

Chapter 10

Surface Structure of Sound Emission Organs in *Urania* Moths

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10.1 Introduction

The scales of Lepidoptera (butterflies and moths) are famous for specialized surface structures that interact with light to produce color. Such reflective scales occur in a variety of species, and like other scales and bristles of the arthropod cuticle develop from a single epidermal cell (review: Ghiradella 1994). An unusual function for scales, namely the production of acoustic signals was reported for male moths of the Uraniidae family (Lees 1992). The sound emission organs of male *U. leilus*, *U. brasiliensis* and *U. fulgens* are situated on the prothoracic legs and consist of two zones of specialized scales located on opposite sides of the coxa and the femur of each foreleg. On the external side of the coxa, opposite the femur, there is a peg which consists of a bundle of elongated scales that are hooked at the tip. In the proximal part of the femur, in front of the peg, there is a shallow concave surface, densely covered with scales that differ from scales on other parts of the femur (Lees 1992).

Trains of brief clicks are produced by rapid forward jerks of the forelegs in perching males or males handheld by the wings likely to result from stridulatory movements of the femur scales over the peg scales. The signals contain sonic and ultrasonic components with peak frequencies between 25–30 kHz. They possibly serve intraspecific communication. Female moths do not emit sound and lack stridulatory organs (Lees 1992).

The aim of this paper is to describe the main acoustic features of the clicks and to investigate in detail the structure of the sound emission organ in males of *Urania boisduvalii*, (Fig. 10.1), an endemic Cuban species (Barro and Rodríguez 2005) which has not been studied previously.

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Fig. 10.1 A live specimen of *Urania boisduvalii* perching on the subsurface of a leaf of one of its host plants, *Omphalea trichotoma*



10.2 Materials and Methods

To study the structure of the sound emission organ in *U. boisduvalii*, the prothoracic legs of males (N=9) and females (N=5) were separated from the thorax at the junction between the coxa and the prothorax with forceps. Four prothoracic legs from males with separated coxa and femur were photographed with a digital camera attached to a binocular (Leica MZ APO). Individual prothoracic legs from 7 males, also with coxa and femur separated, were mounted on small aluminum stubs using adhesive tape and conductive carbon cement (Leit-C). These preparations were dried for more than 24 hours in a desiccator. They were sputtercoated with gold (Agar-Sputter Coater) and observed and photographed with a scanning electron microscope (SEM Hitachi S4500) equipped with a digital camera. All the photographs were processed using Adobe Photoshop version 6.0.

In the laboratory, sound emissions were recorded from 4 male *U. boisduvalii* that were individually kept in 51 plastic containers. During recording, the moth was perching on a gauze net at a distance of 3–4 cm from the microphone. Within the same stridulatory sequence, motion of both front legs or only one front leg could occur. Due to the high speed and the irregularity of leg motions it is not possible with the employed techniques to directly correlate leg movements and sound emission patterns. Recordings were made with a U-30 Mini Bat Detector (Ultrasound Advice, England) that has a flat (+/-2 dB) spectral response characteristic in the range between 10 and 150 kHz. The high-frequency output of the bat detector was connected to a PCM-DAS 16S/330 (Computer Boards) data acquisition card set to a sampling frequency of 200 kHz. For data acquisition and analysis, Batsound (version 2.1) software was used. To detect the sound emissions in field conditions, and during long term observations of mating behaviour in the laboratory, a bat detector with headphones was used.

Temporal features were analysed for 10 pulses of each individual and included: duration of the short acoustic pulses, duration of the pulse trains and the mean pulse repetition rate during the train. Pulses were considered to be grouped in pairs or

trains if the pulse interval (defined as the temporal distance between amplitude maxima of consecutive clicks) was ≤ 6.6 ms, corresponding to a repetition rate of ≥ 150 Hz. Power spectra were obtained from individual pulses, emitted either isolated or forming part of trains, using fast Fourier transform (FFT) analysis (Batsound version 2.1) with a Hanning window and 64 data points at $5 \mu\text{s}$ interval between them ($320 \mu\text{s}$ time of analysis). From the power spectra, the peak frequency and the bandwidth 20 dB below the peak frequency were determined (10 from each of the 4 specimens). The shape of the power spectra (single peaked, with a broad plateau or double peaked) was classified for 267 spectra from the 4 specimens. The basal noise level of the recordings was more than 30 dB below the level at the peak frequency.

