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# TYMPANAL HEARING IN INSECTS

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## ABSTRACT

Specialized hearing organs, known as tympanal organs, have evolved in at least seven different orders of insects. Tympanal organs are usually defined by the presence of a tympanal membrane (or eardrum). They are backed by an air-filled space or cavity and are innervated by a chordotonal sensory organ. In some insects, however, a recognizable tympanal membrane may not be easily identified by visual inspection, yet may possess tympanal hearing organs. In insects that possess them, tympanal hearing organs may mediate the detection of predators, prey, and potential mates and rivals. Unlike the ears of vertebrates, which are localized to cranial segments, the ears of insects may be found in a bewildering variety of locations on their bodies, depending on the species. The embryological and evolutionary origins of tympanal organs are related to ancestral states as proprioceptive chordotonal organs.

## INTRODUCTION

An insect, like any animal, depends on specialized organs for remote sensing of other animals: potential predators, prey, and mates or rivals. To see, hear, smell, or feel the presence of others, insects use eyes, auditory organs, olfactory organs, and internal proprioceptors and cuticular hairs sometimes borne on specialized appendages such as cerci or antennae. Compared with vision and olfaction, the ability of insects to hear may at first seem to be relatively uncommon. No one doubts that cicadas, crickets, and katydids have good hearing, because of their conspicuously loud calls, which mediate their conspecific reproductive and territorial interactions (5, 37, 51), but among the most speciose of insect taxa, such as the Coleoptera, Hymenoptera, and Diptera, reports of conspicuous sound emissions are rare. Nevertheless, even these groups appear to emit acoustic signals in various behavioral contexts (12, 50,

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52). However, whether they have the means to detect such signals is not always clear.

An acoustic signal is generated by the vibrations of a sound-producing structure, and its reception requires the detection of those vibrations by appropriate mechanoreceptive organs. When an insect produces sound, part of the vibrational energy may be propagated through the substrate upon which the sender is standing and part through the air. Substrate-borne signals are generally omitted from the domain of acoustic signals, and for the sake of brevity, we do not discuss them either, although they are deserving of a thorough review (19, 44, 45). However, substrate signals can be considered part of a general class of signals that includes acoustic (airborne) signals, and when considering the structure, function, and evolution of the organs for signal production and reception, we ought to view them together. Certainly, if the discussion includes those insects that produce substrate signals and are sensitive to them, we are no longer talking about an apparent small minority of insects (46).

Even if we restrict ourselves to the domain of hearing organs that are sensitive to the airborne component of a vibrational sound source, we face the problem of defining an insect "ear" (85). An airborne sound signal has two components that affect its reach or effective communication range. The effective range, in turn, depends on several factors, including distance from the sound source, such as the size of the sound radiator relative to the wavelength of the sound (10, 11); the physical features of the sound itself, such as frequency and initial intensity of the signal; environmental factors; and the sensitivity of the receiver (49, 70). Very near the sound source, within a radius measuring one wavelength of the emitted signal, the adjacent air molecules experience relatively large translational movements that represent a significant proportion of the total intensity in the sound signal (this proportion decreases sharply as the distance to the sound source increases and rapidly becomes negligible from the sensory point of view). Within this nearby space of signal propagation, a detector is said to be in the near-field of the sound source (49).

Examples of near-field detectors include the cercal organs of cockroaches, the Johnston's organs of mosquitoes, and the aristae of drosophilid flies (46). Although these are indeed examples of auditory organs, they lack eardrums and are not tympanal organs. Depending on species and behavioral context, these organs are generally restricted in their range of communication to short distances—a few body lengths in *Drosophila melanogaster* (12) to one meter for male mosquitoes (44). In general, the range of frequency sensitivity of near-field auditory receivers is also restricted to sounds containing relatively low frequencies—a few hundred (75–500) Hertz. For example, *D. melanogaster* (12) and mosquitoes (44, 45) respond to sounds corresponding to the wingbeat frequencies of their mates, and caterpillars respond to the wingbeat frequencies of predatory wasps (78, 79). Sensory hairs borne on the insect's body or on specialized appendages, such as the cerci of orthoperans or the antennae of mosquitoes, also serve as receptors for sound vibrations (46).

