

Chapter 2

Evolutionary and Phylogenetic Origins of Tympanal Hearing Organs in Insects

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Abstract Among insects, tympanal ears evolved at least 18 times, resulting in a diversity of auditory systems. Insects use their ears in different behavioural contexts, mainly intraspecific communication for mate attraction, predator avoidance, and parasitic host localisation. Analysing the evolution of insect ears aims at revealing the phyletic origins of auditory organs, the selection pressures leading to the evolution of ears, the physiological and behavioural adaptations of hearing, and the diversification of ears in specific groups or lineages. The origin of sensory organs from preadapted proprioceptive or vibroceptive organs has now been established for different ear types. In this review, we embed research on insect hearing in a phylogenetic framework to reconstruct the ancestral sensory situation in different taxa, and the series of morphological changes during the evolution of an ear. The importance of sensory and neuroanatomical data is discussed for either mapping onto a phylogeny or as characters for phylogenetic analysis.

2.1 Evolutionary Diversity of Insect Ears in Structure and Function

Insects are among the oldest land animals, and exist for more than 400 million years. For a large portion of this time, the majority of animal sounds stemmed from insects. Insects were probably also the first animals to evolve sound perceiving organs. Ears are found in different recent insect taxa and hearing is involved in

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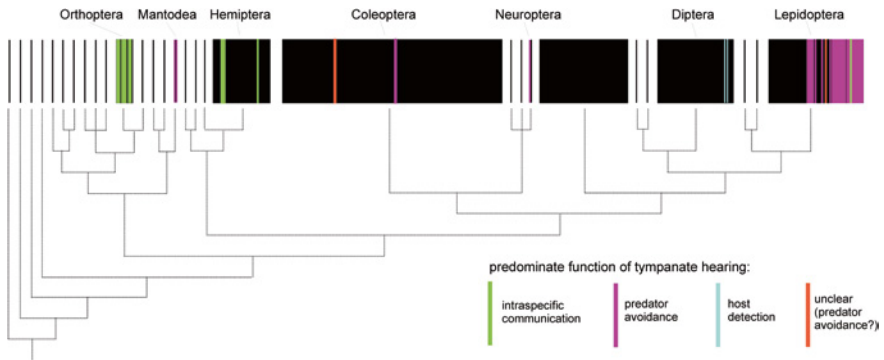


Fig. 2.1 Phylogeny of insect taxa as adapted from Wheeler et al. (2001) and Grimaldi and Engel (2005) indicating the presence of tympanate auditory organs. The top row depicts recent tympanate taxa with their relative number of species; the main or basic function of hearing is indicated by colour: for intraspecific communication, predator detection or host detection. In these taxa, except for Neuroptera hearing organs evolved more than once. Secondary reduction of hearing also occurred but has not been depicted

three major behavioural contexts: (1) intraspecific communication e.g. mate attraction, courtship and rivalry behaviour, (2) detection and avoidance of predators and (3) host localisation by parasitoid insects.

Communication systems based on species-specific acoustic signalling evolved repeatedly among animals (Webster et al. 1992; Yager 1999; Christensen-Dalsgaard and Carr 2008). Sound signals are effective means for signalling and intraspecific communication as they are independent of the photophase, provide directional cues in cluttered environments and may convey the sex or behavioural state of the sender. The complex temporal pattern and frequency content of sound signals represents an important pregametic isolation mechanism (Pollack 2000; Greenfield 2002). Intraspecific acoustic communication is well described in Orthoptera and Hemiptera (Fig. 2.1) (see Chap. 6 by Greenfield on Lepidoptera). In many nocturnally flying insects (Mantodea, Neuroptera, Lepidoptera; Fig. 2.1) auditory systems are used to detect and avoid predation by bats (reviews: Hoy 1992; Conner and Corcoran 2012; Yager 2012; see Chap. 5 by Conner). By contrast, only a few species of two taxa of Diptera possess ears for the highly specialised function of host detection (Fig. 2.1; see Chap. 4 by Hedwig and Robert).

For different insect taxa, typical tympanal ears are located on specific tagmata of the body (Fullard and Yack 1993; Hoy and Robert 1996; Yager 1999; Stumpner and von Helversen 2001; Yack 2004). Auditory organs with tympana evolved at least 18 times independently in diverse taxa of seven insect orders as: in butterflies and moths (Lepidoptera), locusts, crickets and bush crickets or katyids (Orthoptera), flies (Diptera), cicadas and water striders (Hemiptera), beetles (Coleoptera), mantids (Mantodea) and lacewings (Neuroptera) (Fig. 2.1). The auditory systems can usually be assigned to a main behavioural function, although hearing in a species might be involved in more than one of these behaviours, e.g.

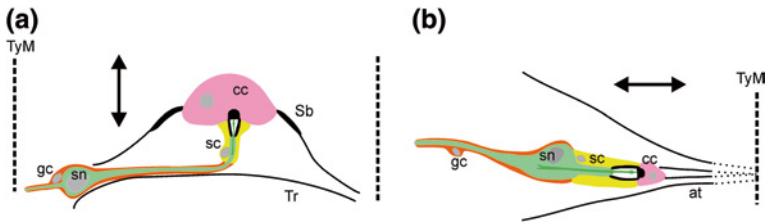


Fig. 2.2 Schematic scolopidial unit from a tettigoniid (after Schumacher 1979) and a diptera (after Lakes-Harlan et al. 2007). Each unit consists of a sensory neuron (sn, *mint*), glial cell (gc, *orange*), scolopidial cell (sc, *yellow*) and a cap cell (cc, *pink*). The proposed direction of sensory activation (arrow) in the tettigoniid is perpendicular to the tracheal wall and the unit is attached to a supporting band (sb) holding the cap cell. In the diptera, the tympanum is attached longitudinally to the sensory organ (at, attachment tissue). TyM tympanal membrane (not to scale)

in both mate recognition and predator detection (Moiseff et al. 1978; Wyttenbach et al. 1996; Rodriguez and Greenfield 2004).

