Chapter 15
Vibrational Communication in Heelwalkers (Mantophasmatodea)

Monika J. B. Eberhard and Mike D. Picker

Abstract Mantophasmatodea (Heelwalkers), described in 2002, is the most recently discovered insect order. Additionally, with only 21 species described to date, it is also among the smallest insect orders known. Mantophasmatodea are 1–4 cm long, secondarily wingless predators. They inhabit bushes, herbs, shrubs, or hide within grass tussocks in open semi-arid landscapes of sub-Saharan Africa. Adult males and females use percussive signals to communicate with one another, mainly for mate localization, recognition of male vs female, and potentially also for species recognition. Females drum their entire abdomen onto the substrate, producing single pulses spaced at regular intervals. Males use a special drumming organ located on their subgenital plate to generate groups of pulses (pulse trains), also repeated at regular intervals. Although most of the species investigated thus far occur in allopatry and have limited dispersal abilities, male vibrational signals are still surprisingly distinct from each other at an interspecific level, and most species can be distinguished by the structure of the male signal. Behavioral experiments additionally suggest that some information about species identity is encoded in male and female vibratory signals. However, the signals are probably mainly used for the localization of a potential mate within the structurally complex vegetation that the heelwalkers inhabit. Moreover, Mantophasmatodea possess very sensitive scolopidial organs to detect substrate vibrations—the well-developed subgenual organ complex within the tibia of all legs is probably most sensitive to the species-specific communication signals. Despite their recent discovery, comparatively little is known about their biology, behavior, and diversity.

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15.1 Introduction

Mantophasmatodea (Heelwalkers; Fig. 15.1) is the most recently described insect order; it was discovered in 2001 and formally described in 2002 (Klass et al. 2002). The description was based on two preserved museum specimens, collected in Namibia in 1909 and Tanzania in 1950. This discovery elicited a lot of scientific as well as public interest, since it was not expected that a new insect order comprising comparatively large species would have slipped the taxonomists' attention. The first extant specimens of Mantophasmatodea were found in 2002 in Namibia (Picker et al. 2002; Klass et al. 2003). Some autapomorphies of the order are the antennae that exhibit a well-separated basi- and distiflagellum and unusual antennomere structure (Drilling and Klass 2010), a median process on the subgenital plate of males (used for drumming), a triangular process on the third tarsomere (Buder and Klass 2013), and various details of the tentorium and female ovipositor. Unique characteristics are also found in the behavior of Mantophasmatodea, which keep their large arolia and last (fifth) tarsal segments of all legs lifted up and off the substrate. Only when walking on smooth surfaces, during copulation attempts, or when handling large prey, the arolia are lowered and used for firm attachment to the substrate (Eberhard et al. 2009). This unique habit gave rise to the vernacular name "Heelwalker" for the order. Another distinctive feature of Mantophasmatodea is their communication system, where both males and females drum their abdomens on the substrate to generate vibrational signals. The order is one of the smallest, with currently only 21 extant species described (Zompro 2001, 2005, 2008; Klass et al. 2002, 2003; Zompro et al. 2002, 2003; Engel and Grimaldi 2004; Arillo and Engel 2006; Zompro and Adis 2006; Huang et al. 2008; Eberhard et al. 2011; Wipfler et al. 2012, 2018). However, it is restricted to relatively poorly explored and inventoried southern African countries (South Africa, Namibia, Tanzania, Malawi, and likely Angola) (Roth et al. 2014; Dool et al. 2017) and the number of species is likely to increase with more intensive study in these areas. Additionally, fossil Mantophasmatodea have been found in Baltic amber from the Eocene (Arillo and Engel 2006; Engel and Grimaldi 2004; Zompro 2001, 2005, 2008) and in China from the Middle Jurassic (165 Mya) (Huang et al. 2008), indicating that the extant species are a relictual fauna. Extant Mantophasmatodea are known from sub-Saharan Africa, namely Namibia, South Africa, Malawi, Angola, and Tanzania. Adult individuals are ca. 1–4 cm in body length, and females are usually larger than males (Hockman et al. 2009; Roth et al. 2014). Their body has a brown, gray, green, or yellow basic color, often overlain by a mottled pattern. Dorsal, longitudinal striping patterns are common in many of the species. These secondarily wingless insects inhabit bushes (Fig. 15.2c, d), small trees, herbs, and grass in various semi-arid landscapes where they prey on other arthropods, catching them with their spinose fore- and midlegs (Fig. 15.1g). Their superficial resemblance to juvenile mantids (order Mantodea) likely contributed to their being overlooked for such a long time.

