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Tympanal and atympanal ‘mouth-ears’ in hawkmoths (Sphingidae)

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The labral pilifers and the labial palps form ultrasound-sensitive hearing organs in species of two distantly related hawkmoth subtribes, the Choerocampina and the Acherontiina. Biomechanical examination now reveals that their ears represent different types of hearing organs. In hearing species of both subtribes, the labral pilifer picks up vibrations from specialized sound-receiving structures of the labial palp that are absent in non-hearing species. In Choerocampina, a thin area of cuticle serves as an auditory tympanum, whereas overlapping scales functionally replace a tympanum in Acherontiina that can hear. The tympanum of Choerocampina and the scale-plate of Acherontiina both vibrate maximally in response to ultrasonic, behaviourally relevant sounds, with the vibrations of the tympanum exceeding those of the scale plate by *ca.* 15 dB. This amplitude difference, however, is not reflected in the vibrations of the pilifers and the neural auditory sensitivity is similar in hearing species of both subtribes. Accordingly, morphologically different—tympanal and atympanal—but functionally equivalent hearing organs evolved independently and in parallel within a single family of moths.

Keywords: auditory mechanics; bioacoustics; hawkmoths; insect hearing; mechanoreception; sound perception

1. INTRODUCTION

In insects, the sensation of the pressure component of air-borne, high-pitched sounds at frequencies in the kilohertz range is usually mediated by tympanal ears (for reviews see Michelsen & Larsen (1985), Hoy & Robert (1996), Hoy (1998) and Yager (1999)). Although insect tympanal hearing organs have evolved several times independently and can occur on a variety of body parts (Yack & Fullard 1990), their basic architecture is surprisingly uniform. By definition, tympanal hearing organs comprise a sound-receiving tympanum, i.e. a more or less thin-walled area of cuticle that is apposed on an air space and vibrates in response to sound. Tympanal vibrations, in turn, are transduced by a chordotonal sensory organ that is associated with the tympanum (Hoy & Robert 1996; Hoy 1998; Yager 1999).

A few examples seem to show that insect ears can be fully functional in spite of the lack of a tympanum. Usually when a tympanum has been reported to be absent, the region of the cuticle that forms the sound receiver is simply not differentiated and conspicuous enough to call it a tympanal membrane (Nelson 1980; Lakes-Harlan *et al.* 1991; Van Staaden & Römer 1998; for a review see Hoy & Robert (1996)). There is, however, one reported case in which a whole mouthpart has been suggested to replace a tympanum. Hawkmoths of the subtribe Choerocampina use hearing to detect the ultrasonic echolocation signals of insectivorous bats, and thus to escape them (Roeder *et al.* 1968). Their ears are located on either side of the head (for reviews see Roeder (1976), Hutchings & Lewis

(1983), Michelsen & Larsen (1985), Scoble (1992) and Yager (1999)). Each ear comprises a chordotonal organ with a single sensory cell that attaches to the base of the labral pilifer, a small, bristled process located laterally to the tongue (Roeder *et al.* 1970; Göpfert & Wasserthal 1999*b*) (figure 1*a*). The auditory function of this chordotonal sensory organ is accompanied by structural modifications of two mouthparts, the labral pilifer itself and the labial palp (figure 1*a*). The pilifer of Choerocampina is characteristically bilobed and, in addition, the second segment of the labial palp is swollen, devoid of scales, and filled by a large air sac. In the natural arrangement, the distal lobe of the pilifer and the inner surface of the second palp segment are closely apposed to each other—a physical contact that appears to be a prerequisite for sensitive hearing. Indeed, deflection of the palp from the pilifer causes a drop in acoustic sensitivity by *ca.* 35–40 dB (Roeder *et al.* 1968, 1970; Roeder & Treat 1970; Roeder 1972). Accordingly, the labial palp has been proposed to serve as a sound-receiver that deflects the labral pilifer by its vibrations. In this way, sound energy appears to be transmitted to the auditory sensory cell at the pilifer’s base (Roeder *et al.* 1970; Roeder 1972; Göpfert & Wasserthal 1999*b*). Although the presence of a tympanum on the palp of choerocampine hawkmoths has not rigorously been tested, the ears of these hawkmoths are generally considered to be atympanal (Hutchings & Lewis 1983; Michelsen & Larsen 1985; Cook & Scoble 1992; Scoble 1992).