Despite the different positions and forms of tympanal ears, shared functional elements in ears have become evident across taxa: tympanal ears are characterised by tympanal membranes or ear drums of thinned cuticle which vibrate in response to airborne sounds. The tympanum is typically backed by a tracheal space. There are notable exceptions of ears which are not backed by an acoustic trachea but by fluid, like the ear of the green lacewing (Miller 1970) and of some aquatic hemipterans (Arntz 1975). In some cases, an auditory trachea transfers the sound signal to the inside of the body. The third and crucial element is a sensory organ. This consists of scolopidial sensory units which are directly or indirectly activated by sound-induced tympanum oscillations and function as auditory receptor neurons (Hoy and Robert 1996; Yager 1999; Yack 2004). Scolopidial sensilla (Fig. 2.2a, b) are widespread among insects in proprioceptive and vibration-sensitive receptor organs (Moulins 1976; Field and Matheson 1998). Each scolopidial sensillum consists of four distinct cell types, only one of which is a primary sensory neuron. The dendrite of the sensory neuron extends distally into a cilium; the tip of the cilium is covered by a specific cap cell (this cap cell characterises the mononematic type of scolopidia, irrespective whether tympana are developed or not). Dendritic cilia of homogenous diameter are called type 1 scolopidia (Field and Matheson 1998; Yack 2004). Additional cell types of the scolopidium are the glia (sheath) cell and scolopale cell. The latter forms a rod-like structure, the scolopale, which surrounds the dendrite. Within the scolopale, the dendrite is surrounded by fluid which may be secreted and homeostatically regulated by the scolopale cell. In tympanal ears, the dendrite of a single sensory neuron resides in the scolopale (monodinal type) and the ears have mononematic type 1 scolopidia (Yack 2004). In auditory systems, the sensory neurons are ultimately activated by sound stimuli which mechanically stretch the dendrites of sensory neurons (Kernan 2007).

The different evolutionary origins and functions correspond to a great diversity of ear morphologies (see Fig. 2.3 for anatomy of selected insect ears). The differences are also reflected in the varying number of scolopidial sensilla and their organisation.

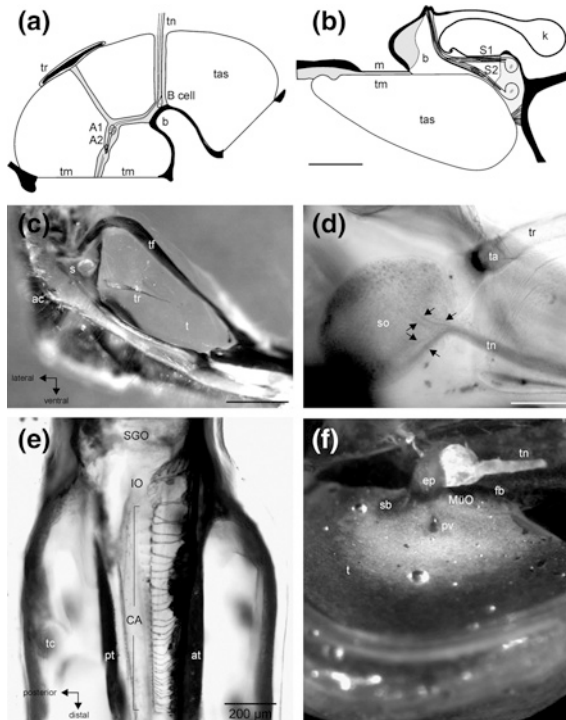


Fig. 2.3 Morphological diversity of insect tympanal ears. **a** Schematic transvers section of the tympanal organ of noctuoid moths containing only two transversscolopidial sensory neurons (A1, A2) attached to the tympanal membrane (tm). Axons of the sensory neurons form the tympanal nerve (tn). Another sensory cell, the B cell, is not directly connected to the tympanum. The tympanum is backed by tracheal air sacs (tas) and a trachea (tr). **b** Schematic section through the mesothoracic tympanal organ of a waterboat man, *Corixa punctata* (Heteroptera). Two sensory neurons (S1, S2) are connected to the tympanal membrane (tm) via a knob-shaped process (k) which upon tympanum movement stretches the dendrites. Sound input is delivered to sensory cells from the tracheal sac (t). Abbreviations: b, base of knob; m, membrane; S1/S2, sensory neuron 1/2; t, tracheal sac; tm, tracheal membrane. **c** External view of the tympanal organ of the cicada, *Okanagana rimosa*. The tympanum (t) is surrounded by a tympanal frame (tf) and contains a thickened tympanal ridge (tr). Close to a spiracle (s), the auditory capsule (ac) harbours the sensory organ, which is connected to the tympanal ridge by the tympanal apodeme (ta). **d** Internal view of the sensory organ (so) of *O. rimosa*. Distinct minor nerve branches of the tympanal nerve (tn) run within the mass of the sensory organ (arrows). Sensory cells are coupled via the tympanal apodeme (ta) to the tympanal ridge (tr), which transfers the resonant vibrations of the tympanum. **e** The complex tibial organ in the foreleg of a tettigoniid *Tettigonia viridissima* containing three scolopidial organs, the subgenual organ (SGO), intermediate organ (IO) and *crista acoustica* (CA) located behind the tympana (at, anterior tympanum, pt, posterior tympanum) in tympanal chambers (tc). Note the parallel organisation of dendrites of auditory CA neurons. **f** Internal view of the tympanum and auditory organ (Müllers organ, MüO) of the desert locust *Schistocerca gregaria*. Auditory receptors have different attachment sites directly on the tympanal membrane: the folded body (fb), ep (elevated process), pyriform vesicle (pv), and styli-form body (sb). **a** redrawn from Roeder (1967), **b** redrawn from Prager (1976), **c–f** Strauß and Lakes-Harlan unpublished. Scales: **b** 100 μm , **c** 1 mm, **d** 400 μm and **e** 200 μm

Insect ears may contain only one or two scolopidial sensilla like in moth (Fig. 2.3a) or water striders (Fig. 2.3b) or may contain over 2000 as in cicadas (Doolan and Young 1981) (Fig. 2.3c, d). The orientation of dendrites and the attachment of sensory neurons to the tympana or trachea vary greatly in different ears. Frequency analysis may be based on attaching the sensory cells specifically to sound-transmitting structures like in the ears of tettigoniids where receptor cells are linearly arranged (Fig. 2.3e) or in locusts where distinct neuron groups attach to specific areas of the tympana (Fig. 2.3f). Comparative analysis of auditory structure and function has recently expanded the understanding of evolutionary origins of insect ears both empirically and conceptually. In the following, the evolution of tympanal sound pressure receivers for different tasks is reviewed in relation to phylogenetic analysis.