As is known thus far, Mantophasmatodea are annual, univoltine species (Tojo et al. 2004; Roth et al. 2014), appearing in the rainy season. Females oviposit in the

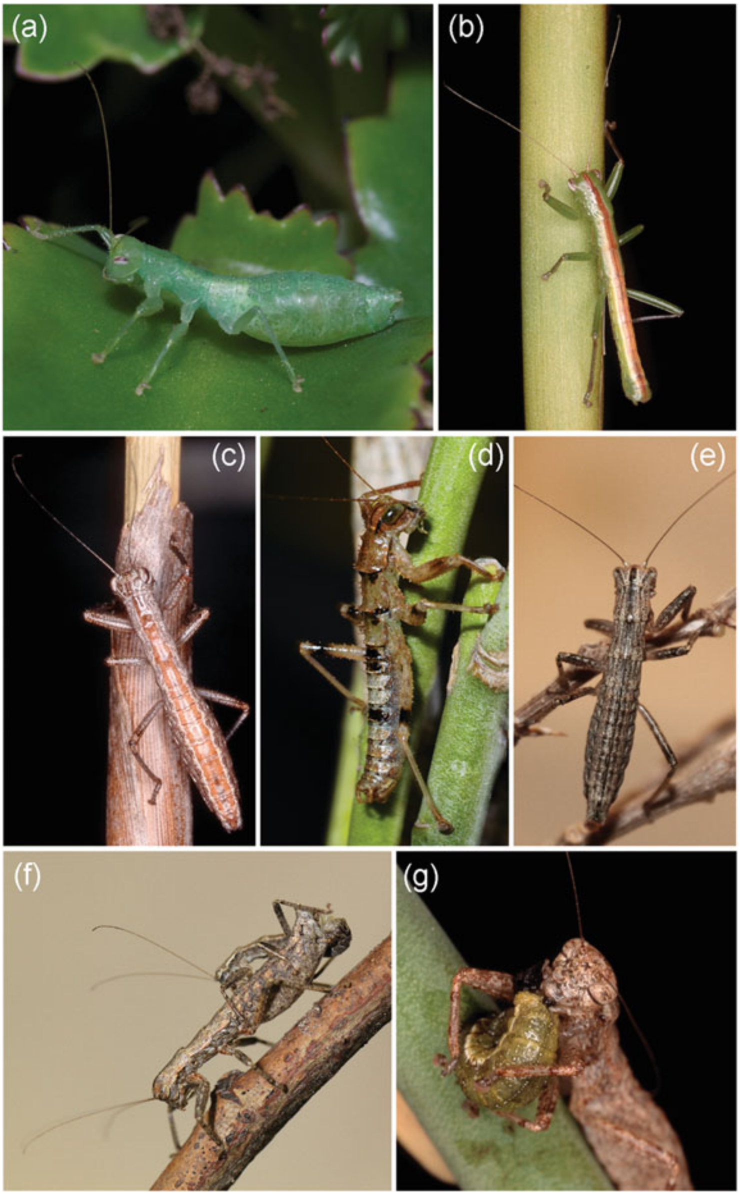


Fig. 15.1 Habitus of adult Mantophasmatodea: (**a**) Female *Viridiphasma clanwilliamense*, (**b**) male *Austrophasma caledonense*, (**c**) female *Lobatophasma redelinghuysense*, (**d**) male *Tyrannophasma gladiator*, (**e**) female *Karoophasma biedouwense*, (**f**) mating pair (male on top of female)—*K. biedouwense*, (**g**) female *Namaquaphasma ookiepense* eating a caterpillar. Photos by M. Eberhard (**e**), A. Lamboj (**a**), G. Nigro (**f**), M. Picker (**b**–**d**, **g**) (**a** and **f** are reprinted from Eberhard et al. 2018, with permission from John Wiley & Sons)