Recently, ultrasound-sensitive hearing organs have been identified in some species of another hawkmoth subtribe, the Acherontiina (Göpfert & Wasserthal 1999*a,b*). Remarkably, hearing in these hawkmoths involves the same sensory and accessory structures that also form the ears in Choerocampina (Göpfert & Wasserthal 1999*a,b*). The structural specializations that accompany hearing in

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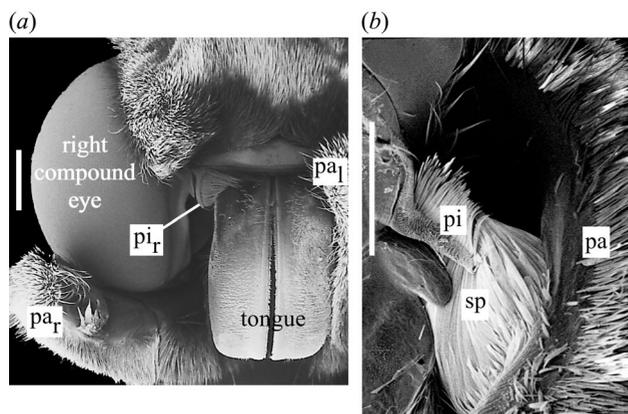


Figure 1. Anatomy of pilifer–palp hearing organs in hawkmoths. (a) Head of the hearing acheroiine species *A. atropos* (frontodorsal view). The left labial palp (pa_l) is in its natural, adducted position, completely concealing the left pilifer. The right palp (pa_r) has been deflected from the head, thus exposing the right pilifer (pi_r). (b) Contact between the palp (pa) and pilifer (pi) in *A. atropos*. A characteristic feature of hearing Acherontiina is the pilifer in close contact with the scale-plate (sp) of the palp. Scale bars, 1 mm. ((b) is reprinted from Göpfert & Wasserthal (1999a), with permission from the Company of Biologists Ltd.)

the two subtribes are, however, vastly different. The pilifer of Acherontiina lacks a distinct distal lobe (figure 1a), and the second palp segment is neither swollen nor void of scales as in Choerocampina, but deeply depressed on its inner surface (figure 1b). Despite these anatomical differences, hearing in Acherontiina apparently also involves the transmission of vibration from the palp to the pilifer. As in Choerocampina, deflection of the palp causes a decrease in sensitivity, which, in Acherontiina, drops by ca. 20–25 dB (Göpfert & Wasserthal 1999a,b).

The similar auditory functions but different anatomy of the pilifer–palp system in hearing Choerocampina and Acherontiina gave rise to the present study, which focuses on the process of sound reception in hawkmoths. In order to identify sound-receiving structures and, more generally, to evaluate the auditory significance of the structural specializations observed, we compared the mechanical response of the pilifers and palps in a hearing choerocampine, a hearing acheroiine, and a non-hearing acheroiine species. To assess the auditory relevance of the palp mechanics, we also examined the response characteristics of auditory neurons, thus facilitating comparisons between mechanical and neural responses.

2. MATERIAL AND METHODS

Three hawkmoth species were examined, including the hearing choerocampine species *Hippotion celerio* L., the hearing acheroiine species *Acherontia atropos* L. (the death's head moth), and the non-hearing acheroiine species *Panogena lingens* Butler. All animals were raised in the laboratory at the University of Erlangen, the stocks originating from the Canary Islands (*H. celerio*), Kenya (*A. atropos*) and Madagascar (*P. lingens*).

For mechanical examination, the animals were transferred to Odense University. Prior to the analysis, the animals were decapitated and the heads were mounted with modelling clay

on a holder. To facilitate mechanical measurements, the medially facing pilifer–palp system had to be exposed on one side of the head. This was performed either by removing the palp on the head's other side or, alternatively, by splitting the whole head in the median axis with a razor blade. The latter approach, which provided better accessibility, was preferred. When this approach was used, measurements were only taken immediately after the surgery, and desiccation was prevented by perfusing the preparation with saline (Kaissling & Thorson 1980). Both surgical approaches, when subsequently conducted in the same animal, revealed comparable vibrational responses, indicating that the splitting of the head did not affect the mechanical properties of the pilifer and the palp.