2.2 Comparative and Phylogenetic Studies of Tympanal Organs

Several sources of information are relevant to understand the evolution of tympanal organs. Descriptive data on the neuroanatomy and functional morphology of tympanal organs analyse sensory organs in different species. Comparative and phylogeny-based studies are based on relationships of organisms. These latter studies aim to reconstruct the evolutionary sequences of e.g. morphological and functional changes. The concepts of cladistics are used to identify the ancestral (plesiomorphic) lineages and anatomical features of sense organs, or the derived (autapomorphic) situations (so-called “tree-thinking”). Phylogenetic analysis indicates in which lineage tympanal organs evolved or became secondarily reduced and may point out suitable recent taxa for understanding evolutionary transitions. Reconstructing phylogenetic relationships by molecular techniques has provided numerous phylogenies for insect taxa, which however, have so far not resolved evolutionary processes for all taxa with tympanal ears. Combined approaches including neuroanatomy, behaviour, and physiology of auditory systems should provide important characters for a phylogenetic analysis, which may also allow identifying the selection pressures acting upon during evolution.

2.2.1 Fossil Record of Insect Ears

The fossil record for insect ears is scarce and only known from Ensifera (Orthoptera) (Rust et al. 1999; Plotnick and Smith 2012) and date back to the Eocene (~56–34 million years ago). Some well preserved specimen of gryllids and tettigoniids from this era (dating at ~48 my) show tympana reminiscent of the tympanal ears of recent species (Plotnick and Smith 2012). By that time, intraspecific acoustic communication was probably long established. Fossils from the wing stridulation apparatus allow even to reconstruct the ancient sounds. Analysis of stridulation teeth distance in the Jurassic (165 my ago) haglid *Archaboilus musicus* suggests a carrier

frequency of 6.4 kHz in their pure-tone song (Gu et al. 2012). Songs from the tettigoniid *Pseudotettigonia amoena*, in the Eocene (55 my ago), were likely broad-banded, with a carrier frequency around 7 kHz (Rust et al. 1999). Importantly, an ancestral bat species dated to the early Eocene at ~52 my shows no indications of ultrasonic sound production (Simmons et al. 2008). Thus, hearing in Ensifera likely evolved prior to bat echolocation, and its ancestral function was presumably linked to intraspecific communication (Stumpner and von Helversen 2001).

2.2.2 Comparative Neuroanatomical Approaches

Comparative anatomical studies compare sensory organs of related species (interspecific comparison), or serially homologous organs, i.e. sensory organs occurring in similar positions in different body segments of the same species (intraspecific comparison).

In interspecific comparisons the homologous sensory structures in hearing (tympanate) species may be compared to closely related recent atympanate species (Orthoptera: Meier and Reichert 1990; Lepidoptera: Yack and Fullard 1990; Yack et al. 1999, Mantodea: Yager 2005; Diptera: Edgecomb et al. 1995; Lakes-Harlan et al. 2007) assumed to be representative of the ancestrally deaf situation (Fullard and Yack 1993) though they might also result from secondary reduction (see below). Homology is usually evaluated based on the morphological analysis of adult ears or their development (Yager 1999). To identify sensory organs in non-hearing species which are homologous to ears in related species, the three morphological criteria of homology are to be met. These criteria are those of location (homotopy), the special quality of organisation (homomorphy), and of continuity (either in several species, thus “linking” morphological forms, or during ontogenetic development of one species). Homology analysis of ears is usually based on the location and quality of organisation.

Comparative studies provided considerable insights into the origin of insect ears and importantly have identified homologous sensory organs in tympanate and atympanate species. Auditory sense organs are derived from pre-existing sensory organs which served functions other than hearing, e.g. proprioception (see below). The lineage-specific anatomical structures indicate which changes accompanied the transformation of ancestral non-hearing mechanosensory organs into ears. For example, the embryonic development of the locust (*Schistocerca gregaria*) ear indicated that the auditory sense organ evolved among scolopidial organs present in all abdominal segments (Meier and Reichert 1990; Schäffer and Lakes-Harlan 2001) and derived from a rather unspecialised, proprioceptive organ. The early development of the auditory sense organ and the serially homologous pleural chordotonal organs is highly similar. However, part of the neurons in the differentiating auditory sense organ migrate anteriorly during embryogenesis and generate the anterior group of receptors. Thereby they establish the morphology of the adult hearing organ which contains more neurons than the unspecialised

scolopidial organs. Among tettigoniids, tympanal organs occur in the foreleg while homologous sensory organs develop in the mid- and hindleg without tympana (Rössler 1992). Adaptations for hearing are the tympanal membranes in the foreleg (Bailey 1993) and an acoustic spiracle and trachea as main sound entrance to the auditory system (Lewis 1974; Nocke 1975).

2.2.3 Phylogeny-Based Approaches

Given a reliable phylogenetic tree, neurosensory data can be projected onto it in order to deduce the most likely sequence of evolution. Such neurosensory data concern the anatomy of the scolopidial organs, their innervation, their serial organisation, the sensory attachment, or ultrastructural features. In combination with the species' phylogenetic relationships, it is possible to infer in which lineage(s) and therefore in which succession, the corresponding changes in sensory structures evolved. A phylogenetic framework can become particularly important for the identification of two distinct evolutionary processes: secondary reduction of tympana, and their parallel evolution. If tympana have been secondarily reduced, insects might be mistaken for primarily atympanate. Parallel evolution in independent lineages has resulted in ears with high structural similarity based on the same ancestral organ. One example of parallel evolution concerns the ears of flies. Among Diptera, tympanal hearing evolved only in two groups, the parasitoid Emblematomini and Ormiini, whose ears are located in the prothorax. As both taxa are not closely related phylogenetically, a parallel evolution of hearing can be deduced (Fig. 2.4) (Lakes-Harlan et al. 1999). Diptera possess a prothoracic chordotonal sense organ which twice has been modified and incorporated into an ear together with the development of a prosternal tympanal membrane

Fig. 2.4 Prothoracic tympanal organs in two lineages of calyptate Diptera Emblematomini and Ormiini. This phylogenetic mapping supports independent evolution of the hearing organs. Adapted from Lakes-Harlan et al. (1999) with a phylogeny modified after Kutty et al. (2010)