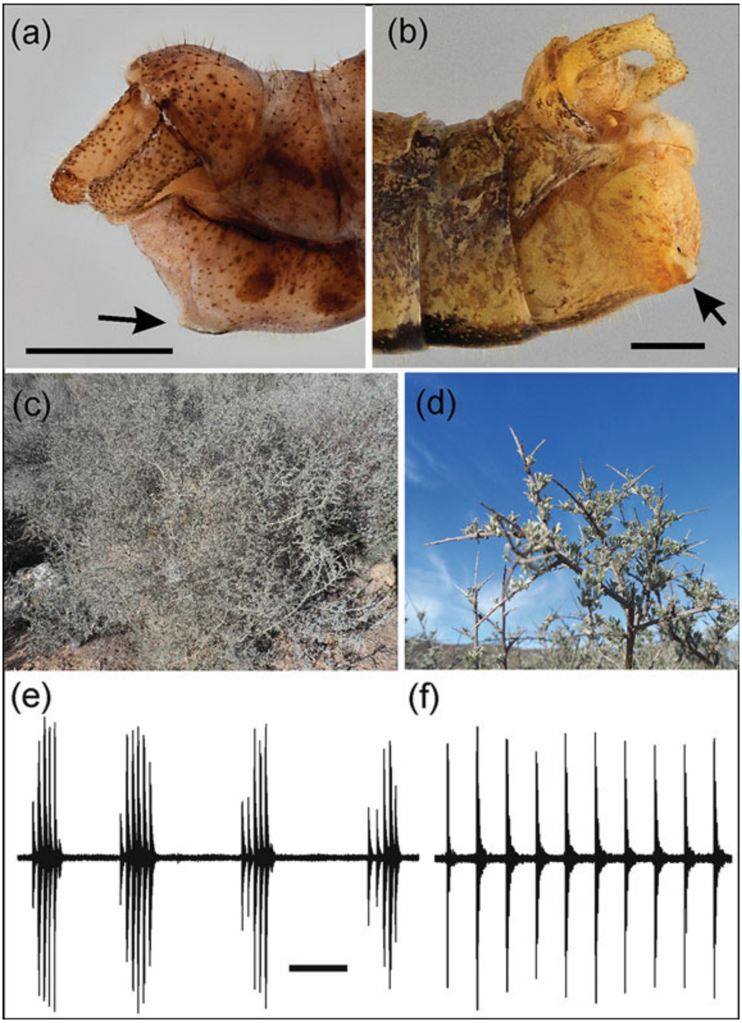


Fig. 15.2 Vibrational communication in Mantophasmatodea: (**a**) Postabdomen of a male *K. biedouwense* (Austrophasmatidae) and (**b**) *Tyrannophasma gladiator* (fam.n.) showing the drumming organ on the subgenital plate (arrows; photos by T.M. Dederichs, bars = 1 mm). (**c**, **d**) host plant (*Wiborgia* sp., Fabaceae) of *K. biedouwense* consisting of thin, woody branches (photos by S. Dool). (**e**, **f**) vibrational signals of Mantophasmatodea: the male signal (**e**) consists of regularly repeated pulse trains, whereas the female signal (**f**) comprises repeated single pulses (both signals from *Austrophasma gansbaaiense*). Bar = 1 s

ground, usually at the base of a shrub. By mixing eggs with a secretion and sand, they produce hard, water-resistant egg pods containing 10–12 (Tojo et al. 2004) or 20–30 eggs (Roth et al. 2014). A recent study showed that the number of eggs within an egg pod corresponds to the number of ovarioles in the paired ovaries of the females (Küpper et al. 2019). The hard, resistant egg pods are adapted to endure the hot and dry seasons; diapause lasts at least 8 months (Tojo et al. 2004; Roth et al. 2014), and egg pods maintained in the laboratory can undergo diapause for a number of years. Egg hatching is initiated by the first heavy rains of the rainy period; nymphs subsequently disperse on the nearest bushes and/or grass tussocks. Nymphs molt five times, each instar can be identified by the number of annuli within the basiflagellum of the antenna: Two annuli are added at each molt, deriving from the most basal annulus (meriston) in each instar, until the final (fifth) adult instar, which possesses 14 annuli in the basiflagellum (Hockman et al. 2009). The time between hatching of nymphs and reaching adulthood is between 2 and 4 months (Zompro et al. 2003; Hockman et al. 2009), depending on habitat and weather conditions (Tojo et al. 2004).

First observations on biotremology in heelwalkers were reported by Zompro et al. (2003) and Tojo et al. (2004), who referred to a “drumming” behavior of both males and females prior to mating. Since their discovery, Mantophasmatodea have been investigated in many different contexts, including taxonomy and phylogeny (e.g., Klass et al. 2003; Terry and Whiting 2005; Damgaard et al. 2008), morphology (e.g., Baum et al. 2007; Eberhard et al. 2009; Drilling and Klass 2010; Wipfler et al. 2015), fossil record (e.g., Zompro 2001; Arillo and Engel 2006; Huang et al. 2008), etc. Still many aspects concerning their ecology and behavior remain unknown. This chapter aims to outline the current knowledge of vibratory communication in Mantophasmatodea, the production and function of substrate-borne vibrational signals, as well as the detection of such signals by extremely sensitive leg scolopidial organs.

15.2 Production and Characteristics of Vibrational Signals

In Mantophasmatodea, individuals communicate via percussive signals generated by both sexes. Males use the median process on their subgenital plate (also called drumming organ) to tap on the substrate (Fig. 15.2a, b), while females drum the entire abdomen against the ground (Eberhard and Picker 2008). Through this behavior, heelwalkers produce substrate vibrations of a defined temporal pattern, transmitted through the branches of bushes or blades of grass on which they reside.