Although near-field sound receptors are certainly interesting, they are not discussed further in this review because they are not tympanal ears and are discussed in several excellent reviews (23, 46, 51, 70).

Farther from the sound source, the air molecules experience the propagation of the sound as a pressure wave. The term ears, whether applied to insects, frogs, elephants, or humans, usually refers to auditory detectors sensitive to the pressure wave of the sound field. In insects, such auditory detectors are sensitive to a wide range of high frequencies (2 to more than 100 kHz) and that, depending on species, permit the detection of sounds over relatively long distances, up to tens of meters. In this article, we restrict ourselves to these far-field acoustic detectors, which are commonly designated tympanal hearing organs.

This review covers (*a*) the definition and taxonomic distribution of tympanal hearing organs (i.e. ears); (*b*) the morphology and function of tympanal ears in selected insects, including sexually dimorphic ears; (*c*) the developmental origins of some tympanal organs; and (*d*) recent studies on possible evolutionary origins of tympanal organs.

## TYMPANAL HEARING ORGANS IN INSECTS

Tympanal ears are morphologically characterized by three features: a tympanal membrane; an air-filled sac or tracheal expansion, upon which the tympanum is appressed; and an associated chordotonal sensory organ. The tympanum (or eardrum) is a specially differentiated region of cuticle that is thinner than the surrounding cuticle and often appears silvery because of the way it reflects light. The chordotonal organ is a complex cellular unit consisting of a bipolar sensory neuron, the dendrite of which inserts distally into a scolopale cell. The dendrite and the scolopale cell are connected to several glial and support cells and together form the scolopophorous or scolopidial organ (46, 54). Airborne sound waves from the emitting source impinge upon the tympanum and make it vibrate. These vibrations are then sensed by the chordotonal sensory organ. In many insects, such as crickets, katydids, cicadas, moths, and locusts, the chordotonal organ may be excited not only by sound impinging directly on the external surface of the tympanum, but also by sound waves impinging on the tympanum's internal surface. For instance, in crickets, an airsac associated with the tympanum is part of the spiracular tracheal system and provides a pathway for sound to reach the internal side of the tympanum. The ability to sense the difference in sound pressure on both sides of the tympanum is the key to the directional properties of some insect auditory systems, which are known as pressure-difference receivers (51). The complex interaction between the acoustic excitation of the tympana and the anatomy of the internal tracheal pathways in pressure-difference auditory receivers exemplifies the diversity of (fundamentally different) hearing mechanisms found in insects (51).

Tympanal hearing has been well documented in seven orders of insects (Table 1). Other workers have compiled similar lists (e.g. 85). The number of orders has grown in the past few years, and not only are other orders likely to be added to that list in the near future, but more examples within each order

**Table 1** The occurence of tympanal hearing organs in seven orders of insects

| Order | | Superfamily/ family | Species | Ear location | Reference |
|---|---|---|---|---|---|
| Neuroptera | 1 | Chrysopidae | *Chrysopa carnea* | Wing base | 53 |
| Lepidoptera[a] | 2 | Geometroidea/ Geometridae | *Larentia tristata* | Abdomen | 18 |
| | 3 | Noctuoidea/ Noctuidea | | Metathorax | 20a |
| | | Notodontidae | *Phalera bucephala* | Metathorax | 62b |
| | | Arctiidae | *Cycnia tenera* | Metathorax | 73 |
| | 4 | Papilionoidea/ Nymphalidae | *Heliconius erato* | Base of fore- or hind-wing | 77 |
| | 5 | Hedyloidea/ Hedylidae | *Macrosoma hyacinthina* | Fore-wing base | 72a |
| Coleoptera | 6 | Cicindelidae | *Cicindela marutha* | Abdomen | 76 |
| | 7 | Scarabaeidae | *Euetheola humilis* | Cervical membranes | 26 |
| Dictyoptera | 8 | Mantodea | *Mantis religiosa* | Ventral metathorax | 88 |
| | | Blattoidea[b] | *Periplaneta americana* | Metathoracic leg | 75 |
| Orthoptera | 9 | Acrididae | *Locusta migratoria* | First abdominal segment | 30a |
| | 10 | Gryllidae | *Gryllus bimaculatus* | Prothoracic leg | 72 |
| Hemiptera | 11 | Cicadidae | *Cystosoma saundersii* | Abdomen | 91 |
| | 12 | Corixidae | *Corixa punctata* | Mesothorax | 62a |
| Diptera | 13 | Tachinidae | *Ormia ochracea* | Ventral prosternum | 66 |
| | 14 | Sarcophagidae | *Colcondamyia auditrix* | Ventral prosternum | 75a[c] |