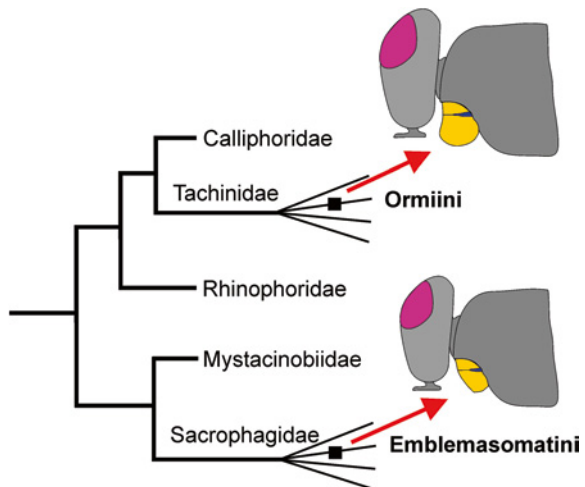
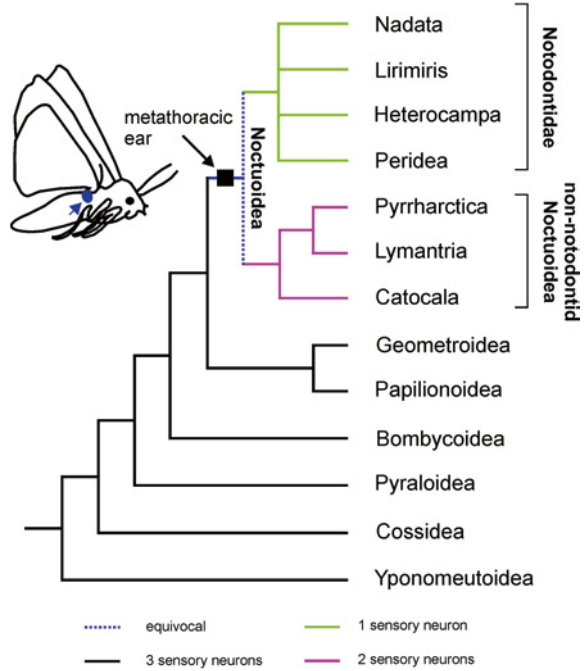


Fig. 2.5 Number of sensory neurons in the metathoracic ear of lepidopteran species. Tympanal ears evolved in the lineage of Noctuoidea (black square). The number of scolopidial sensillae is indicated by colour. The ancestral number is three neurons, which was reduced to two neurons in most Noctuoidea or one neuron in Notodontidae. Adapted from Yack et al. (1999), animal redrawn from Yack and Fullard (2000)



(Lakes-Harlan and Heller 1992; Edgecomb et al. 1995). The prosternal chordotonal organ is a vibration sensor (Stölting et al. 2007; see below). Consistent with a parallel evolution of hearing organs is the fact that the host species of these parasitoid flies belong to different taxa: Ormiini infest species of Orthoptera while Emblematomatini infest cicadas (see Chap. 4 by Hedwig and Robert). However, the physical conditions and constraints making the scolopidial organ and structures a suitable base are unclear.

In the case of Macrolepidoptera, a reduction of the number of sensory neurons in ears became evident by blending comparative neuroanatomy of diverse lepidopteran taxa with phylogenetics. The metathoracic tympanal ears in some Lepidoptera derived from the wing-hinge chordotonal organ, an (atympanate) receptor organ to monitor wing movements with three scolopidial neurons (Yack and Fullard 1990). The tympanal ears of recent species contain either two or just one single sensory neuron (Figs. 2.3a and 2.5). Mapping the neuroanatomical details onto the phylogeny identifies the situation with three neurons as the ancestral atympanate organisation, while the lower numbers reveal an evolutionary reduction: ears of Notodontidae house a single sensory unit (Surlykke 1984; Yack et al. 1999), while all other noctuoid ears have two (Yack et al. 1999). The reduction in neuron number may even be adaptive, as noctuoids do not use frequency discrimination for bat avoidance; multiple neurons might be functionally unnecessary, and would be redundant (Yack et al. 1999). The evolutionary transition from proprioceptor to auditory organ might also implicate a loss of the original function but it is unclear

how this loss is compensated. Reduction of tympana or at least hearing sensitivity has been documented in Lepidoptera (Cardone and Fullard 1988; Fullard et al. 2007) Mantidae (Yager 1990), Orthoptera (Otte 1990; Pollack and Martins 2007; Lehmann et al. 2010) and is often associated with a regression or loss of wings, indicating that flying insects are under particular selection pressure from echolocating bats (Yager 2012). If the ability of flight is lost, the selection on hearing may decrease so that ears are undergoing regression and might also be lost.

Phylogenetic mapping and any inference drawn crucially depend on the quality of the phylogenetic analysis available and its resolution. When relationships between taxa and identification of outgroups were not (yet) reliably established, improvement of phylogenies resulted in new concepts of ear evolution. As mentioned above, ultrasonic hearing evolved repeatedly among Lepidoptera, with ears in different positions on the body, including metathoracic and abdominal ears (Yack and Fullard 2000; Yack 2004). Among three groups of Lepidoptera (Pyraloidea, Geometridae and Drepanidae), abdominal ears appeared to have evolved in parallel (independently) from a lateral scolopidial organ in the first abdominal segment (Hasenfuss 1997). As the relationships among Lepidoptera was recently revised based on molecular sequence data, the parallel evolution of hearing organs was questioned and instead a singular evolution of ears discussed (Regier et al. 2009). However, the singular evolution of ears in the lineage of all tympanate groups can be ruled out based on morphological analysis of homology as ears are located in different segments (Kristensen 2012). A similar incongruence occurs for Ensifera as morphological and molecular phylogenetic analysis (Legendre et al. 2010) lead to different scenarios regarding the evolution or reduction of tympanal ears. In general, the homology of ears and especially their sensory organs has to be established independently of the phylogenetic relationships. This neuroanatomical approach is crucial for homology analysis, as sensory organs which are not homologous cannot share a common evolutionary origin.