Sound-induced mechanical vibrations were examined using a Dantec laser Doppler vibrometer (model GLG53650; Dantec Dynamics A/S, Skovlunde, Denmark). Acoustic stimuli were 5 ms broadband frequency sweeps (bandwidth 1–100 kHz) generated by a dynamic signal analyser (HP3562A; Hewlett-Packard, Palo Alto, CA, USA). The stimuli were power-amplified (Xelex type DD10-P9; distributed by Xelex Corporation) and broadcast from a Technics leaf tweeter (4288; Technics Music Canada, distributed by Panasonic Technologies Company) positioned at a distance of ca. 35 cm from the preparation (intensity at the position of the animal 85–90 dB sound pressure level (SPL) (re. 2×10^{-5} Pa)). Amplitude spectra of the vibration velocity were normalized to the acoustic stimulus by the computation of transfer functions, calculated as the energy spectrum of the laser vibrometer signal divided by the energy spectrum of the stimulus, measured by a reference microphone (B&K, type 4138; Brüel & Kjaer, Naerum, Denmark) placed at the ear.

Neural threshold curves were determined at the University of Erlangen by recording extracellularly from auditory neurons. In *A. atropos*, we examined the afferent response of the single auditory sensory cell by recording from the labral nerve using a dorsal approach (Göpfert & Wasserthal 1999b). In *H. celerio*, this nerve is less accessible for electrophysiological recordings. Therefore, we analysed the response of a descending, second-order interneuron in the cervical connective (Roeder 1972), which is expected to exhibit frequency characteristics comparable to the afferent, but may have higher thresholds. The descending interneuron examined is characterized by receiving input from both ears with little or no summation (Roeder 1972). To preclude any binaural summation, the contralateral ear was destroyed prior to the experiments by removal of the pilifer. In *P. lingens*, auditory responses could neither be detected in the labral nerve nor in the neck connectives, even when exposed to intense acoustic stimuli (≤ 95 dB SPL). Correspondingly, previous behavioural experiments also revealed no evidence for ultrasonic hearing in this apparently non-hearing species (Göpfert & Wasserthal 1999a).

The set-up and stimulus protocol for electrophysiological recordings have been described (Göpfert & Wasserthal 1999b). In brief, acoustic stimulus pulses (30 ms duration, 0.3 ms rise/fall time, 3 Hz repetition rate) were broadcast by a Technics leaf tweeter (10TH400C) positioned 40 cm from the hawkmoth preparation. For threshold determination, the responses to acoustic stimuli at frequencies between 5 kHz and 80 kHz were examined with a frequency resolution of 5 kHz. Intensity was varied in 3 dB steps, with each intensity being presented five times. Based on these measurements, intensity–response plots were computed for each frequency tested. Threshold intensity, defined as the intensity eliciting an average response of one spike