[a] These four superfamilies are considered to have independently evolved tympanal organs.
[b] Absence of well-differentiated tympanal membrane.
[c] Evidence of phonotactic behavior.

will certainly be discovered. In recent years, tympanal hearing has been demonstrated in the speciose orders Coleoptera (76, 89) and Diptera (39, 65).

Does the lack of a recognizable tympanal membrane preclude audition in the far field? In a few examples of audition reported from Dictyoptera and Gryllidae, no well-defined tympanal membrane was associated with the chordotonal sensory organ. Even if the putative tympanal membrane does not consist of a transparent or translucent delimited area of cuticle, it may still be thinner than the adjacent cuticle, as in praying mantises (87, 88). Other insects also lack obvious tympana. Some cockroaches, notably the Madagascar hissing cockroach, *Gromphadorhina portentosa,* use acoustic signals for courtship and territorial displays (55, 57). The auditory organs are tibial subgenual organs (28, 56), but no obvious tympanal region or thin cuticle was found. Recently, Shaw (75) reported that the cockroach *Periplaneta americana* can detect airborne sounds. The auditory tuning curve displays a best-frequency of about 1.8 kHz, with thresholds in the range of 55–60 dB sound pressure level, which is comparable to the threshold range of other tympanate insects (51). The putative auditory sensory organ of *P. americana* is the metathoracic tibial subgenual organ (75).

Shaw used isolated cockroach legs. Such dissection quite possibly alters the acoustic characteristics of the leg tracheal system. Intact preparations are preferable, as are tuning curves from single unit recordings. However, Ritzmann et al (63) had previously reported evidence of hearing (also in *P. americana*), based on the acoustic responsiveness of identified interneurons with a striking resemblance to auditory interneurons from other insects, as discussed below.

Thus, in two distantly related genera of cockroaches, the tibial subgenual organ, which is usually thought of as a detector of substrate vibrations, has auditory sensitivity and consequently serves a dual function. Yet both species lack any obvious overlying region of thin cuticle corresponding to a tympanum. Nonetheless, two of the three structures that typically compose a tympanal organ—a scolopidial organ (the subgenual organ) and closely apposed tracheae—are present. Auditory function has also been reported for an atympanate tettigoniid, *Phasmodes ranatriformes* (38). This insect lacks any recognizable tympanal membranes and tracheal expansions in the tibiae of its forelegs. Nonetheless, neural recordings showed that a putative homologue of the auditory organ (the crista acustica) was excited by sound, although it exhibited considerably less sensitivity than that associated with a tympanum. *P. ranatriformes* looks more like a stick insect than a bushcricket or katydid, and Lakes & Schikorsky (38) posit that it may be a primitive tettigoniid.

What are the implications of these studies? For one, auditory function may be even more widespread in insects than previously reported, especially if functional hearing can occur without a clearly differentiated external tympanal membrane.