The examples discussed so far have all used given phylogenies to discuss the evolution of hearing organs. However, auditory features can become an integral part of a phylogenetic study if included in the cladistic analysis. The most prominent example so far is hearing in Mantidae (Yager and Svenson 2008). The mantid ear is located at the ventral metathorax and forms an “auditory cyclops”. Based on functional anatomy and neurophysiology, five distinct ear types can be distinguished in the metathorax of mantids. While the ear shows some variability in morphology, the sensory physiology and behavioural response to ultrasound are remarkably similar. Using different structural features a morphological data matrix was created and an “auditory phylogeny” generated (Yager and Svenson 2008). Outgroup cockroach species as well as mantid instars, which lack fully developed auditory systems, clustered at the base. The topography of the phylogenetic tree supported a single origin of the metathoracic ear, while another hearing organ in the mesothorax with auditory sensitivity to frequencies lower than ultrasound may have evolved repeatedly. Comparison with mantid phylogeny based on molecular sequences supports that the metathoracic ear evolved once. In addition, a distinct type of the metathoracic ears which is rather unelaborate as it lacks clearly defined acoustic chambers is not the

ancestral ear type, but developed repeatedly (Yager and Svenson 2008) and may represent a regression associated with wing reduction. Thus, neurosensory characters can provide a data set for reconstructing ear evolution using cladistic approaches. Analysis of, e.g., hearing organs and their organisation could therefore be included for cladistic analysis to distinguish homology from convergence (e.g. Desutter-Grandcolas et al. 2005), especially if ear homology is contentious.

Neurobiology and phylogeny are both important to reconstruct the evolution of tympanal ears. Phylogeny alone cannot sufficiently explain how the tympanal ears of insects formed; for this the function of the ancestral receptor organ and its evolutionary modification has to be considered. Phylogenies are decisive to distinguish between monophyly versus polyphyly of hearing, but only data on the sensory organs can reveal the direction of anatomical change by identifying the ancestral structure of sensory organs.

2.3 The Evolutionary Origin of Auditory Sense Organs

Scolopidial sensilla occur in tympanal organs, but moreover in numerous organs of proprioceptive or vibroceptive function in insects (Field and Matheson 1998). Scolopidial organs in similar locations and even with similar organisation to auditory sensilla are often present in related tympanate and atympanate species. As the sensory structures and the mechanism of activation are conserved among proprioceptive, vibroceptive and auditory organs (Kernan 2007), insect ears apparently evolved from pre-existing mechanoreceptor organs (Meier and Reichert 1990; Boyan 1993; Fullard and Yack 1993; Yager 1999) which were termed “precursor organs” (Yager 1999). This concept of a precursor organ as basis of the evolution of ears was conceived already in the nineteenth century (Graber 1881). However, the idea of a mechanoceptive origin of auditory organs usually addressed only specific taxa of insects (but see Radl 1905), and it took some time to identify precursor organs and their ancestral function for several insect ears. According to the precursor concept, the scolopidial sensilla were already present prior to an auditory function; only the medium for effective stimulation changed by acquiring sensitivity for airborne sound. For any scolopidial organ at least two criteria have to be met to identify it as an ear precursor: (1) It has to be homologous to the sensory organ of tympanate taxa as derived from morphological analysis. (2) A phylogenetic analysis has to establish that the tympanate and atympanate taxa share a common atympanate ancestry which the recent atympanate species might still represent. An alternative scenario would be that ears evolved by generating additional sensory organs (“de novo”) which directly evolved as the auditory sense organ. Though this is in principle a valid possibility, it has so far not been supported for any insect ear. Apart from location, precursor organs also match in their innervation, their axonal projection to mechanosensory areas of the CNS, and their synaptic connections to interneurons in atympanate and tympanate species (Yack and Fullard 1990; Boyan 1993;

Table 2.1 Chordotonal precursor organs of insect ears

Taxon	Position of auditory organ	Precursor	Reference
Diptera			
Sarcophagidae	Prothorax	Prosternal CO	Lakes-Harlan et al. (1999)
Tachinidae	Prothorax	Prosternal CO	Lakes-Harlan et al. (1999)
Coleoptera			
Cicindelidae	1st abdominal segment	Pleural CO	Yager and Spangler (1995)
Acrididae	First abdominal segment	Pleural CO	Meier and Reichert (1990)
Ensifera			
Grylloidea	Foreleg tibia	Intermediate organ	Strauß and Lakes-Harlan (2009)
Tettigonioidae	Foreleg tibia	Crista acustica homolog	Strauß and Lakes-Harlan (2009)
Mantodea	Ventral metathorax	N7 chordotonal organ	Yager (2005)
	Ventral mesothorax	N7 CO of mesothorax	
Lepidoptera			
Sphingidae	Pilifer	Single SO	Göpfert and Wasserthal (1999)
Noctuoidea	Metathorax	Wing-hinge CO	Yack and Fullard (1990)
Pyraloidea	Ventral 1st abd segment	Lateral scolopal organ	Hasenfuss (1997)
Geometridae	Anterior 1st abd segment	Lateral scolopal organ	Hasenfuss (1997)
Drepanidae	1st abdominal segment	Lateral scolopal organ	Hasenfuss (1997)
Uraniidae	2nd abdominal segment	Lateral CO	Hasenfuss (2000)

CO chordotonal organ; SO scolopial organ

Yager 1999). The precursor organs of ears have been identified for several taxa, but not yet in Hemiptera, Coleoptera (scarab beetles) and some Lepidoptera (in Hedyllidae and Nymphalidae) (Table 2.1).

Evolution of tympanal ears was apparently rather complex in Ensifera. Gryllids, tettigoniids and few related taxa have tympanal ears within the tibia of the forelegs with usually two tympana in the anterior and posterior tibia, respectively (Fig. 2.3e). In the atympanate Rhaphidophoridae (cave crickets), the subgenual organ and the intermediate organ are present, but no sensory neurons homologous to the auditory receptors (Jeram et al. 1995). This organisation may well be the ancestral atympanate situation of Ensifera. In the tettigoniids and gryllids, the hearing organs are similar in neuroanatomical structures, but important differences exist. In tettigoniids, wetas (Anostomatidae) and haglids, three sensory organs form the complex tibial organ: the subgenual organ, the intermediate organ, and the sensory neurons in the *crista acustica* responding to airborne sound. In a majority of the non-hearing Ensifera including Stenopelmatidae and Gryllacrididae, sensory structures are present in the complex tibial organ which is clearly homologous to the