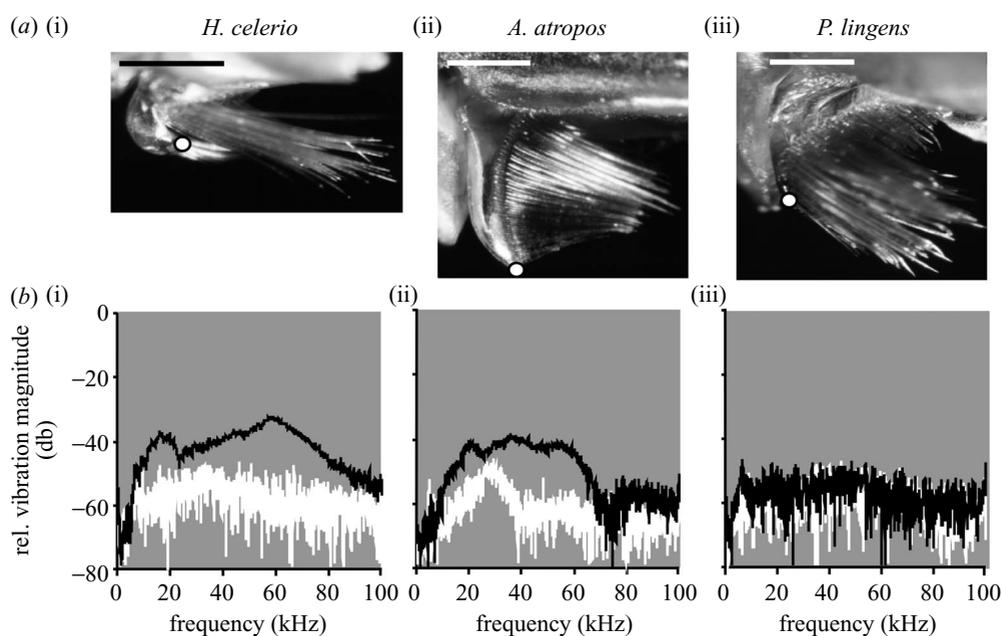


Figure 2. Pilifer anatomy and vibration. (a) Pilifer anatomy: (i) *H. celerio*; (ii) *A. atropos*; (iii) *P. lingens*. White circles mark the distal tip of the pilifer. Scale bars, 0.5 mm. (b) Pilifer vibration: (i) *H. celerio*; (ii) *A. atropos*; (iii) *P. lingens*. Velocity response of the pilifer-tip measured before (black traces) and after (white traces) deflection of the labial palp (data from one animal per species). In the case of *A. atropos*, (b) shows the atypical specimen, where some pilifer vibration was retained *ca.* 30 kHz even after palp deflection.

per stimulus, was finally extrapolated by fitting fifth-order polynomial functions to the plots.

3. RESULTS

(a) *Mechanics of the labral pilifer*

In the first set of measurements, we examined the mechanical response of the labral pilifer. With respect to their anatomy, the pilifers of the three species studied exhibit the characteristic anatomical features previously described (Roeder *et al.* 1970; Roeder 1972; Göpfert & Wasserthal 1999*a,b*) (figure 2*a*). As in all Choerocampina, the pilifer of *H. celerio* is bilobed, comprising an enlarged distal lobe, whereas the pilifers of the acherontiine species *A. atropos* and *P. lingens* are only unilobed. The pilifer is distally prolonged and stiff in the hearing *A. atropos*, but rather short, broad and soft in the non-hearing *P. lingens*. For reasons of detectability and comparability, pilifer vibrations were always measured on the tip of the pilifer (figure 2*a*), the response of which was examined from various directions. During the mechanical examination, the pilifer was initially left in contact with the labial palp, with the latter being in its natural, adducted position. In the course of measurement, however, the labial palp was transiently deflected to evaluate whether the pilifer's mechanical response is affected by the palp.

As long as the palp was in its natural position, pilifer vibrations were detected in the two hearing species, but not in the non-hearing species (figure 2*b*). High-amplitude, sound-induced vibrations that clearly exceeded the noise floor were observed on the distal pilifer lobe of *H. celerio*, the hearing choerocampine species, and on the tip of the prolonged, stiff pilifer of *A. atropos*, the hearing acherontiine species. By contrast, the broad, soft pilifer of the non-

hearing acherontiine species *P. lingens* never exhibited vibrations that exceeded the noise floor ($n =$ two to four animals per species, figure 2*b*). In the hearing species, the frequency characteristics and also the amplitude of the pilifer changed with the direction of the measurement. Maximum pilifer vibrations were detected when the laser beam was focused either on the inner (*H. celerio*) or on the lower side of the pilifer tip (*A. atropos*), corroborating the lateral (*H. celerio*) and dorsoventral (*A. atropos*) direction of vibration indicated by their respective pilifer anatomies (Roeder *et al.* 1970; Göpfert & Wasserthal 1999*a*). The pilifers vibrated with maximum amplitudes at ultrasonic frequencies, i.e. between *ca.* 15 kHz and 70 kHz (*H. celerio*) and *ca.* 20 kHz and 60 kHz (*A. atropos*) (figure 2*b*). The maximum response magnitudes in these two species were comparable, exceeding the noise floor—and, thus, the pilifer vibrations in *P. lingens*—by up to *ca.* 20 dB (figure 2*b*).