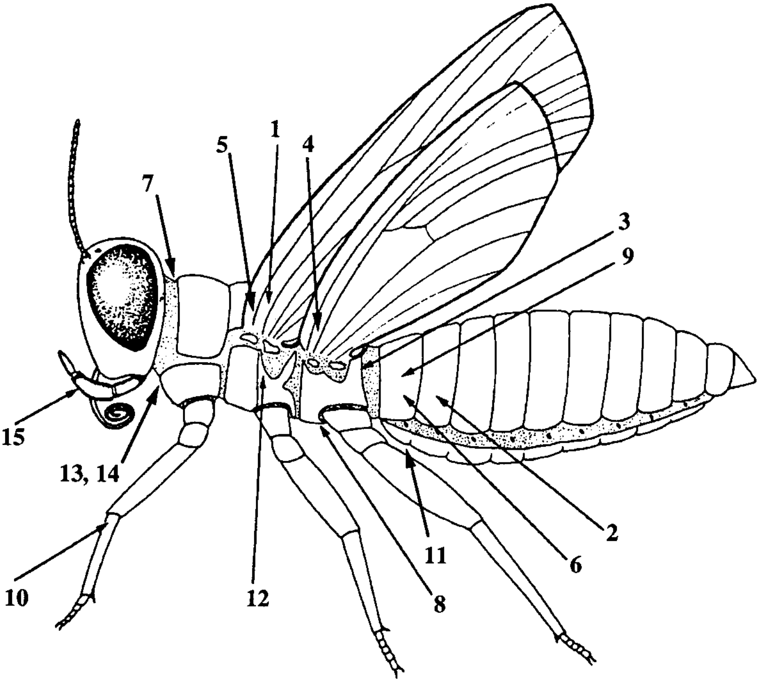

*Figure 1* Diagrammatic view of a "generalized" insect, which shows the locations on the body where tympanal hearing organs have been described in various species of insects. The numbers refer to the second column of Table 1, except for number 15, which refers to the pilifer organ of hawkmoths (Lepidoptera: Sphingidae). (Modified from Reference 85.)

Tympana, whether cryptic or conspicuous, may be found at various body locations, from the head to the abdomen and on appendages, including mouthparts (68), wings (53), and legs (72), depending on species. Among insects within an order but from different families, tympanal ears may have different locations (Figure 1) (18, 30a, 73, 84). In many insects, such as in the Orthoptera and at least ten families of Lepidoptera, the tympana are anatomically conspicuous (73), a silvery eardrum can be identified on the tibial segment (crickets, bushcrickets, and katydids) or on the body (moths and grasshoppers). In other groups, e.g. the praying mantis, the tympanum is inconspicuous or hidden from view (87). It may also be cryptic, as in some heliconid butterflies (77) and the green lacewing (53), in which the effective tympanum is associated with the wing veins.

Thus, the identification of tympanate insects on the basis of morphology is not straightforward. Strictly speaking, should only those insects that possess a frankly differentiated tympanal membrane be included? Must the tympanal membrane be obvious to (human) visual inspection? These questions arise because some insects that lack a visually obvious tympanum perform similar acoustic behaviors as insects with tympana—namely, detect high-frequency sounds at long distance in the acoustic far-field—and also possess scolopophorous sensory organs associated with acoustic tracheae. Such insects, e.g. the praying mantis, possess a functionally equivalent tympanum, i.e. a thin (1–10 μm) cuticle that overlies the acoustic tracheae and the scolopophorous organ.

Table 1 and Figure 1 indicate the impressive taxonomic and locational diversity of tympanal organs among insects. Indeed, no other group of animals exhibits such a bewildering diversity of ear placement. One can find tympanal ears in almost any segment of the insect body!

## THE BEHAVIORAL FUNCTION OF TYMPANAL HEARING

In the conspicuously tympanate insects, such as cicadas (91), crickets (4, 26, 37), and katydids (31, 69, 80), conspecific communication related to reproduction and territoriality is clearly mediated by loud songs. However, in insects, hearing involves not only mates and rivals, but also predators and prey. In particular, a surprising number of night-flying insects possess tympanal ears that are tuned to ultrasound (36). This is presumably an evolutionary response to predation by insectivorous bats, which detect their prey by means of echolocation using ultrasonic biosonar (24, 67). A brief summary of acoustic behavior follows in which we present a few examples out of the many hundreds in the literature.