Male vibratory signals consist of repeated groups of pulses (pulse trains, Fig. 15.2e), and the simpler female signals comprise repeated single pulses (Fig. 15.2f, pulse = one tap with the abdomen on the ground). Analysis of the vibrational signals of 13 species of heelwalkers revealed that signals of the different species are of similar overall structure but differ in temporal characteristics such as pulse rate or pulse train duration (Fig. 15.3). Male signals particularly exhibit great interspecific differences concerning their temporal patterns. A principal component analysis (PCA, Fig. 15.4) of all measured parameters revealed that most of the species could be identified by the structure of the male calls alone (Eberhard and Eberhard 2013). This is rather surprising given that most of the extant species do not

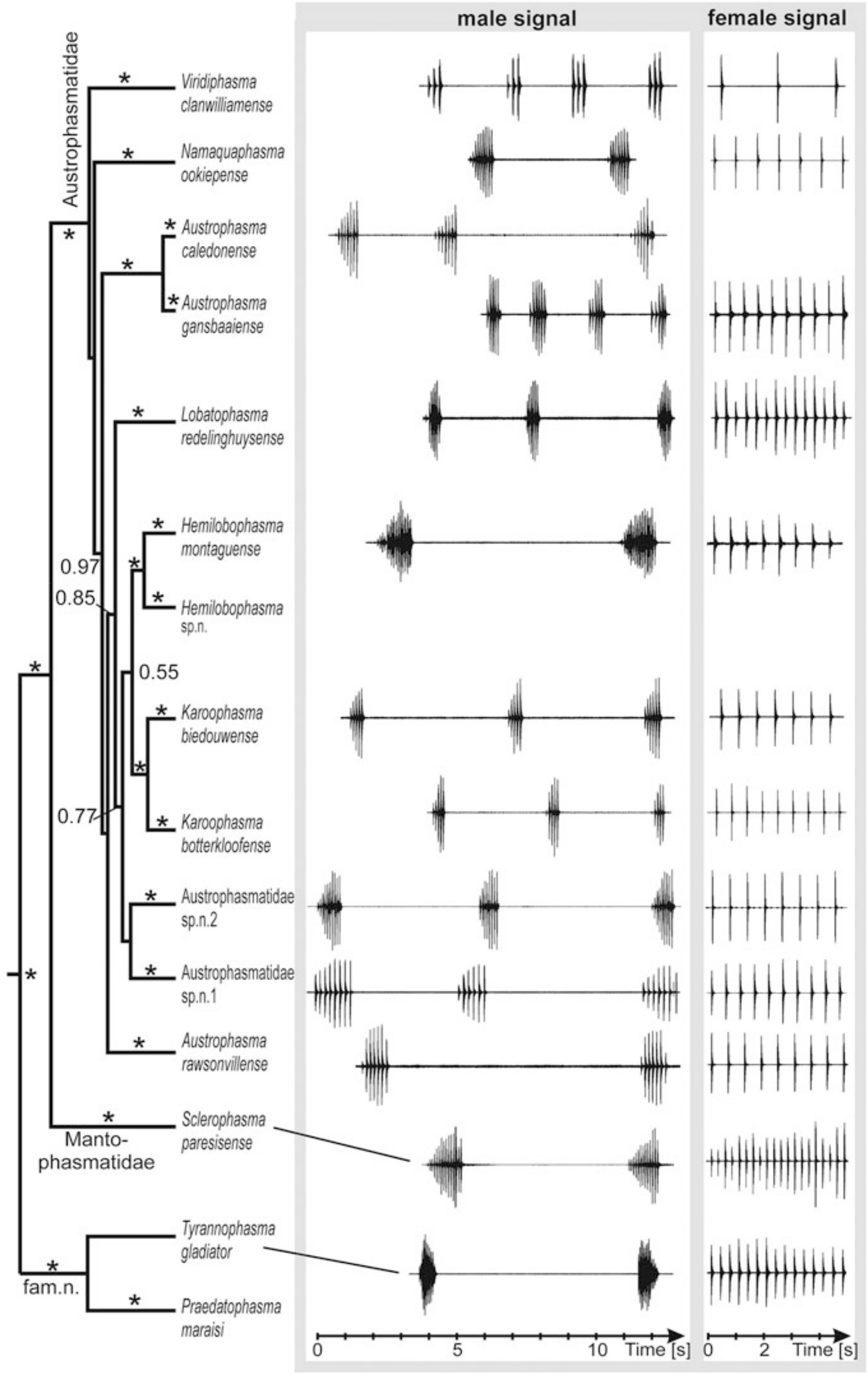
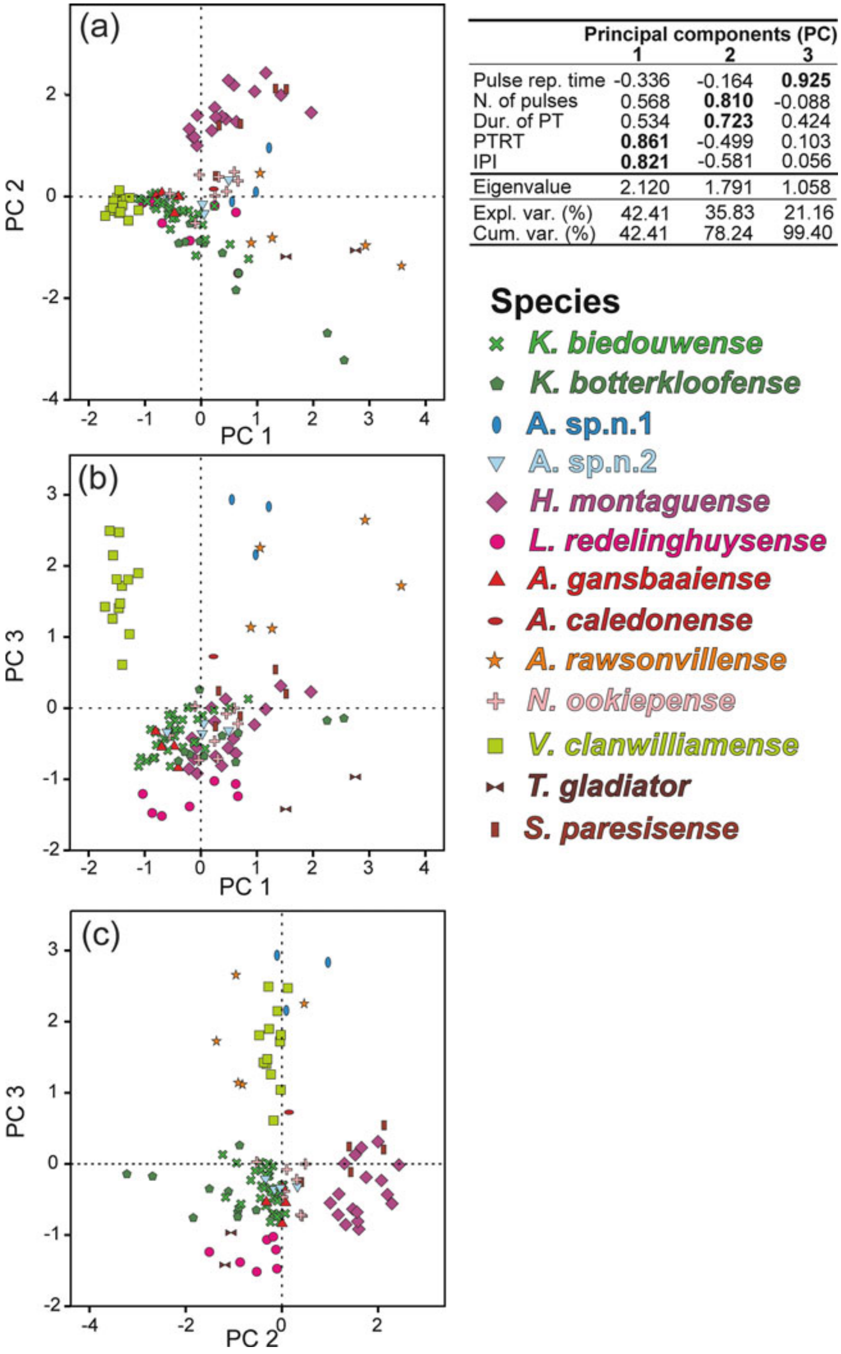