When the palp was deflected from the pilifer, the pilifer vibrations in *H. celerio* and *A. atropos* changed (figure 3*b*). The pilifer vibrations observed before palp deflection infallibly decreased in amplitude and usually vanished into the noise floor. The only exception was one of the four *A. atropos* studied, where pilifer vibrations above noise level were still detected after palp deflection. Here, the pilifer continued to vibrate at frequencies *ca.* 30 kHz, but the vibrations at other frequencies also disappeared in this animal (measurements from this animal are shown in figure 2*b*). The reduction of the pilifer vibrations caused by deflection of the labial palp was reversible. When the palp was moved back to its natural position, the initially observed vibrations reappeared in both *H. celerio* and *A. atropos*. A comparable effect was, however, never observed in *P. lingens*. In this species, no pilifer vibrations

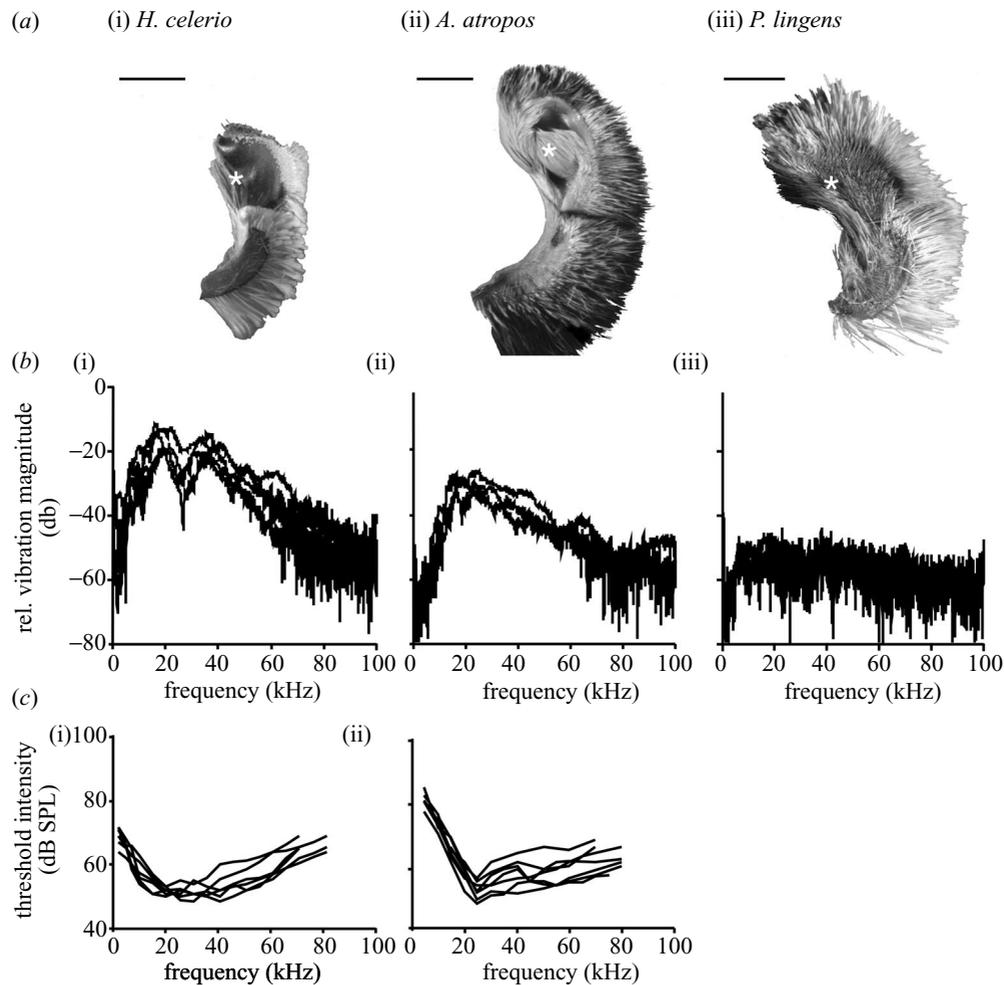


Figure 3. Palp anatomy, vibration and neural threshold curves. (a) Palp anatomy: (i) *H. celerio*; (ii) *A. atropos*; (iii) *P. lingens*. Asterisks mark the region on the inner surface of the second palp segments, which usually is in contact with the pilifer. Scale bars, 1 mm. (b) Palp vibration: (i) *H. celerio*; (ii) *A. atropos*; (iii) *P. lingens*. The superimposed velocity responses measured on the region of the palp that is marked with asterisks in (a) are shown (data from three to four animals per species). (c) Threshold curves of auditory neurons, i.e. a second-order interneuron of (i) *H. celerio* (six animals) and the auditory sensory cell of (ii) *A. atropos* (seven animals).

could be detected, irrespective of whether the palp was adducted or deflected.

(b) *Mechanics of the labial palp and neural response characteristics*

In a second set of measurements, we compared the mechanical response characteristics of the labial palps. The labial palp anatomy, specifically that of the second palp segment, is notably different in the three species studied (figure 3a). The inner surface of this segment lacks scales and is thin-walled and transparent in the hearing choerocampine species *H. celerio*, but deeply depressed and roofed over by a scale-plate in the hearing acheroitiine species *A. atropos* (figures 1b, 3a). In the non-hearing acheroitiine species *P. lingens*, it is totally covered by short scales and lacks any obvious structural specializations. Sound-induced palp vibrations were evaluated by measuring the mechanical response of various parts of the palps, including various measurement points on the inner and outer surfaces of the first and the second palp segments. To ensure that only sound-induced palp vibrations were measured—and to expose that region of the palp that usu-