### *Calling, Courtship, and Territorial Signals*

Long-distance mate calling is characteristic of insects in several insectan orders. In the most common pattern, the male produces the calling song and the female usually responds by either flying or walking to his location (23, 37). The Orthoptera (crickets, katydids, grasshoppers) and Hemiptera (cicadas) include the most conspicuous of the acoustically signaling insects. In some grasshopper signaling systems, the female produces a stridulation in response to the male's call, resulting in a duet (43, 80a, 80b). Cicadas are among the loudest of daytime singing insects, and their hearing is mediated by a tympanal hearing organ (91). Among the Orthoptera, the songs of mole crickets (Gryllotalpidae) are especially loud because males sing from subterranean burrows dug in the shape of an exponential horn; the males actively adjust the tuning of this burrow (10, 80). The male's call is thus amplified and broadcast high into the air, where it attracts females on the wing (10, 27).

In field crickets, once the male has attracted a female onto his territory with his calling song, his courtship includes a stridulatory act called the courtship song. This song, which is distinct from the calling song, is initiated by mutual antennation (1, 80b) and is strictly a short-range signal. In field crickets, courtship song influences mating success under laboratory conditions (15, 42). The rivalry song that accompanies male-male aggression is also emitted at short range (2, 4, 80b).

### *Predator Detection*

In many insects, particularly the nocturnally active, flying insects, ultrasonic frequencies elicit an acoustic startle or escape response. In general, a series of suprathreshold tone pulses with frequencies ranging from 20 to 50 kHz, although the upper frequency limit may exceed 100 kHz (24), is sufficient to elicit the startle responses (25, 36, 67). These reactions are presumably to insectivorous bats, which hunt insects on the wing by detecting them with the aide of ultrasonic biosonar (32). The best-known example is bat predation upon nocturnally flying moths (67). But since the publication of Roeder's pioneering work (67), many examples have been documented (36), and ultrasound-mediated startle responses have been demonstrated in laboratory experiments on five orders of insects (Lepidoptera, Dictyoptera, Neuroptera, Orthoptera, and Coleoptera). Whether hunting bats actually elicit such startle responses in all cases has not been rigorously demonstrated by field observations; however, predatory acts are rarely observed in nature, and most bat-insect interactions are especially difficult to observe because they occur in darkness, high above the ground.

In insects such as moths preyed upon by bats, ultrasound-sensitive ears appear to have evolved directly as a result of predation (67). In other insects, such as crickets and short- and long-horned grasshoppers, ultrasound sensitivity may have been added onto preexisting auditory capabilities that had mediated social interactions (36, 41, 64).

### *Acoustic Parasitism*

Acoustic parasitism was first demonstrated by Cade (16), who reported that the field cricket *Gryllus integer* is parasitized by the tachinid fly *Euphasiopteryx ochracea*. The larviparous females of this fly, now reclassified as *Ormia ochracea* (83), localize their hosts, male crickets, by hearing and homing in on the mating calls of these crickets (16). Live larvae are then deposited upon or near the singing male cricket, which becomes infested (3). The auditory organ of *O. ochracea* females was described recently (65), and a similar organ was reported in females of another tachinid parasitoid, *Therobia leonidei* (39). The hearing organs of *O. ochracea* and *T. leonidei* were shown to be a typical tympanal ear; it has a well-defined membrane, backed by an air-filled acoustic chamber, and a scolopophorous sensory organ is attached directly to the membrane (65, 66). The ears of female *O. ochracea* appear to be most sensitive to sound in the range 4–6 kHz, which encompasses the dominant frequency of its host's song (4.8 kHz). However, the fly also exhibits sensitivity in the ultrasonic region, 20 to at least 60 kHz. Males of *O. ochracea* also have tympanal hearing organs, but these ears are quite different from those of the females, in both form and function (65, 66). They are relatively insensitive to the 5-kHz frequencies that characterize cricket calls, but they are just as sensitive to ultrasounds as the female fly's ears. Because these parasitoids have adopted the activity cycle of a nocturnally active cricket, and like crickets, they fly at night, they presumably must also be vulnerable to the cricket's predators, such as insectivorous bats that hunt on the wing by echolocation. Therefore, the ultrasound sensitivity in the ears of male and female *O. ochracea* may have arisen from the need to detect and avoid predation by bats.