Fig. 15.3 Bayesian COI topology (810 bp) for the order Mantophasmatodea, together with vibrograms of male and female vibrational signals, recorded at ca. 20 °C. Bayesian posterior probabilities are indicated on the branches when ≥0.75 (asterisk indicates 0.99 or 1), outgroups not shown. Sequence data taken from Damgaard et al. (2008), processed by Serena Dool



	Principal components (PC)		
	1	2	3
Pulse rep. time	-0.336	-0.164	**0.925**
N. of pulses	0.568	**0.810**	-0.088
Dur. of PT	0.534	**0.723**	0.424
PTRT	**0.861**	-0.499	0.103
IPI	**0.821**	-0.581	0.056
Eigenvalue	2.120	1.791	1.058
Expl. var. (%)	42.41	35.83	21.16
Cum. var. (%)	42.41	78.24	99.40

Fig. 15.4 Scatter plots of principal components resulting from PCA of male call parameters of 13 Mantophasmatodea species—slightly modified after Eberhard and Eberhard (2013). (**a**) PC1 vs. PC2, (**b**) PC1 vs. PC3, (**c**) PC2 vs. PC3. Three PCs with eigenvalues >1 were extracted; parameters most strongly associated with a PC depicted in bold in the table. Most species cluster in groups and are separated from each other by at least one PC; however, there is also some overlap. *Dur* duration, *IPI* inter-pulse train interval, *N* number, *PT* pulse train, *PTRT* pulse train repetition time, *rep* repetition

occur in sympatry but are strictly allopatric with little overlap in distribution ranges. Investigation of male vibratory signals recorded from *Striatophasma naukluftense* [which exhibits an unusually long pulse train of 5–6 s duration, see Roth et al. (2014)] and from individuals belonging to the Sclerophasma/Mantophasma clade collected at different localities in Namibia suggests some intraspecific variation in vibratory signals at the population level (Roth et al. 2014). However, this variability might relate to species complexes. Due to the lack of behavioral (mate choice) experiments and detailed taxonomic investigations on these specimens, these questions remain to be solved. Typically, variability of vibrational signal traits within a species is rather low, with mean intra- and interindividual coefficients of variation (CV) below 20% (Eberhard and Eberhard 2013; Roth et al. 2014). This is in accordance with the mean CVs found for acoustic communication signals in insects and amphibians (23.6 and 20.7, respectively; see Reinhold 2009), and substrate vibrational signals in arthropods (26; see Eberhard and Treschnak 2018). Additionally, a positive correlation of the CV with duration of the respective signal trait, as found by Reinhold (2009) for acoustic signals of various insect and amphibian species, is also apparent in heelwalkers (Eberhard and Treschnak 2018).

Eberhard and Eberhard (2013) defined repeated pulse trains as male calls and repeated pulses as female calls, while Roth et al. (2014) argued that each pulse train might be termed a “call”. We suggest using the term “vibratory signal” instead of “call” to avoid such problems of definition. Irrespective of definition of terms, the repetition times of pulse trains within male signals seems to play a role in species recognition (M. Eberhard, personal observation).

Since vibratory signals in heelwalkers are produced by tapping the abdomen (in case of females) or the drumming organ (in case of males) onto the substrate, the spectral properties of the resulting signals mainly depend on the resonant characteristics of the substrate. A single tap on a solid surface produces a complex wave pattern that varies according to the nature of the substrate (Markl 1983; Henry 2006; Eberhard and Picker 2008; Eberhard et al. 2010; Chapman 2013; Mortimer 2017). Dominant frequency patterns elicited by a male heelwalker tapping on different substrates, measured with an accelerometer, changed with the substrate and distance between the accelerometer and the drumming insect; however, frequencies of the signals were similarly low, ranging between 50 and 1000 Hz (Eberhard et al. 2010). More recent investigations using a laser Doppler vibrometer revealed similar results (S. Küpper and M. Eberhard, unpublished data). Due to the complications resulting from the excitation by drumming on nonhomogeneous substrates with frequency-dependent attenuation during transmission of the signals (Mortimer 2017), information is rather coded in the time pattern of vibration pulse series (which remain constant across a range of excitatory substrates) and not in the spectral fine structure of the signals (Markl 1983). Accordingly, the temporal pattern of the vibrational signals is not affected during transmission through the heelwalker’s host plants (which mainly consist of thin stiff woody branches or more flexible grass culms, Fig. 15.2c, d). Recordings of male vibrational signals played back at the bottom of a bush in the natural habitat of *Karoophasma biedouwense* revealed that pulse repetition times, pulse train repetition times, and durations remained unchanged throughout the whole plant—even after several bifurcations and up to a distance of 70 cm. The vibration amplitude, measured as velocity with a laser Doppler vibrometer, even slightly increased (by +1.5 dB) at distances of 39 and 46 cm, but was attenuated by ca. –16 dB (but still detectable over background noise) after several bifurcations at a measuring distance of 70 cm from the source of vibration (D. Metze and M. Eberhard, unpublished data).