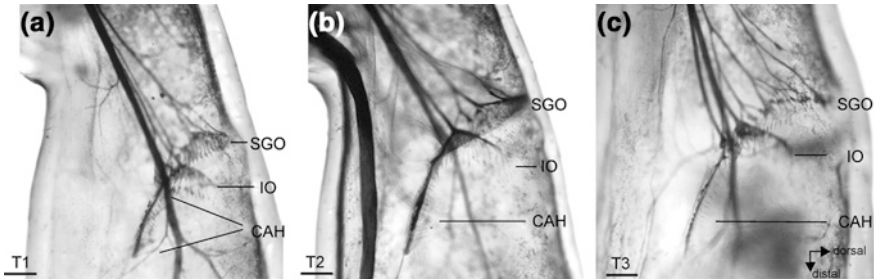


Fig. 2.6 The complex tibial organ of *Stenopelmatus spec.* in the thoracic leg pairs (T1; foreleg, T2; midleg, T3; hindleg). In this species, no tympana are developed in the foreleg but the *crista acustica* homolog corresponds to the auditory sensilla of related tettigoniid groups. No differences in the neuronal organisation are evident between leg pairs. CAH crista acustica homolog; IO intermediate organ; SGO subgenual organ. Scale: 1 mm

auditory receptors in tettigonioids (Fig. 2.6). As they resemble the *crista acustica* of hearing taxa, they have been termed *crista acustica homolog* (CAH) (Strauß and Lakes-Harlan 2008a, b, 2010). The sensory organ of the *crista acustica homolog* is highly similar between all leg pairs and shows no sensory specialisations relating to hearing in the foreleg; therefore it is assumed to represent the ancestral and atympanate organisation. For several of these atympanate Ensiferan taxa, which do not use acoustic signals for intraspecific signalling, communication with vibratory signals plays an important role in intraspecific behaviour (e.g. Field and Bailey 1997; Weissman 2001; Gwynne 2004). Many insects perceive vibration signals with highly sensitive subgenual organs which in Ensifera are also part of the complex tibial organ besides the atympanate *crista acustica homolog*, which might have developed with a role in vibration detection (Strauß and Lakes-Harlan 2009; 2010). The *crista acustica homolog* in atympanate taxa might thus be the precursor organ for the *crista acustica* in Tettigoniodea (Fig. 2.7). While the phylogeny of Ensifera is still debated, the neuroanatomy of sense organs suggests a consistent scenario how ears may have originated amongst Ensifera (Fig. 2.7). Improved taxon sampling and phylogenetic analysis should help to delineate the sensory adaptations.

The functional changes in a mechanosensory organ are also interesting in respect to the upstream sensory pathways in the central nervous system: in tettigoniids and grasshoppers, support for a vibratory origin of the auditory system is given by many interneurons with bimodal vibratory and auditory response properties (Kalmring and Kühne 1980; Kalmring et al. 1997). In this case, audition seems to be an evolutionary addition onto the vibration-sensitive system.

In the grylloid group with e.g. crickets and mole crickets, ears also occur in the foreleg but the neuroanatomy of the complex receptor organ differs from that in tettigoniids. It consists of only two main organs, the subgenual organ and the tympanal organ, the latter being the auditory receptor cells proper. Most likely, this tympanal organ does not correspond to the *crista acustica*. Presumably, the cricket tympanal organ derived from the intermediate organ or distal organ found in many

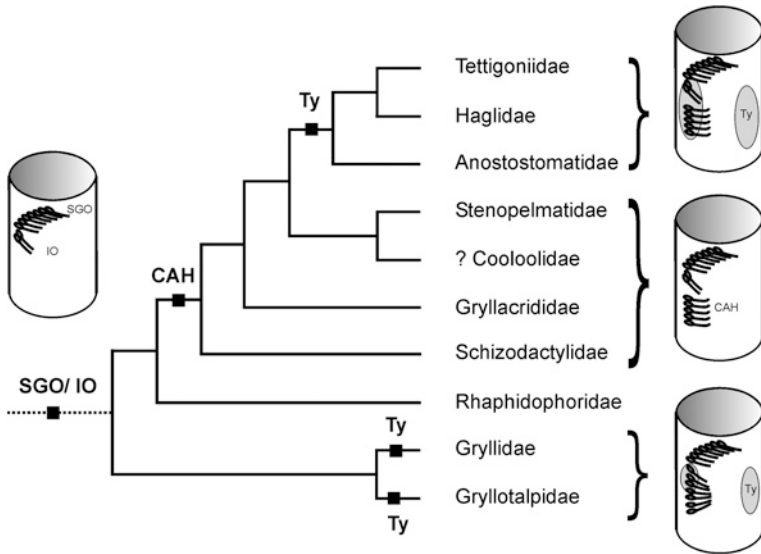


Fig. 2.7 Evolution of tympanal ears in Ensifera. The complex tibial organ consisted ancestrally of the subgenital organ (SGO) and the intermediate organ (IO). In the tettigoniid lineage a third part evolved, the *Crista acustica homolog* (CAH). Tympana (tymp) occur only later to form an auditory organ. In the gryllid lineage, tympanal hearing organs evolved presumably repeatedly from a dipartite sense organ, the plesiomorphic intermediate organ. In the Cooloolidae, the neuroanatomy of the ears is not yet known. Phylogeny based on Desutter-Grandcolas (2003); neurosensory data after Strauß and Lakes-Harlan (2009)

taxa. Remarkably, a much greater anatomical diversity exists for ears in crickets than in tettigoniids, including an ear type in *Cycloptiloides canariensis* (Gryllidae: Mogoplistinae) with a single anterior tympanum and very few scolopidia (Michel 1979). Phylogenetic analysis even suggested the independent origin of tympana in crickets and mole crickets (Desutter-Grandcolas 2003). Presumably, the hearing organs in gryllid and tettigoniid lineages evolved independently, and from different sets of sensilla.

2.4 The Evolutionary Origin of Physiological Hearing

Identification of the precursor organ reveals from which structure the sensory organ derived. With respect to its functional evolution, additional information on accompanying physiological changes and the ecological context of auditory behaviour are necessary.