### *Sexual Dimorphism in Tympanal Organs*

Reports of sexual dimorphism in the auditory systems of insects have been relatively rare, although dimorphism was recently observed in species from four different orders of tympanate insects: a tettigonid (6), the gypsy moth (17), several praying mantis (86, 88), several species of cicadas (89a), and two tachinid parasitoid flies (39, 66). Interestingly, the dimorphism often takes the form of differences in auditory sensitivity, instead of in the gross morphology of the hearing organ itself (17, 88). In at least some of these examples, e.g. mantises and tachinid flies, differences may be more closely related to predator or prey detection than to intraspecific communication. Nonetheless, sometimes following a lead from functional investigations, researchers have established a firm morphological basis for the dimorphism in tachinid flies (66), tettigonids (6), uraniid moths (18), and praying mantises (86).

## DEVELOPMENTAL ORIGINS OF TYMPANAL ORGANS

### *Introduction*

The tympanal organs most thoroughly studied from a developmental viewpoint are those of the acoustically active Orthoptera, in particular those of the Caelifera (grasshoppers and locusts) and the Ensifera (katydids and crickets). The Orthoptera undergo hemimetabolous development, and so the ontogenesis of the auditory organ takes place both embryonically, before the first-instar larva hatches from the egg, and postembryonically, as development proceeds through a variable number of larval instars (up to 11 in some field crickets) (13, 90). Because fully differentiated tympanal organs are not usually expressed until the imago stage, postembryonic development must be considered an important part of their ontogenesis. Detailed studies of the auditory organs during both the embryonic and postembryonic stages have been made mainly on acridids and katydids (48, 71) and crickets (7). The following account therefore focuses primarily on the development of the various components of ensiferan organs.

### *Development of the Tympanal Membrane*

In crickets, definitive eardrums do not appear on the surface of the tibia of the foreleg until the adult stage (90). In the katydid *Ephippiger ephippiger,* the foreleg tympana are recessed within tympanal cavities and not visible on the surface, but as in crickets, the tympana are not fully morphologically differentiated until the adult molt (71). In the Australian field cricket, *Teleogryllus commodus,* the first sign of the tympanum is a thinning of hair sensilla on the region of the cuticle that will become the eardrum; this thinning does not occur until the eighth instar (three molts from the adult). By the tenth instar (one molt to adulthood), an area devoid of hair sensilla clearly has taken on the elliptical shape of the posterior tympanal membrane (90). At adulthood, the thin, translucent tympanal membrane takes on a silvery hue because it overlies the air-filled trachea within the leg. This is the membrane upon which sound impinges, and it serves as part of a complex sound-receiving system.

### *Development of Leg Tracheae*

Sound is conducted through leg tracheae in crickets and katydids. These air-filled tubes or chambers are crucial elements of insect audition and are associated with both eardrums and the sensory scolopidial organs (40). In *T. commodus,* the tracheae of the forelegs develop over the course of the 11 instars. As development proceeds postembryonically, the tracheae branch and, during the last few instars, increase considerably in diameter. By the adult stage, these prothoracic acoustic tracheae are proportionally larger than their serial homologues in the meso- and metathoracic tibiae (90). The acoustic tracheae in the forelegs of *E. ephippiger* similarly take on their adult form over the course of six larval instars, becoming adult-like in the fourth instar (71).

### *Development of the Scolopidial Sensory Organ*

The scolopidial sensory organ undergoes an embryonic and a postembryonic stage of development. Meier & Reichert (48) conducted the most definitive study of embryonic development in the Ensifera using two tettigoniids, *Metaplastes ornatus* and *Poecilimon affinis.* In the prothoracic limb buds of embryos 40% into their development, a cluster of ectodermal cells invaginates the lumen of the tibia. It then separates from the epithelium of the leg, migrates, and eventually differentiates into the subgenual organ and the auditory sensory organ, i.e. the crista acustica. The characteristic linear array of scolopidia, which in the adult is correlated with tonotopic representation of frequency (61, 92), is apparently already established in embryos 50% into their development. Moreover, the use of molecular markers for sensory cell identity has shown that, in katydids, the full complement of scolopidia is generated during embryonic development (48), a finding confirmed by postembryonic studies (71). However, whether the embryonic development of these organs occurs in crickets is questionable. In *T. commodus* (7), light microscopic examination of paraffin-embedded and stained legs taken from different larval instars, showed that although the full adult complement of scolopidia in the subgenual organs had appeared by the first instar, no scolopidia in the crista acustica were present until the third instar. During postembryonic development, scolopales are systematically added in a proximal-to-distal order, and the shape of the scolopidia and associated support cells changes as the instars progress toward the adult stage.