15.3 Function of Vibrational Signals

The only detailed behavioral study on heelwalker vibrational communication to date used two Austrophasmatid species, which occur in sympatry at Clanwilliam Dam, South Africa (Eberhard and Picker 2008). Here, both male and female vibrational signals differed significantly in all measured parameters between the two species. Male and female *K. biedouwense* did not react to heterospecific vibratory signals of *Viridiphasma clanwilliamense*. In contrast, when presented with vibrational signals of conspecific mates, female *K. biedouwense* ceased locomotion and started tapping continuously. Additionally, opening of the ovipositor valves was observed. None of the tested females reacted with continuous tapping to the playback of *V. clanwilliamense* males. In contrast, they increased locomotor activity. When subject to the playback of a conspecific female, *K. biedouwense* males exhibited enhanced locomotion, antennation, drumming, and searching behavior (Eberhard and Picker 2008). Before drumming, many males rubbed their abdomens against the substrate; the function of this unusual behavior is unknown. The searching behavior of males at bifurcations is noteworthy: when arriving at a furcation, excited males stopped and placed their forelegs on the branches of the fork, while keeping their mid- and hind legs on the original stem. After having received some signals from the continuously calling female, the male moved forward, placing its fore- and middle legs first onto both branches and finally onto the one branch that they had selected as being associated with the drumming female. Eberhard and Picker (2008) suggested that males might be able to detect minute differences in reception time of the female signal between their stretched legs and use this to localize the female, similar to the situation in chelicerates (Brownell and Farley 1979; Hergenröder and Barth 1983), stink bugs (Čokl and Virant-Doberlet 2003), and termites (Hager and Kirchner 2014). Males significantly decreased their reaction when presented with the playback of the sympatric, heterospecific female signal. However, they sometimes emitted a few vibratory signals in the absence of any playback stimulus. This suggests that adult males emit signals at random to test their environment for nearby, receptive females (Eberhard and Picker 2008).

As mating occurs in the absence of vibrational communication when males and females are in very close proximity (8–10 cm) (Eberhard and Picker 2008; Roth et al. 2014), vibratory signals are thought to serve for mate localization at the mid-range, mainly to bring the sexes together in the structurally complex bushes in which they reside. However, the playback experiments conducted by Eberhard and

Picker (2008) suggest that at least some information about species identity and sex is encoded in the vibratory signals, since male and female *K. biedouwense* did not react (or had a significantly lower reaction) to signals of the heterospecific, sympatric *V. clanwilliamense*.

When the male arrives at the female's position, he slowly approaches her and then quickly leaps onto her back, grabbing her with his legs. Both male and female do not display any vibratory signaling at this stage of mating (Eberhard and Picker 2008). The male bends his abdomen down in an S-shape around the right side of the female, who lifts up her abdomen. The male's large cerci facilitate the coupling, when the membranous phallus is expanded and inserted into the female vagina (Tojo et al. 2004; Eberhard and Picker 2008; Roth et al. 2014). Copulation lasts up to 3 days, during which the male does not feed, while the female still continues to capture prey and feeds (Zompro et al. 2003; Tojo et al. 2004; Klass 2009; Roth et al. 2014). Multiple matings have been observed, but no critical experiment has been conducted yet to investigate this in detail.

15.4 Detection of Vibrational Signals

Sensory organs (leg chordotonal organs) within all six legs detect substrate vibrations (Eberhard et al. 2010). These sensory organs consist of groups of scolopidia—details on the fine structure of such sensilla can be found in the extensive review by Field and Matheson (1998).

Eberhard et al. (2010) studied the anatomy and sensitivity of the leg scolopidial organs in *K. biedouwense* and *V. clanwilliamense* using serial semithin sections (light microscopy), SEM, micro-CT, and electrophysiology. They found five different scolopidial organs within each leg: a femoral chordotonal organ (FCO) spanning the femur, a subgenual organ (SGO), distal organ (DO), tibiotarsal scolopidial organ (TTO) within the tibia, and a tarso-pretarsal scolopidial organ (TPO) in the tarsus (Fig. 15.5). Additionally, groups of campaniform sensilla are located at the proximal tibia, in close proximity to the SGO inside. The number and location of scolopidial organs within the legs of the two heelwalker species corresponds well with that found in most other insect orders (Debaisieux 1938; Field and Matheson 1998; Lakes-Harlan and Strauß 2014).

The FCO consists of two separate scoloparia: the proximal scoloparium contains at least 20 scolopidia, located close to its proximal attachment site, whereas the distal scoloparium contains scolopidia and connective tissue dispersed along the whole length of the scoloparium. Such a separation of the FCO into two distinct scoloparia has also been described for orthopterans, stick insects, and stoneflies (Debaisieux 1938; Field and Matheson 1998). In locusts, the proximal scoloparium of the FCO was suggested to be a functional low-frequency receiver (Field and Pflüger 1989). This is probably also the case in Mantophasmatodea, since summed recordings from the leg nerve showed a response to vibrational stimuli of 5–80 Hz, even after destruction of all scolopidial organs distal to the FCO, whereas additional