ally touches the pilifer for mechanical analysis—the ipsilateral pilifer was removed.

Significant vibrations of the labial palp, clearly exceeding the noise floor, were detected in the hearing *H. celerio* and *A. atropos*, but not in the non-hearing *P. lingens* (figure 3b). The palp vibrations observed in the two hearing species did not, however, extend to the entire palp; sound neither induced vibrations of the first palp segment, nor of the outer surface of the second palp segment. Instead, the vibrations were restricted to those structures on the inner surface of the second palp segment that are usually in direct contact with the pilifer. In *H. celerio*, the whole thin area of cuticle found in this region of the palp vibrated with high amplitudes when stimulated acoustically. In *A. atropos*, high-amplitude vibrations were detected on the inner surface of the second palp segment. The vibrations were observed on the entire surface of the scale-plate, but extended neither to the cuticle around the scale-insertions nor to the depressed area behind the plate. Consequently, the scale-plate on the palp of *A. atropos* must be driven directly by sound.

Both the thin membrane on the palp of *H. celerio* and

the scale-plate on the palp of *A. atropos* vibrated maximally in response to acoustic stimulation at ultrasonic frequencies (figure 3*b*). The frequency of the best mechanical response varied between *ca.* 20 and 40 kHz in *H. celerio* and between *ca.* 20 and 30 kHz in *A. atropos*. The response amplitudes differed between the two species. When measured in that region of the palp which usually touches the pilifer, the maximum vibration amplitudes of the membrane of *H. celerio* exceeded those of the scale-plate of *A. atropos* by on average 15 dB (range = 14–20 dB, $n =$ four animals of *H. celerio* and three animals of *A. atropos*; figure 3*a,b*). In comparison, the respective palp region of *P. lingens* exhibited much lower vibration amplitudes, not or hardly exceeding the noise floor. In this species, the maximum amplitudes were at least 18 dB and 33 dB lower than those measured on the scale-plate and the membrane, respectively (figure 3*b*).

