorrhyncha, Fulgoromorpha, Cicadomorpha, Coleorrhyncha and Heteroptera).

Vibrational communication was observed in three (Aleyrodoidea, Aphidoidea and Psylloidea) of the four groups that compose the Sternorrhyncha. The production mechanisms of communication differ slightly (Virant-Doberlet & Čokl 2004), but the substrate is always the support for signal propagation. Only the Coccoidea have not been reported to communicate by substrate-borne vibrational signals. Further investigation on the intraspecific communication system of this group is required to assess whether substrate-borne vibrational signals also play a role in male recognition and/or location, or whether this communication system has been replaced by another kind of communication. Within the Cicadomorpha, the ability to produce substrate-borne signals has been observed in five families: Aphrophoridae (Cercopoidea), Tettigarctidae and Cicadidae (Cicadoidea), Cicadellidae and Membracidae (Membracoidea) (Virant-Doberlet & Čokl 2004). However, the use of such a communication channel in Cicadidae is only documented in a single species (Stölting *et al.* 2002). Rather, air-borne signals are the main way used by cicadas to communicate (Sueur 2001). The Tettigarctidae that only use substrate vibrations are often considered as relict survivor of a primitive Mesozoic cicada radiation (Claridge *et al.* 1999). They are recognised as sister-group to the Cicadidae (Cryan 2005). It is therefore very likely that air-borne acoustic communication appeared later historically than substrate-borne acoustic communication and has to be considered as an autapomorphic

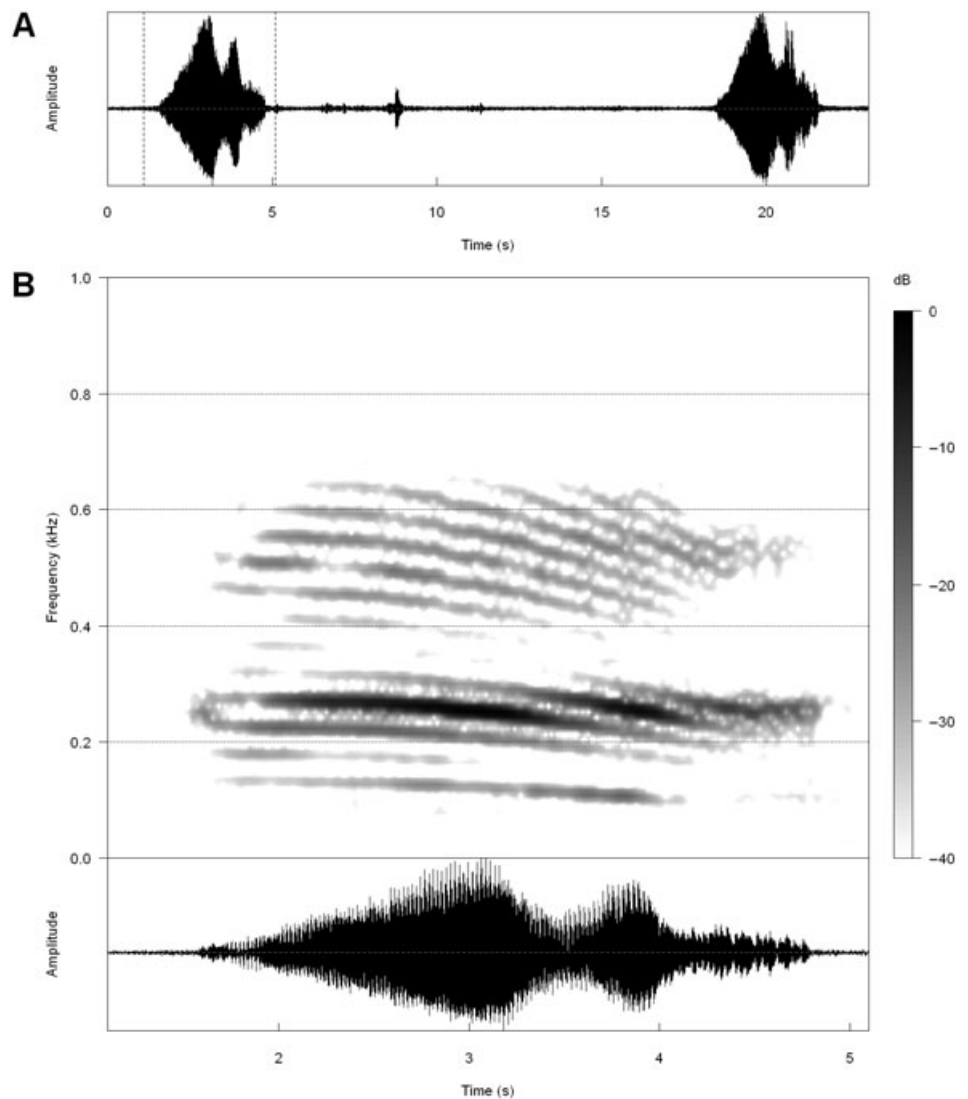


Fig. 1. (a) Oscillographic (amplitude vs. time) representation of two successive calls. (b) Oscillographic (amplitude vs. time) and spectrographic (frequency vs. time, amplitude following the grey scale) representations of a single call (call between vertical dotted lines in (a)).