During the evolutionary transformation of scolopidial organs to functional ears structural changes occur which alter the range and quality of stimuli to which the chordotonal organ responds. The sensory precursor systems may have

been sensitive to high amplitude sound without any specific sound-propagating structures. For example, in cockroaches, the subgenual organ is sensitive to low-frequency sound (Shaw 1994). Similarly, the hind wing chordotonal organ of locusts reacts to sound, beside its proprioceptive function (Pearson et al. 1989). It appears that precursor organs were sensitive to high amplitude sounds only, and that sound-propagating structures evolved in consecutive steps transforming cuticle into the tympana and in some groups a respiratory trachea into an acoustic trachea (Fullard and Yack 1993). Accordingly, atympanate sensory organs which are (serially) homologous to auditory organs have been shown to respond to high amplitudes of low-frequency sounds in Lepidoptera (Yack and Fullard 1990) and Tettigoniidae (Kalmring et al. 1994; Jeram et al. 1995). This suggests that during evolution a gain of auditory sensitivity occurred in a continuum of sensory activity.

With respect to auditory sensilla numbers it is difficult to identify evolutionary trends. As mentioned above, in Noctuoidea, a decrease of sensilla occurred (Yack et al. 1999), however, in other Lepidoptera, the number of sensilla did not change during the evolution of tympanal hearing from the precursor organ (Hasenfuss 2000). In general, it might be assumed that sensory neurons in tympanal auditory organs may have been added to enhance sensitivity and frequency range. In insect taxa with intraspecific acoustic communication, the number of auditory afferents can vary almost over two orders of magnitude. Cicada which process very distinct and complex frequency modulated song patterns (Fonseca et al. 2000) have ears with over 2000 sensory neurons (Doolan and Young 1981). Also the pneumorid Caelifera *Bullacris membracioides* (a Bladder grasshopper) house 2000 auditory afferents in their main—atympanate—hearing organ (van Staaden and Römer 1998). For cicadas and pneumorid grasshoppers the functional role of the large number of receptor neurons is not resolved and the ancestral situation has not been investigated. Ensifera with intraspecific acoustic communication have 15–70 auditory sensilla. In several tettigoniids, the number of sensory neurons is not markedly higher than that in the atympanate precursor (22–35 sensilla; Strauß and Lakes-Harlan 2008a, b). However, the number of auditory sensilla in tympanate species is always significantly higher in the foreleg. In the genus *Poecilimon*, all species have well developed ears, but in few species less than 25 auditory sensilla occur (Lehmann et al. 2007; Strauß et al. 2012). This suggests a secondary reduction and may correlate to an adaptive decrease in auditory sensitivity due to shortened communication distances or even parthenogenetic reproduction (Stumpner and Heller 1992; Lehmann et al. 2007).

In non-hearing flies, the atympanate scolopidial prosternal organ, which is homologous to the ear, responds to vibrations of the legs (Stölting et al. 2007). In tachinid ears, functional specialisations for auditory perception can be identified as a widening of trachea backing the ear, the formation of tympana, an increase in neuron number and the elaboration of sensory cell attachment to the tympanal membrane. Tympanate Tachinidae have several hundred sensory neurons (Edgecomb et al. 1995; Lakes-Harlan et al. 2007), whereas non-hearing sarcophagids and the tympanate sacrophagid *E. auditrix* possess about 30–35 scolopidial units (Lakes-Harlan et al. 1999; Stölting et al. 2007). In

hawkmoths, the structure of ears indicates that hearing evolved independently in *Choerocampina* and *Acherontiina*. In both groups, ears locate on the pilifer, but the *Choerocampina* have developed tympana proper while the *Acherontiina* use overlapping scales to pick up mainly ultrasonic sound (Göpfert et al. 2002).

A central question is how the physiological properties of the precursor organ changed for the functional transition to an auditory organ proper, but remarkably few insights have been established so far. With the gain of auditory sensitivity, the chordotonal organ might alter or lose the ancestral function of vibroception or proprioception. Different solutions are possible:

1. The hearing organ might still be bifunctional, responding to auditory as well as vibration/stretch stimuli. For example, the dipteran ear might represent a bifunctional sensory organ as it responds to sound and to substrate vibrations transmitted over the fly's body as in atympanate species (Lakes-Harlan et al. 1999). The ear of the grass moth *Pleuroptya ruralis* is located ventrally in the first abdominal segment. Auditory neurons are not completely mechanically isolated as they are activated by muscles located in the ventral diaphragm which is indirectly coupled to the receptor organ (Hasenfuss 2000). In this case, the auditory neurons might also be functional proprioceptors.
2. The original function of the precursor is compensated for by other sense organs. In Ensifera, presumably the sense organs in the atympanate legs took over the task of vibration reception.
3. The ancestral sensory function might no longer be necessary. The praying mantis ear presumably evolved with a loss of proprioceptive function (Yager and Svenson 2008), as it might be the case in the Noctuid moth.

2.5 The Evolutionary Origin of Auditory Behaviour

Driven by natural and sexual selection, insect ears evolved mainly for intraspecific communication and predator detection. Therefore, the behavioural and ecological context of auditory systems is important for understanding their evolution. The most prominent example is the “arms-race” between echolocating bats and nocturnal flying insects (reviews: Hoy 1992; Conner and Corcoran 2012; Yager 2012). Bat detecting ears should be highly sensitive to ultrasound (Stumpner and von Helversen 2001) and physiological data show that they are usually tuned to a broad ultrasonic spectrum (Yack and Hoy 2003). Loosing predation pressure results in partial regression of auditory systems (Fullard et al. 2007). In Cicadidae, intraspecific acoustic signalling derived from ancestral vibration signalling in Auchenorrhyncha (Claridge et al. 1999; Hoch et al. 2006) (Fig. 2.8). Hemiptera of small body size use ancestrally tymbal mechanisms to generate vibration signals and Cicadidae produce auditory sounds by identical means of tymbal mechanisms. Thus, the biomechanical way of signal production was retained, but the signal's mode of transmission changed, as did the sensory mode of reception. Tympanal hearing probably evolved in parallel to this change in transmission mode.