Additional examination of the neural response characteristics (figure 3*c*) in the hearing *H. celerio* and *A. atropos* supports the putative function as sound-receiving structures of the membrane and the scale-plate, respectively. In *H. celerio*, minimum neural thresholds occurred at *ca.* 20–40 kHz, corresponding to those frequencies at which the maximum vibrations of the membrane on the palp were observed (figure 3*b,c*). A similar match between the mechanical and the neural frequency characteristics was found in *A. atropos*, in which minimum neural thresholds occurred at *ca.* 20–25 kHz, the best frequency of the scale-plate vibrations (figure 3*b,c*). Not only the best frequencies, but also the overall shape of the mechanical and the neural tuning curves was remarkably similar within both species. However, the neural auditory sensitivity did not reflect this difference in amplitude between the mechanical vibrations of the membrane of *H. celerio* and the scale-plate of *A. atropos*. Although the membrane vibrated with *ca.* 15 dB higher amplitudes than the scale-plate, minimum neural thresholds were comparable, ranging between 49 and 53 dB SPL in *H. celerio* (mean \pm s.d. = 50 ± 1.5 dB SPL, $n =$ six animals) and between 49 and 57 dB SPL in *A. atropos* (mean \pm s.d. = 53 ± 3 dB SPL, $n =$ eight animals).

4. DISCUSSION

While ultrasonic hearing is widespread within many families of moths (Spangler 1988; Surlykke 1988; Fullard 1998; Yager 1999; Minet & Surlykke 2002), most of the approximately 1050 hawkmoth species known (D'Abrera 1986) appear to be deaf. Acoustic sensitivity has been evaluated in a variety of hawkmoths (Roeder & Treat 1970; Roeder 1972; Göpfert & Wasserthal 1999*a*; M. C. Göpfert and L. T. Wasserthal, unpublished data), but until now ultrasound-sensitive ears have only been identified in representatives of the subtribe Choerocampina (approximately 150 auditory species; Roeder 1972; Scoble 1992) and in some species of the subtribe Acherontiina (13–14 hearing species; Göpfert & Wasserthal 1999*a*). Choerocampina and Acherontiina are only distantly related to each other (Grieveaud 1959; D'Abrera 1986; Pittaway 1993; Kristensen 2002). Nevertheless, in these two subtribes, hearing has been shown to involve homologous sensory cells and, in addition, homologous accessory structures, the labral pilifers and the labial palps (Roeder

et al. 1970; Roeder 1972; Göpfert & Wasserthal 1999*a,b*). Hence, the hearing organs of choerocampine and acherontiine hawkmoths presumably evolved independently on the basis of homologous structures. The results of the present study corroborate such parallel evolution; choerocampine and acherontiine ears are demonstrated to actually represent two different types of hearing organs—tympal ears and atympal ears.

Our comparative approach reveals that hearing in Choerocampina and Acherontiina is accompanied by improved mechanical properties of the pilifer–palp system. Sound induces mechanical vibrations of the pilifers and palps in hearing species of these subtribes, but not in non-hearing species. In the hearing species, the labral pilifer vibrates with significant amplitudes only when in contact with the labial palp, whereas the pilifer vibrations strongly decrease in amplitude when the palp is deflected. Accordingly, rather than being driven directly by sound, the pilifer senses vibrations of the palp. Indeed, our mechanical measurements demonstrate that sound induces labial palp vibrations in hearing Choerocampina and Acherontiina. These palp vibrations are restricted to specialized structures on the inner surface of the second palp segment. Accordingly, these structures, but not the whole palps, appear to serve as sound receivers.