behavioural character for the Cicadidae. This change in acoustic channel selection probably allowed the emitters to be heard by a larger number of receivers, and not limited to those individuals in physical contact with the plant. Within the Coleorrhyncha, vibrational signalling was recorded recently for a Peloridiidae (Hoch *et al.* 2006), which is often considered as a Gondwanan relict insect group. Within the Heteroptera, there is evidence for communication by vibrational signals in 18 families of the Cimicomorpha, Gerromorpha, Nepomorpha and Pentatomorpha (Virant-Doberlet & Čokl 2004), although production mechanisms are diverse. The optimisation shows uncertainty at the base of the heteropteran group, and research effort directed towards the Enicocephalomorpha and Dipsocoromorpha would aid in resolving this issue.

The optimisation on the Hemiptera phylogenetic hypothesis points to groups, which are in need of further investigation. We are convinced that further research focusing on acoustic communication will hold exciting discoveries and help elucidate

the evolutionary history of this largest non-holometabolous insect taxon.

ACKNOWLEDGEMENTS

We would like to express our sincere gratitude to Paul Zborowski, Kuranda, Queensland (Australia) for his generous hospitality extended to A.S.-P. and H.H. during fieldwork in Australia. We also thank T. Bourgoïn, MNHN, Paris, and M. Asche, Museum für Naturkunde, Berlin, for their help in the field, for their support and valuable comments on the manuscript. We are indebted to Thierry Aubin, CNRS, Paris for his help in acoustic analysis. Financial support was provided by the Germaine Cousin grant to A. Soulier-Perkins and the German Research Council (DFG) to H. Hoch. This publication is a contribution to the 'Biodiversity and Evolution of Fulgoromorpha' – a global Research Initiative (BEFRI) (<http://bach.snv.jussieu.fr/befri/>).

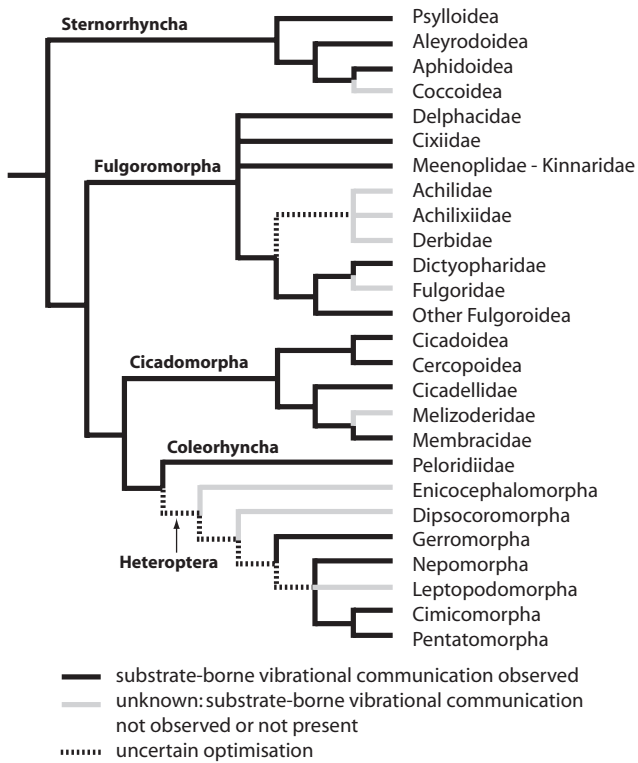


Fig. 2. Scenario for the evolution of substrate-borne communication for the Hemiptera. The hypothesis requiring the fewest steps is that substrate-borne vibrational signalling is ancestral for the entire group (seven steps). The composite phylogenetic hypothesis is extracted from Bourgoïn and Campbell (2002). Note, fossil taxa have been pruned.