### *Functionality of the Developing Tympanal Organ*

Evidence indicates that the immature ear in both crickets and katydids, although lacking frank tympanal membranes, is already sensitive to sound. Hill & Boyan (34) demonstrated that auditory interneurons in the last instar of *T. commodus* had a similar tuning curve to those in adults. By recording compound action potentials from larval tympanal nerves, Rössler (71) demonstrated that the auditory spectral sensitivity is already adult-like by the fourth instar. The intensity thresholds of the earlier-instar organs tended to be considerably higher than those of the adult by at least 20 dB.

In the adult katydid, the proximal-to-distal linear array of scolopidia has functional significance. The frequency sensitivity of the tympanal organ ranges from low in the proximal regions of the crista acustica to high in the distal regions. This tonotopic organization of scolopidia within the katydid crista acustica was inferred from extracellular recordings (92) and shown directly from intracellular recordings from single cells in the scolopidial complex (60). A very similar tonotopic organization occurs in gryllids and was also confirmed at the receptor cell level (61, 93).

## EVOLUTIONARY ORIGINS OF TYMPANAL ORGANS

The early histological studies by Friedrich of the anatomy of insect tympanal organs suggested that they arose from proprioceptive chordotonal organs (29, 30). Based on his studies on postembryonic instars and adults, he proposed that the crista acusticae in crickets and katydids shared a common origin with the subgenual organ. The argument that the auditory organ and the subgenual organ are in fact homologous is now confirmed by unequivocal evidence for the common embryonic origin of both subgenual and auditory organs in katydids (48). This embryological study also established that the subgenual organs in meso- and metathoracic legs develop in the same way as the specialized auditory organs in the prothoracic legs, which demonstrates that all of these organs share segmental homology. In moths, Yack & Fullard (84) present evidence that the metathoracic tympanal organ of noctuid moths may have evolved from a chordotonal stretch receptor that serves other functions in atympanate moths. For example, in the tobacco hornworm, *Manduca sexta,* it measures movements of the wings during flapping flight. Meier & Reichert (48) argue that the pair of tympanal organs of locusts, which are located in the first abdominal segment, also evolved from a chordotonal stretch receptor. These authors noted that the other abdominal segments contain pleural chordotonal organs that are serially homologous to the specialized pleural tympanal organ. Their argument is compelling, as it is based on developmental evidence. In tachinid flies, the auditory chordotonal organ is apparently also derived from a chordotonal proprioceptive organ, which has an unknown function in various outgroups of closely and distantly related higher flies (21).

In the past decade, findings on the developing nervous system of the locust, combined with anatomical data on the auditory systems of several insect species, have led to interesting general hypotheses about the functional and evolutionary relationships of tympanal hearing in insects. In locusts, the lineage of a given neuron in the adult can be traced back to its origins in the neuroblasts of the early embryo. This work was begun by the pioneering American entomologist WM Wheeler (81), and its modern-day revival has reinvigorated the studies of homology and evolutionary biology in insect neural systems (9, 62), in particular the developmental and evolutionary origins of tympanal organs in insects.

New ways of thinking about the auditory system in insects have come from the developmental work of Bastiani et al (8), Doe & Goodman (20), and Meier & Reichert (48), combined with a large body of literature on the structure and function of several species' tympanal organs and their neural projections in the central nervous system. In particular, a recent review by Boyan (14) provides an important synthesis of this information from disparate sources. These authors argue that all tympanal organs arise developmentally from a common set of segmentally homologous precursors that have mechanoreception, such as stretch sensitivity, as a primitive function. Moreover, the sensory afferent nerves of these chordotonal organs, whether auditory or not, project into specific areas of ganglionic neuropiles, where they possibly form synapses with at least some common second-order interneurons that in turn project ascending or descending axons in the central nervous system. This arrangement implies that at least some chordotonal organs in insects have a modular structure, if not multiple functions.