In Choerocampina, the thin area of cuticle exhibits not only all the morphological, but also the mechanical key features characterizing auditory tympana (Hoy & Robert 1996; Hoy 1998; Yager 1999). Apart from being thin-walled, it lacks scales and is backed by a large air sac (Roeder & Treat 1970). As shown by the comparison of mechanical and neural response characteristics, it also vibrates in response to sounds at ultrasonic and auditory relevant frequencies. Accordingly, the ears of choerocampine hawkmoths are tympal hearing organs, similar to those found in other insects. However, choerocampine ears are unconventional with respect to the absence of a sensory organ associated with the inner surface of the tympanum. Instead, vibrations are picked up from the outer tympal surface by means of a mechanical interface, the pilifer. The ears of hearing Acherontiina apparently lack a conventional auditory tympanum. They are atympal ears. According to our mechanical analysis, the scale-plate covering the depressed inner palp surface functionally replaces a tympanum in those acherontiine species that can hear. This plate vibrates in response to ultrasonic sounds with frequency characteristics resembling those of the auditory sensory cell at the pilifer's base. Thus, it provides mechanical properties comparable to those of a tympanum. Three facts support the auditory significance of the tympanum of Choerocampina and the scale-plate of hearing Acherontiina. First, both structures are present in hearing species only, but absent in non-hearing species (Roeder 1972; Göpfert & Wasserthal 1999*a*). Their presence seems to be directly linked to audition. Second, the tympanum and the scale-plate are the only palp structures in hearing Choerocampina and Acherontiina that are in contact with, and thus can transmit vibrations to, the pilifer. Third, additional evidence is provided by ablation experiments. Deflection or amputation of the labial palp causes a loss in acoustic sensitivity (Roeder *et al.* 1968, 1970; Roeder & Treat 1970; Roeder 1972; Göpfert & Wasserthal 1999*a,b*) which, in Acherontiina, is also

observed when only the scale-plate of the palp is removed (Göpfert & Wasserthal 1999a). Remarkably, subtribe-specific differences in the strength of this effect correlate with the difference in the vibration amplitudes revealed by this study. The tympanum of Choerocampina vibrates with ca. 15 dB higher amplitudes than the scale-plate of Acherontiina. Correspondingly, the decrease in neural auditory sensitivity caused by palp amputation in Choerocampina (ca. 35–40 dB; Roeder *et al.* 1970; Roeder 1972) exceeds that in Acherontiina (ca. 20–25 dB; Göpfert & Wasserthal 1999a,b) by about the same amount.

Interestingly, the difference in vibration amplitude of the labial palps in hearing Choerocampina and Acherontiina is not detectable in the mechanical response of the pilifer tips or at the neural level. Here, sensitivity appears to be similar in hearing species of both subtribes, indicating that some subtribe-specific difference in the auditory mechanics compensates for the reduced vibration in Acherontiina. Evidence suggests that this compensation is related to the mechanics of the pilifer base. After palp deflection, no more pilifer-tip vibrations were observed in most animals of the hearing acherontiine and choerocampine species examined. Accordingly, one would expect that this treatment also abolishes the neural response to sound, but this is not the case. A residual acoustic sensitivity of the sensory cell at the pilifer's base has been reported for both hearing Choerocampina and Acherontiina, with the sensitivity being higher in Acherontiina (ca. 70–75 dB SPL in Acherontiina versus ca. 80–90 dB SPL in Choerocampina; Roeder & Treat 1970; Roeder *et al.* 1970; Roeder 1972; Göpfert & Wasserthal 1999a,b). In Acherontiina, this residual sensitivity has been demonstrated to be only weakly affected by the ablation of the pilifer tip (Göpfert & Wasserthal 1999b). Hence, sound appears to induce vibrations of some part of the basal pilifer region of the pilifer close to the sensory cell. At high stimulus intensities those vibrations are sufficient to elicit neural responses. Since the mechanical sensitivity of this vibrating part seems to be higher in Acherontiina than in Choerocampina, it presumably compensates for the different vibration amplitudes of the labial palps in the two hawkmoth subtribes. Although this proposed, palp-independent mechanical pathway still awaits a direct, mechanical confirmation, it has interesting implications for the evolution of 'mouth-ears' in hawkmoths. Possibly, the insensitive, palp-independent auditory mechanism found in some Choerocampina and Acherontiina gave rise to the subsequent evolution of ears by the mechanical coupling between the pilifer and the palp and the evolution of sound-receivers on the inner palp surface. Such an evolutionary scenario, though still being rather speculative, could explain the fact that distantly related hawkmoths independently evolved ears made of mouthparts, whereas in all other hearing moths the ears are located around the thorax–abdomen connection (Minet & Surlykke 2002).

A general message from this study is that high-frequency hearing in insects is not essentially linked to the presence of a tympanum; there are alternatives. In fact, the scale-plate of hearing acherontiine hawkmoths may just be one example out of many. Thus further examination of insect audition, in structure and function, promises fundamental insights in the diversity and evolution of arthropod sensory systems.

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