10.3 Results

In the laboratory, males of *Urania boisduvalii* may produce acoustic emissions while perching with their head downwards when other males or females approach or are nearby. Sound emissions are also produced by males handheld by the wings and stimulated with light touches to the head, the antennae or the distal end of the abdomen. Acoustic signals are generated by characteristic motion of the prothoracic legs (Fig. 10.2D) when the proximal end of the femur is moved against the distal end of the coxa of the same leg. No sound emission was ever detected in females or in males in which the prothoracic legs were removed or in males simply walking or flying.

In different places in the western part of Cuba (Viñales Valley, Guanahacabibes Peninsula, the East coast of Havana City) we detected sound emissions from specimens that were flying in pursuit of other conspecifics or other insects (different species of Lepidoptera, Hymenoptera and mainly Odonata), or humans. All sound emitting specimens were identified after capture as males based on the clear sexual dimorphism of the tympanic organ (Coro 1986). Typically, sounds were produced when the *U. boisduvalii* male was in close vicinity of one of its perching trees (*Persea americana*, *Ficus* sp., among others) or on one of its host plants (*Omphalea trichotoma* or *O. hypoleuca*). Usually the male pursued the “intruder”, which in most cases was identified as a male conspecific, during several seconds while emitting acoustic signals, and when the latter left the territory, the *U. boisduvalii* male returned to its perching site or flew in circles around the plant from which he started the pursuit and then stopped the sound emission. This behavior was observed throughout daytime, from shortly after sunrise until just before sunset.

In laboratory conditions, seven matings were observed, and in none was sound emission ever detected. Thus, all the behavioral data obtained so far in *U. boisduvalii*, both in the laboratory and in the field, suggest that sound emission is related to territorial behavior of the males.

The sound sequences produced by stridulatory behavior of individual *U. boisduvalii* males while perching in the laboratory are characterized by an irregular overall temporal pattern. Within one sound sequence there are trains of short pulses at a high repetition rate (above 150 Hz), isolated pulses and pulse pairs (Fig. 10.2A).

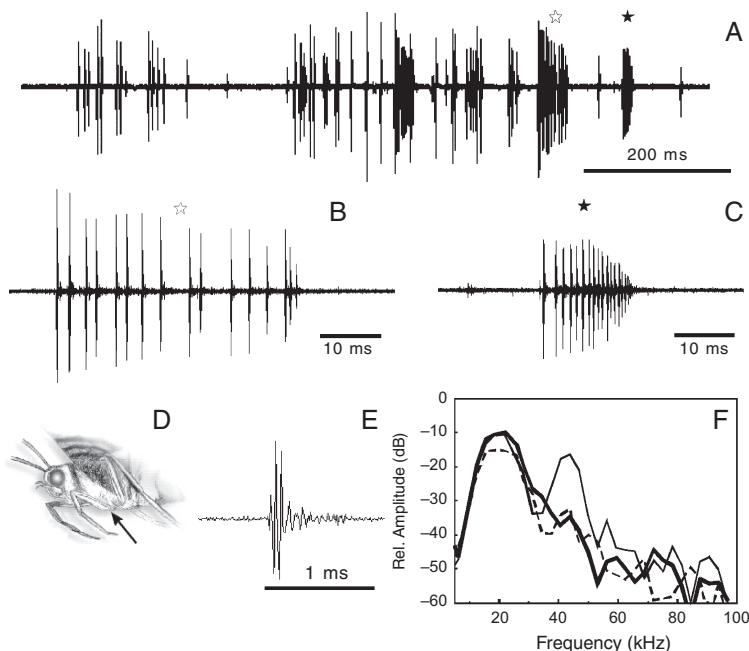


Fig. 10.2 A–C, E. Digitized oscillograms of sound emissions produced by a male of *U. boisduvalii* while perching. A. Sequence of one second showing the temporal variability of sound emissions which occur either as isolated pulses or as pulse trains. B and C show pulse trains from the same recording at higher temporal resolution. D. Artist's view of the frontal part of a *U. boisduvalii* male, showing the typical forward extension of prothoracic legs during stridulation. The arrow points to the femur. E. Time course of an individual click. The main acoustic energy is within the first three cycles. The amplitude spectrum is shown in F (thick solid line). F. Amplitude spectra of three representative clicks. The main acoustic energy is between 16–28 kHz. For further explanations see text