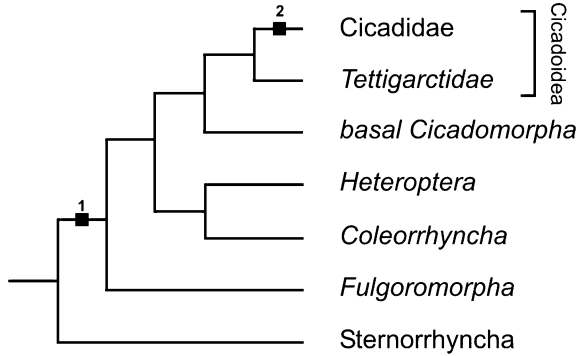


Fig. 2.8 Phylogenetic origin of cicada acoustic signalling revealed by mapping of signalling behaviours on the phylogeny of Hemiptera. Signal production by tymbals is present in all Hemiptera excluding the basal Sternorrhyncha, and thus presumably monophyletic (indicated as autapomorphy, a novel trait [1]). In ancestral taxa (names in italics) tymbals were used for the production of substrate vibration. Only recent Cicadidae use tymbals for sound production and hear with tympanal ears (autapomorphy [2]). Their sister group, the Tettigarctidae, also produce vibration signals. Thus, acoustic communication evolved from tymbal mechanisms used for vibratory signalling. Adapted from Hoch et al. (2006) and from Claridge et al. (1999)

Acrididae commonly have ears but not all groups use acoustic signals for intraspecific communication, and those using auditory cues do so by different mechanisms (Riede 1987). A phylogenetic study indicated a possible order of the evolution of ears (Fig. 2.9): tympana are present in the Acridoidea, including grasshoppers and locusts, and the Pyrgomorphidae in the first abdominal segment while the latter lack stridulation behaviour. These two groups are sister taxa (Flood et al. 2000), making the assumption of an origin of tympana in their common lineage most parsimonious. Some more basal acridid taxa do use stridulation for sound production, though with different mechanisms than Acridoidea. It is thus difficult to match the origins of hearing and of stridulation, as for stridulation repeated gains as well as several losses may have occurred. Two explanations are available to accommodate these findings, conflicting over the ancestral function of hearing (Flood et al. 2000): stridulation and hearing evolved simultaneously within the lineage of Acridomorpha, and either one was lost in specific lineages. This implies that stridulation was initially also present in the lineage of Pyrgomorphidae, but was lost secondarily. As an alternative, the evolution of tympana and stridulation may have occurred independently, with audition presumably functioning in predator detection and evasion. Intraspecific signalling in Acrididae occurs by different sound production mechanisms, including mandibular, femoro-tegmina and femoro-abdominal sounds (Riede 1987). Even within a species, males and females might have different stridulatory structures, indicating their separate evolutionary origins, and hinting that stridulatory structures apparently evolve easily. Stridulation might have evolved in defence rather than intraspecific signalling. The multiple mechanisms of stridulation were also seen as indication that hearing

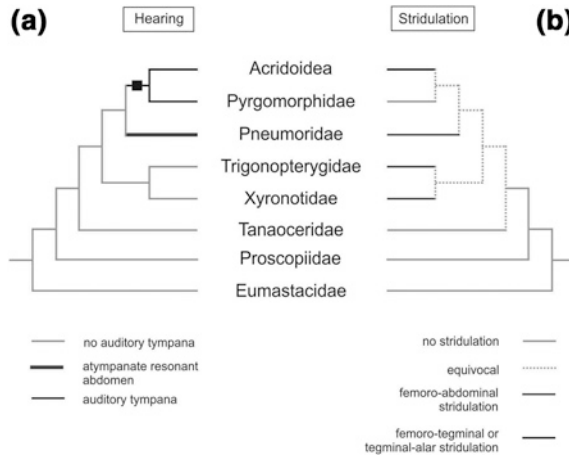


Fig. 2.9 Phylogeny of Acridomorpha with occurrence of **a** tympanal organs and **b** stridulation mechanisms in the different taxa. Comparison of the distribution of hearing and sound production highlights their uneven distribution among Acridomorpha. As the most parsimonious explanation, tympanal hearing originated in the lineage of Acridoidea and Pyrgomorphidae (indicated by *square*). Origins of stridulation are not resolved, indicated by dotted line for equivocal taxa, and may involve repeated losses. The phylogenetic mapping highlights that stridulation occurred prior to hearing in either scenario in at least some taxa. Adapted from Flook et al. (2000)

evolved prior to intraspecific acoustic signalling (Riede 1987; Flook et al. 2000), probably to avoid terrestrial predators like reptiles (Stumpner and von Helversen 2001; Greenfield 2002) or small mammals (Flook et al. 2000). In this case, sound production came before sound perception by tympanal ears.

Amongst Noctuoidea and Pyraloidea moths, an evolutionary succession of acoustic functions seems to have taken place though in another sequence than in acridids. Some species produce intraspecific sound signals, but tympanal hearing is far more common. The evolution of intraspecific communication in this case seems to be facilitated by the hearing sense which evolved earlier in defence against bat predation. Male ultrasonic signalling may have been favoured in evolution due to the auditory system which was already sensitive to ultrasound (Greenfield 2002; see Chap. 6 by Greenfield).

2.6 Conclusion

The evolutionary approach to hearing in insects is a multidisciplinary one where quantitative behavioural analysis, behavioural ecology, and phylogenetics are just as important as functional anatomy and sensory physiology to understand the origin of insect ears. These studies address some central evolutionary questions, which all contribute to a proper understanding of hearing in insects: (1) from

which sensory precursor organ did an ear evolve, (2) where in a given lineage did tympanal ears appear, (3) under which selection pressure(s) did the ear originate, (4) which physiological and behavioural adaptations occurred with a hearing sense, and (5) how did the hearing organ diversify further?

The depth of information is so far not the same for all tympanate taxa of insects. For cicada the ancestry of signalling behaviour has been resolved, but a precursor of the ear is not explicitly identified. However, for some groups, a very consistent scenario of ear evolution has been formed, e.g. for Mantids and Acridids, based on comparative neuroanatomy, physiology, phylogeny and studies of acoustic behaviour. Origins of auditory systems can be illuminated by phylogenetic approaches and “tree thinking”, as they seek to clarify organismic relationships, identify ancestral and derived sensory organisations, and identify evolutionary transitions. These approaches will enforce multi-species studies, which will in turn provide principle insights into the commonalities and diversifications of auditory sensory evolution. Addressing different levels of evolutionary change, such as the origin of ears, the adaptive changes in existing ears, or changes in acoustic behaviour, in a surely cross-disciplinary approach will help to understand the evolution of insect ears.

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