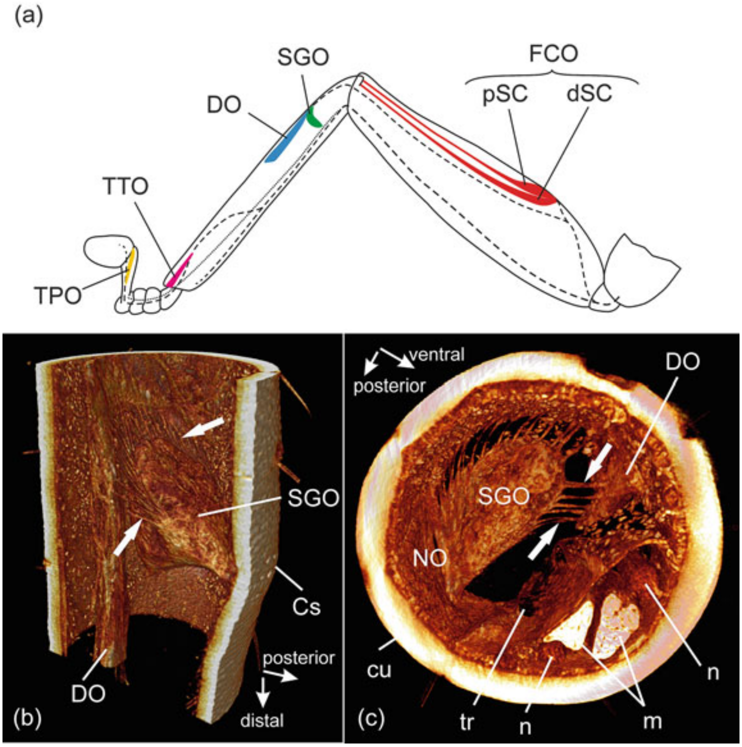


Fig. 15.5 (**a**) Schematic drawing of the leg scolopidial organs found in all six legs of Mantophasmatodea (slightly modified and reprinted from Eberhard et al. 2010, with permission from Elsevier; leg nerves shown as dashed black lines). The femoral chordotonal organ (FCO) consists of a proximal and distal scoloparium (pSC, dSC). The subgenual organ complex, which is probably most sensitive to substrate vibrations, consists of subgenual organ (SGO), Nebenorgan (not shown), and distal organ (DO), whereas the tibiotarsal scolopidial organ (TTO) and tarso-pretarsal scolopidial organ (TPO) are most probably proprioceptors. (**b**) Volume-rendered micro-CT image of an SGO within the hind leg of a *V. clanwilliamense* male in lateral view. (**c**) SGO within the front leg of a female *K. biedouwense* in transverse view. Arrows show scolopidia spanning from their posterior attachment site to the anterior border of the tibial cuticle. *cu* cuticle, *Cs* campaniform sensilla, *m* muscle, *n* nerve, *NO* Nebenorgan, *tr* trachea

ablation of the FCO dramatically decreased all responses to vibrational stimuli (Eberhard et al. 2010). These ablation experiments additionally showed that the TTO and TPO probably serve for proprioception (as joint chordotonal organs) rather than for vibration detection (Eberhard et al. 2010).

Most insect taxa studied so far have scolopidial organs within the proximal tibia, with the exception of Archaeognatha, Coleoptera, and Diptera (Debaisieux 1938; McIver 1985; Field and Matheson 1998; Lakes-Harlan and Strauß 2014). The subgenual organ complex of Mantophasmatodea consists of an SGO, a Nebenorgan [considered as part of the SGO, but see Strauß (2017)], and a DO. The SGO, which consists of 15–30 scolopidia, has a sail-like structure and spans the hemolymph space, approximately perpendicular to the longitudinal axis of the tibia (Fig. 15.5b, c). This organization is similar to other polyneopteran insects such as cockroaches, locusts, bush crickets, stick insects, and praying mantises (Lakes-Harlan and Strauß 2014). As in other insects, the SGO is considered to be most sensitive to substrate vibrations (Čokl and Virant-Doberlet 2003; Lakes-Harlan and Strauß 2014). Mantophasmatodea have one of the most sensitive receptor systems among insects, and are capable of perceiving vibrational stimuli with a threshold of less than 0.001 m/s^2 at a stimulus frequency of 600 Hz (Eberhard et al. 2010).

15.5 Conclusions and Outlook

Given the recent discovery of the order, it is not unexpected that many details on biotremology and mating behavior, as well as the ecology, diversity, phylogeny, and other aspects of mantophasmatodean biology are not, or only superficially, investigated so far—leaving huge research lacunae. Since Mantophasmatodea use a rather simple mode of vibrational communication (percussive signals), this fascinating insect order is perfectly suited to investigate the selective forces at work that produced and maintained the surprisingly high interspecific variability of advertisement signals, despite its low dispersal abilities.

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