The last two pulse trains of this sequence are shown at higher temporal resolution in Figs. 10.2B, C. Figure 10.2B shows a train where pulses occur at irregular interpulse intervals (mean 2.61 ± 1.2 ms; range 0.96–5 ms). In the example shown in Fig. 10.2C, interpulse intervals are shorter (mean 0.83 ± 0.39 ms; range 0.33–1.25 ms) and decrease towards the end of the train. In a sample of 40 pulse trains, train duration ranged from 4 to 39.7 ms; the maximum number of pulses contained in a train ranged from 3 to 27 pulses, and pulse repetition rate ranged from 235 Hz to 1188 Hz. The pulses are brief clicks (Fig. 10.2E) with a duration of 390 ± 45 μ s (mean \pm SD). The spectrograms (Fig. 10.2F) reveal components in the sonic as well as the ultrasonic range and show maximal energy at a peak frequency of 19.9 ± 2.7 (range from 15.6 to 28.1 kHz), and a bandwidth of 25.1 ± 3.7 kHz (range from 15.1 to 36.0 kHz). The majority of amplitude spectra were single peaked ($N=174$; thick solid line in Fig. 10.2F) or showed a broad plateau between 16 and 28 kHz ($N=66$; broken line in Fig. 10.2F). Only rarely, did double peaked spectra occur with a distinct second maximum around 40 kHz ($N=27$; thin solid line in Fig. 10.2F). Clicks

with these amplitude spectra could occur within the same sound sequence and there was no correlation with other parameters such as repetition rate and intensity.

On the pro-femural surface of the coxa and at the proximal end of the pro-coxal side of the femur of the prothoracic legs in *U. boisduvalii* males there are specialized structures (Fig. 10.3), similar to the “peg” and “dish” described by Lees (1992) in other *Urania* moths. The prothoracic legs of females of *U. boisduvalii* lack these specializations (results not shown).

Figure 10.3A schematically shows the spatial relations between peg and dish in situ with the femur partially covering the peg. The photomicrographs in Fig. 10.3B, C were taken after separating the femur from the coxa, and turning the femur such that its pro-coxal surface is visible. The peg (Fig. 10.3B) is formed by a bundle of specialized elongated scales which at first glance resembles an old fashioned shaving brush but the structure is not radially symmetrical. The black stripe slightly off-center in the top part of the peg corresponds to the functional stridulatory edge described by Lees (1992), and is formed by the pointed tips of the apical ends of elongated scales which are bent such that they form a plate at the top of the peg (compare also Fig. 10.4A, B). In fresh and dried specimens, the peg has an oblique angle of orientation with the functional stridulatory edge pointing towards the femur. Surrounding the peg, there is a cuticula area completely denuded of scales below which there is an air-filled cavity in the coxa that is also observed in fresh specimens.

Near the proximal end of the inner surface of the femur, which in situ faces the peg, there is a widened area forming a shallow concave dish that is covered with a band of scales that appear different from those on the rest of the femur (Fig. 10.3C). The main differences are the much higher packing density of scales, the increased overlap of scales in a basic shingle-like arrangement with a more upright position of the free edges of the scales, and a less obliquely oriented angle of the scales' free edges towards the side of the femur (compare also Fig. 10.5).

A rotating motion of the femur over the coxa (arrow Fig. 10.3A) will move the scales of the dish over the stridulatory edge of the peg. Due to the directional arrangement of the fine surface discontinuities of the band of densely packed overlapping scales, only one direction of motion, namely the extension of the leg, should maximize mechanical resistance to the stridulatory edge of the peg.