The generality of this hypothesis rests on lineage studies done on the central and peripheral sensory systems in two species, the grasshopper, *Schistocerca gregaria* (e.g. 8, 48) and the fruit fly, *D. melanogaster* (47). The notion that the central networks subserving auditory or chordotonal function contain homologous interneurons related by lineage certainly needs more investigation, but tantalizing data in support of it have been reported from cockroaches (63), praying mantises (88), and locusts (8, 14). Certainly, the data supporting a modularity hypothesis based on serial homologies of receptor and ganglionic interneuronal systems appear to be well founded. The assertion of phylogenetic homology of elements between species is always problematic and remains so also for chordotonal sensory and modular interneuronal systems. However, species-by-species investigations into the embryological origins of identified sensory and central neurons would certainly provide a developmental basis on which to establish homologies and would enhance the analysis of the homology question.

## CONCLUDING REMARKS

Among terrestrial animals, only vertebrates and insects are widely endowed with a sense of hearing. In vertebrates, hearing is associated with the possession of an inner ear embedded in the skull. It consists of fluid-filled chambers containing sensory hair cells and various thin membranes that overlie or are associated with the hair cells. This organ system appears to have evolved only once in vertebrate evolution (58), the organs being located in the head and nowhere else. However, in insects, the possession of hearing organs is not related to their position. Insect ears have evolved independently from taxon to taxon and even severally within a taxon (e.g. the Lepidoptera). The reason(s) for this diversity of ears may be related to the roles hearing plays in the life of the insect. Thus, field crickets, bushcrickets, and katydids use hearing not only to receive conspecific communication signals, but also to detect the ultrasound echolocation signals of predaceous bats.

In these orthopteroids, the same hearing organ serves both these functions, and we speculate that ultrasound sensitivity was added on to preexisting sensitivity for lower-frequency conspecific signals. Given that the Orthoptera can be traced back nearly 200 million years (74), whereas the fossil record for bats can be traced back only 65 million years (59), this is not an unreasonable proposal. However, the order Lepidoptera is relatively younger [about 100 million years (22)], and given that many of the acoustically sensitive lepidopteran species have ears that are sensitive exclusively to ultrasound, the predatory pressures from insectivorous bats might have comprised the primary force in auditory evolution. As pointed out above, the auditory receptive apparatus of many insects appears to be derived from a ubiquitous and anatomically widely distributed sets of paired pleural chordotonal receptors. In acoustically sensitive moths, this origin would account for the diversity of ear locations with (a pair of) tympana on the thorax or on one of several abdominal segments.

Tympanal hearing is at one end of a continuum in the insectan mechanoreceptive-based communication system for detecting remote signal sources. This continuum also includes near-field reception, whereas substrate-borne reception is at the other end of the continuum. We can speculate that the most primitive form of mechanoreceptive communication was substrate signaling, given the ubiquitous occurrence of vibration-sensitive chordotonal, campaniform, and sensory hair receptors in insects.

Finally, we believe that the examples of tympanal hearing we have presented above are just the tip of the iceberg with respect to the actual occurrences of tympanal hearing organs in the Insecta. The recent discoveries of tympanal hearing organs in the Coleoptera and the Diptera point to future discoveries in these speciose taxa. We should not be at all surprised by reports of tympanal hearing in the Hymenoptera. An insect's ability to hear may not be necessarily surmised from an anatomical examination of its surface anatomy. More important are the functional attributes; however, these can be difficult to demonstrate, given that many insects use signals with frequencies and amplitudes beyond (both above and below) those detectable by humans and currently available electronic instrumentation, which is designed around human hearing. The fact that some insect auditory behavior may be performed in the dark of night and high in the air provides an additional challenge for the study of hearing in insects.

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