REFERENCES

- Bourgoïn T & Campbell BC. 2002. Inferring a phylogeny for Hemiptera: falling into the 'Autapomorphic Trap'. *Denisa* **4**, 67–81.
- Claridge MF & Vrijer De PWF. 1994. Reproductive behavior: the role of acoustic signals in species recognition and speciation. In: *Planthoppers: Their Ecology and Management* (eds RF Denno & TJ Perfect), pp. 216–233. Chapman & Hall, London, UK.
- Claridge MF, Morgan JC & Moulds MS. 1999. Substrate-transmitted acoustic signals of the primitive cicada, *Tettigarcta crinita* Distant (Hemiptera Cicadoidea, Tettigarctidae). *Journal of Natural History* **33**, 1831–1834.
- Čokl A & Virant-Doberlet M. 2003. Communication with substrate-borne signals in small plant-dwelling insects. *Annual Review of Entomology* **48**, 29–50.
- Cocroft RB & Rodríguez RL. 2005. The behavioral ecology of insect vibrational communication. *Bioscience* **55**, 323–334.
- Cryan JR. 2005. Molecular phylogeny of Cicadomorpha (Insecta: Hemiptera: Cicadoidea, Cercopoidea and Membracidae): adding evidence to the controversy. *Systematic Entomology* **30**, 563–574.
- Desutter-Grandcolas L. 1997. Studies in caves life evolution: a rationale for future theoretical developments using phylogenetic inference. *Journal of Zoological Systematics and Evolutionary Research* **35**, 23–31.
- Gogala M. 2006. Vibratory signals produced by Heteroptera-Pentatomorpha and Cimicomorpha. In: *Insect Sounds and Communication* (eds S Drosopoulos & MF Claridge), pp. 275–295. Taylor & Francis, Boca Raton, USA.
- Grandcolas P, Delporte P, Desutter-Grandcolas L & Daugeron C. 2001. Phylogenetics and ecology: as many characters as possible should be included in the cladistic analysis. *Cladistics* **17**, 104–110.
- Henry CS. 1994. Singing and cryptic speciation in Insects. *Trends in Ecology and Evolution* **9**, 388–393.
- Henry CS. 1997. Modern mating systems in archaic Holometabola: sexuality in neuropterid insects. In: *The Evolution of Mating Systems in Insects and Arachnids* (eds JC Choe & BJ Crespi), pp. 193–210. Cambridge University Press, Cambridge, UK.
- Hill PSM. 2001. Vibration as a communication channel: a synopsis. *American Zoologist* **41**, 1133–1134.
- Hoch H, Deckert J & Wessel A. 2006. Vibrational signalling in a Gondwanan relict insect (Hemiptera: Coleorrhyncha: Peloridiidae). *Biology Letters* **2**, 222–224.
- Kanmiya K & Sonobe R. 2002. Records of two citrus pest whiteflies in Japan with special reference to their mating sounds (Homoptera: Aleyrodidae). *Applied Entomology and Zoology* **37**, 487–495.
- Maddison WP & Maddison DR. 2002. *Analysis of Phylogeny and Character Evolution (Macclade)*, Version 4.05 for OS X. Sinauer Associates, Inc., Sunderland, Massachusetts, USA.
- Mickevich MF & Weller SJ. 1990. Evolutionary character analysis: tracing character change on a cladogram. *Cladistics* **6**, 137–170.
- O'Connell CE, Arnason BT & Hart LA. 1997. Seismic transmission of elephant vocalizations and movement. *Journal of the Acoustic Society of America* **102**, 3124.
- O'Connell-Rodwell CE, Hart LA & Arnason BT. 2001. Exploring the potential use of seismic waves as a communication channel by elephants and other large mammals. *American Zoologist* **41**, 1157–1170.
- Soulier-Perkins A. 2000. A phylogenetic and geotectonic scenario to explain the biogeography of the Lophopidae (Hemiptera: Fulgoromorpha). *Palaeogeography, Palaeoclimatology, Palaeoecology* **160**, 239–254.
- Soulier-Perkins A. 2001. The phylogeny of the Lophopidae and the impact of sexual selection and coevolutionary sexual conflict. *Cladistics* **17**, 56–78.
- Soulier-Perkins A & Bourgoïn T. 1998. Copulatory mechanisms and sexual selection in the Lophopidae (Hemiptera: Fulgoromorpha). *Annales de la Société Entomologique de France* **34**, 149–162.
- Specht R. 2004. *SAVISOF-SAS Lab Pro*. Avisoft, Berlin, Germany.
- Stölting H, Moore TE & Lakes-Harlan R. 2002. Substrate vibrations during acoustic signalling in the cicada *Okanagana rimosa*. *Journal of Insect Science* **2**, 1–7.
- Strübing H & Rollenhagen T. 1988. Ein Aufnehmersystem für Vibrations-signale und seine Anwendung auf Beispiele aus der Familie Delphacidae (Homoptera Cicadina). *Zoologische Jahrbücher Physiologie* **92**, 245–268.
- Sueur J. 2001. Audiospectrographical analysis of cicada sound production: a catalogue (Hemiptera: Cicadidae). *Deutsche Entomologische Zeitschrift* **48**, 33–51.
- Sueur J, Aubin T & Simonis-Sueur C. 2006. *Seewave*, v. 1.1. [Cited October 2006.] Available from URL: <http://cran.r-project.org/src/contrib/Descriptions/seewave.html>
- Virant-Doberlet M & Čokl A. 2004. Vibrational communication in insects. *Neotropical Entomology* **33**, 121–134.

Accepted for publication 17 October 2006.