Using the scanning electron microscope more details of the scales forming the peg, as well as their insertion zone on the surface of the coxa, can be described (Fig. 10.4). The view of the peg presented in Fig. 10.4A, B is towards the stridulatory edge of the highly asymmetric structure. The basic structural unit is an elongated flattened scale with a pointed tip. This shape varies from the stridulatory edge towards the opposite side of the peg. The scales just in front and below the stridulatory edge are straight, at the stridulatory edge their ultimate tips are sharply bent to form a fine hook and the overlying tips of neighboring scales together form an edge. Scales located at the circumference of the peg are buckled and hooked, with the length of the bent (hooked) portion increasing towards the distal side of the peg, but their tips all pointing towards the stridulatory edge. The overlap of the hooked portions of the scales creates the concave thatched roof of the peg. The hooks are directed against the force that is exerted during stridulatory movements and hence

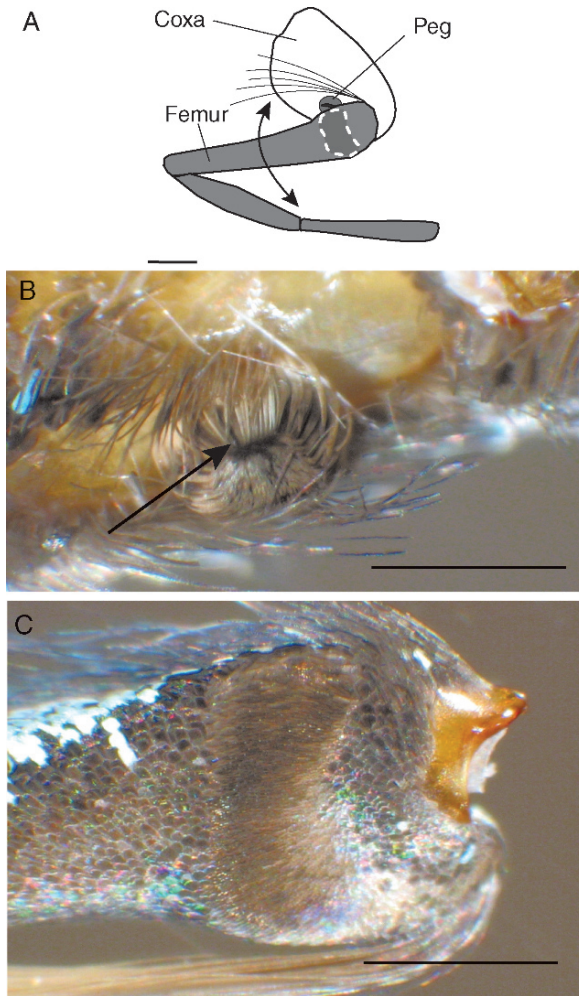


Fig. 10.3 The sound emission apparatus of a male *U. boisduvallii* in light microscopic resolution. **A.** Schematic illustration of the left prothoracic leg in lateral view. The peg arises from the external (pro-femural) side of the coxa. On the subsurface (pro-coxal side) of the femur, there is a band of specialized scales, the shape of which is indicated by the white stippled line. A brush of long bristles arising from the top aspect of the femur close to the coxa-femoral joint is indicated as a landmark. Rotational motion of the femur as expected to occur during stridulation (*double arrow*) will move the band of specialized scales across the peg. Scale bar: 1 mm. **B.** Photomicrograph of the peg. The peg is formed by a group of elongated and partially hooked scales. The functional stridulatory edge appears *black* and is indicated by an *arrow*. **C.** Photomicrograph of the subsurface (pro-coxal side) of the proximal end of the femur. All scales are arranged as overlapping shingles but there is a conspicuous band of very densely packed scales forming the stridulatory surface of the femur. Further explanations see text. Scale bar for B and C: 400 μm

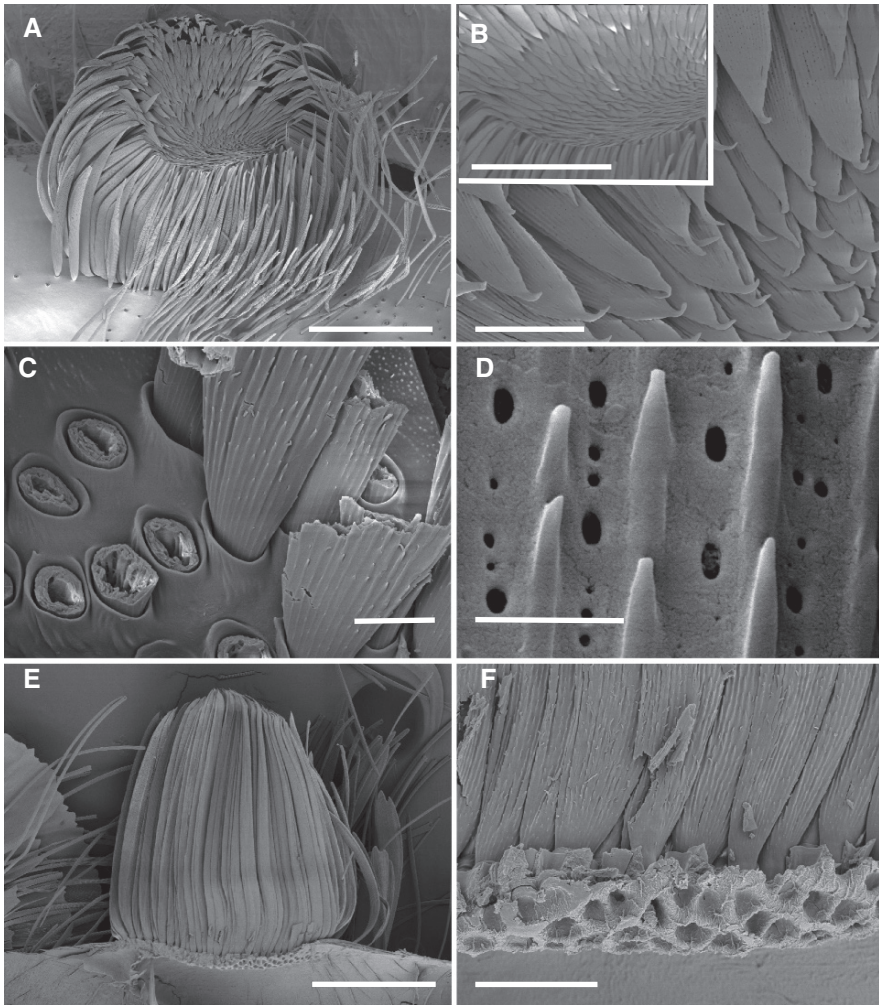


Fig. 10.4 Scanning electron micrographs of the peg on the coxa of the prothoracic leg of a male *U. boisduvalii*. **A.** Low magnification view of the peg. Scale bar: 200 μm . **B.** Stridulatory edge (inset with scale bar of 100 μm) and pointed tips of matted scales that form the peg plate (scale bar: 20 μm). **C.** External view of the insertion zone of the peg scales. Scale bar: 10 μm . **D.** External surface of a peg scale. Scale bar: 2 μm . **E.** The fracture through the peg, parallel to the stridulatory edge, shows the subsurface of the scale insertion site and cavity below. Scale bar: 200 μm . **F.** Higher magnification of the subsurface of the peg insertion site. Scale bar: 30 μm

could increase the stiffness of the peg in a direction dependent manner. Higher magnification of the peg roof surface (Fig. 10.4B) shows that the scales exhibit very fine pointed tips that form “microhooks”.

The insertion site of the peg scales in the coxa surface is depicted in Fig. 10.4C. The scales arise from oval holes in the cuticula that are surrounded by folds which

form extended sockets. This is a basic feature of attachment of butterfly scales (e.g. Greenstein 1972) but the sockets of peg scales are higher than those of scales in other regions of the coxa. Furthermore, due to the exceptionally high packing density of peg scales the walls of adjacent sockets are in tight apposition.

The peg scales conform to the basic architecture of butterfly scales (Downey and Allyn 1975, review Ghiradella 1994). They are hollow, with an oval cross-section at their origin and a flattened profile in their free portion. Their external surface exhibits parallel longitudinal ridges that terminate in apically oriented spines (Fig. 10.4C). In between the ridges and spines, there are scale windows having different diameters (Fig. 10.4D).

Figure 10.4E shows a preparation of the peg that has been fractured parallel to the stridulatory edge to expose the subsurface of the scale insertion site. Below the peg there is a cavity whose cuticular lining is smooth, except for the region just underneath the peg. There, the inner aspect of the cuticula presents a honeycomb structure shown in higher magnification in Fig. 10.4F. This ensures a deep and strong insertion of these scales on the coxa, and creates a specialized region of mechanically reinforced cuticula within the roof of the underlying cavity. The robustness of the insertion site is documented by the facts that the peg scales are very hard to remove mechanically or by treatment with 30% NaOH.

SEM-pictures of the proximal end of the femur of the prothoracic legs in *U. boisduvalii* males are shown in Fig. 10.5. The low power view (Fig. 10.5A)

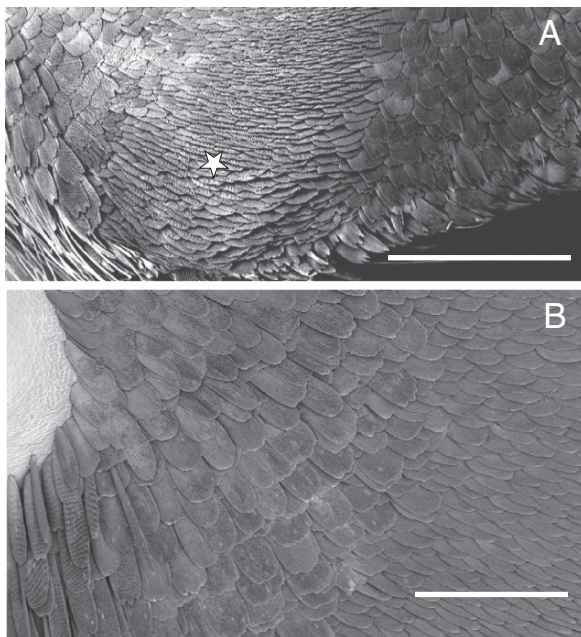


Fig. 10.5 Scanning electron micrographs of the band of specialized scales on the proximal end of the femur of the prothoracic leg in a *U. boisduvalii* male. **A.** Low power view of the lower portion of the band of specialized femur scales (asterisk). Scale bar: 400 μm . **B.** Higher magnification view of the transition zone between unspecialized and specialized femur scale areas proximal to the coxa-femoral joint. Scale bar: 200 μm

demonstrates the more upright position and the higher packing densities of scales within a band across the femur as compared to neighboring regions. The portion of the band indicated by a star is the most ruffled and thus the most likely candidate for generating friction. During femur extension this is the first region which encounters the stridulatory edge of the peg. Figure 10.5B shows the transition between the specialized band of scales and the scales of the neighboring proximal part of the femur at higher magnification. In the non-specialized region, only the bases of the scales are covered by overlap, whereas in the specialized region scale overlap is greatly increased so that only the smooth apical edges of scales are free.

10.4 Discussion

In adult lepidopterans the sound producing structures are more diverse and less well known than their auditory organs (for reviews see Spangler 1988, Scoble 1992, Conner 1999, Minet and Surlykke 2003, and literature cited therein). Sound emission organs have evolved independently in different superfamilies and sound producing surfaces can be located on the legs, the wings, the thorax and the abdomen, including the genitalia. The best studied type is the tymbal organ formed by modified cuticular regions associated with an air-filled cavity. In arctiids, the tymbal organs are on the metathorax and sound is emitted when the surface of the tymbal organ buckles inwards due to the action of the basalar muscle as well as when it buckles outwards during muscle relaxation (Blest et al. 1963). In Galleriinae (Pyraloidea), the tymbals are on the tegule and if the surface is smooth, as in *Achroia grisella* and *Galleria mellonella*, then one short acoustic pulse (less than 500 μ s duration) is produced during inward as well as outward buckling. If the surface features corrugations (microtymbals), as in *Corcyra cephalonica*, each tymbal buckling produces many short pulses (Spangler et al. 1984, Spangler 1986, 1987, review: Conner 1999, Minet and Surlykke 2003).

Sound producing organs involving the interaction of two surfaces, either based on a percussive or stridulatory mechanism, have been studied less than the tymbal organs. The best-studied examples for a percussion mechanism are the Australian “whistling moths” (genus *Hecatesia*: Agaristinae, Noctuidae). Males possess conspicuous cuticular knobs named “castanets”, associated with a large area that acts as an acoustic resonator in the forewings. The “castanets” are clashed against each other during flight but only while defending territory (Bailey 1978, Surlykke and Fullard 1989). Stridulation by rubbing of two hard surfaces has been described in other Noctuidae, e.g. male *Rileyiana fovea* emit sound by scraping a stridulatory area on the hindleg against a resonating blister of the hindwing (Surlykke and Gogala 1986). In male *Syntonarcha iriastis* (Pyraloidea, Crambidae, Odontiinae), the sound emission organ seems to involve modified areas of the genitalia acting as the file, and of the eighth abdominal segment which apparently functions as the scraper (Gwynne and Edwards, 1986).

Stridulation by relative motion of two surfaces of modified scales has only been described in Smerinthinae, Sphingidae and the genus *Urania*. Certain species of Smerinthinae and Sphinginae (Sphingidae, Bombycoidea) produce sound emissions by rubbing modified valvular scales, called “friction scales”, against other modified scales located on the eighth abdominal segment (Nässig et al. 1992).

Although also based on stridulation of surfaces of modified scales, the sound production mechanism first described by Lees (1992) for *Urania* moths is unique. Our data extend his morphological observations concerning details of peg scale structure and their specialized zone of apparently reinforced site of insertion, and support and extend his ideas on the sound production mechanism.

Based on light microscopic observations of artificially induced stridulation in a freshly killed specimen, Lees concluded that the peg does not act as a simple “scraper” working against the specialized scales of the femoral plate (the washboard principle). Rather, friction against the functional scraping edge of the peg induces an elastic deformation of the peg which leads to a percussive motion of the structure against the femur that appears to be the main event in click generation. Amplification of the acoustic signal could occur in the enlarged and hollow chambers situated below the peg and in the femur (Lees 1992).

By using stored elastic energy in the peg, such a mechanism should greatly increase the impact force and hence sound amplitude. In terms of its structural characteristics, the rubbing mechanism depends on the rigidity of the peg roof ensured by the directional orientation of the hooked ends of matted scales (Lees 1992 and present study). Additional factors are the elasticity of the free portions of the peg scales distal from the stridulatory ridge indicated by their distinct curvature, the rigidity of their basal attachments, and the properties of the surrounding scale-free cuticula.

To be able to further elucidate the sound production mechanism it will be necessary to directly correlate sound emission and leg motion, to perform measurements of peg vibration, and to manipulate the resonant properties of the hollow chambers in coxa and femur.

Sound production in male *Urania* will depend on the degree of apposition of the femur cushion relative to the peg, the pressure between coxa and femur which influences friction, and the starting point and duration of leg extension. The joint between coxa and femur is a ball and socket joint, and the degree of freedom in rotation and angulation could be enlarged due to a greatly reduced trochanter. This explains why sound emission is not obligatory during flight or walking but only produced when the males jerk their forelegs during territorial behavior. Together with the fact that males can stridulate by alternating motion of the forelegs or with a single leg (Lees 1992), this also could explain why the temporal pattern of the sound emission is so variable, ranging from production of single pulses up to emitting long pulse trains. The temporal irregularity of acoustic emissions could represent an important information bearing element during territorial behavior of *Urania*. In contrast, arctiids who possess tymbals with corrugations emit in a much more regular temporal pattern (Sanderford and Conner 1990, Sanderford et al. 1998, review: Minet and Surlykke 2003, and literature cited therein).

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