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The Structure and Function of Auditory Chordotonal Organs in Insects

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KEY WORDS hearing; scolopidium; sensory; transduction; tympanum; ears; mechanoreception; evolution

ABSTRACT Insects are capable of detecting a broad range of acoustic signals transmitted through air, water, or solids. Auditory sensory organs are morphologically diverse with respect to their body location, accessory structures, and number of sensilla, but remarkably uniform in that most are innervated by chordotonal organs. Chordotonal organs are structurally complex Type I mechanoreceptors that are distributed throughout the insect body and function to detect a wide range of mechanical stimuli, from gross motor movements to air-borne sounds. At present, little is known about how chordotonal organs in general function to convert mechanical stimuli to nerve impulses, and our limited understanding of this process represents one of the major challenges to the study of insect auditory systems today. This report reviews the literature on chordotonal organs innervating insect ears, with the broad intention of uncovering some common structural specializations of peripheral auditory systems, and identifying new avenues for research. A general overview of chordotonal organ ultrastructure is presented, followed by a summary of the current theories on mechanical coupling and transduction in monodynal, mononematic, Type 1 scolopidia, which characteristically innervate insect ears. Auditory organs of different insect taxa are reviewed, focusing primarily on tympanal organs, and with some consideration to Johnston's and subgenual organs. It is widely accepted that insect hearing organs evolved from pre-existing proprioceptive chordotonal organs. In addition to certain non-neural adaptations for hearing, such as tracheal expansion and cuticular thinning, the chordotonal organs themselves may have intrinsic specializations for sound reception and transduction, and these are discussed. In the future, an integrated approach, using traditional anatomical and physiological techniques in combination with new methodologies in immunohistochemistry, genetics, and biophysics, will assist in refining hypotheses on how chordotonal organs function, and, ultimately, lead to new insights into the peripheral mechanisms underlying hearing in insects. *Microsc. Res. Tech. 63:315–337, 2004.*

INTRODUCTION

Acoustic signals play a prominent role in the lives of many insects. Sounds and vibrations are widely used for detecting and locating predators, prey or hosts, and for various sexual and social interactions (Cocroft, 2001; Hoy, 1998; Hoy and Robert, 1996; Miller and Surlykke, 2001; Stumpner and von Helversen, 2001). Insects have an amazing diversity of hearing organs, from single "hairs" to complex tympanal ears that collectively operate over a frequency range of more than 150 kHz, and an intensity range of over 100 dB (Michelsen, 1979). In different taxa, hearing organs can occur on almost every part of the body, including the mouthparts, wings, and legs, and vary considerably in both their structure and complexity. During the past few decades, the introduction of new acoustic, biomechanical, and physiological techniques have enabled us to broaden our concept of what constitutes a functional hearing organ, leading to the discoveries of new hearing organs in insects previously thought to be earless, including some flies, mantids, and butterflies. The structural and functional characteristics of insect ears have been studied extensively (reviewed by Haskell, 1961; Hoy and Robert, 1996; Michelsen and Larsen, 1985; Robert and Göpfert, 2002; Römer and Tautz, 1992; Yack and Hoy, 2003; Yager, 1999a).

Despite their considerable structural variability, most insect ears are uniformly innervated by a single type of mechanoreceptor, the chordotonal organ (Fullard and Yack, 1993; Hoy and Robert, 1996; Yager, 1999a). Surprisingly little is known about the functional organization of chordotonal organs in general, and just how these structurally complex sensilla convert mechanical vibrations into electrochemical impulses remains one of the leading questions in the study of insect bioacoustics. The goals of this report are: (1) to review the literature on the structure of insect auditory chordotonal organs, with an emphasis on tympanal ears, since this is where most of the liter-

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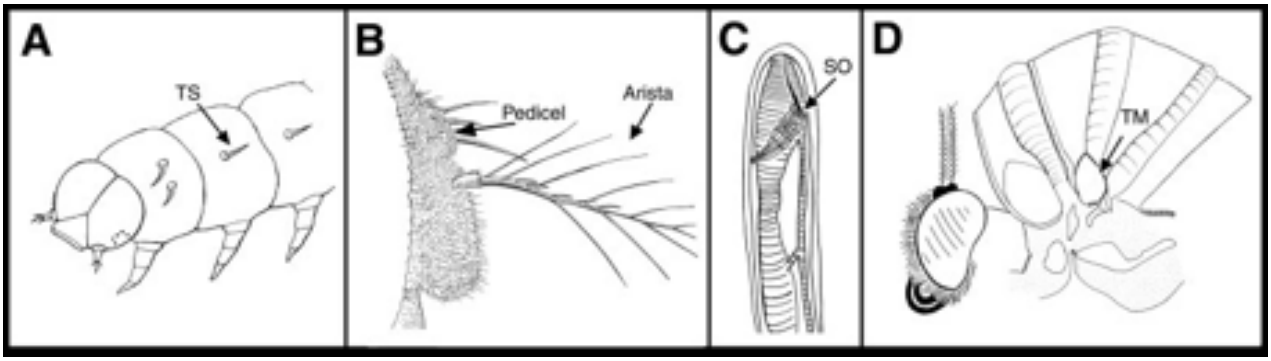


Fig. 1. Schematic illustrations of the four main types of insect auditory receptors: Trichoid sensilla, Johnston's organ, Subgenual organs, and Tympanal organs. **A:** Trichoid sensilla. In *Barathra sp.* caterpillars, thoracic trichoid sensilla (TS) detect near-field sounds produced by the wing beats of predatory wasps. **B:** Johnston's organ. The antennae of some insects are modified to detect near-field sounds produced by the wing-beats of conspecifics. In female *Drosophila*, the arista vibrates in response to male songs. Vibrations are transmitted to Johnston's organ in the pedicel. **C:** Subgenual organ. The foreleg subgenual organ (SO) in a female ant *Formica sanguinea*. Subgenual organs are located in the proximal tibia of most insects, and in some species are highly specialized for detecting solid substrate-borne vibrations. **D:** Tympanal organs. In the butterfly *Hamadryas feronia*, a tympanal membrane (TM) at the base of each forewing functions to detect far-field sounds produced by conspecifics. A–D are redrawn from Markl and Tautz (1975), Bennet-Clark and Ewing (1970), Eggers (1928), and Yack et al. (2000), respectively.

ature is concentrated; (2) to identify structural features common to auditory chordotonal organs that could lead to developing hypotheses linking structural specializations to specific functions; (3) to identify gaps in the literature on the peripheral auditory system. I will concentrate on the structural organization of the chordotonal organ at the level of the receptor. Information coding by primary afferents and processing at the level of the central nervous system have been reviewed by Boyan (1993), Field and Matheson (1998), Pollack (1998), Pollack and Imaizumi (1999), and Stumpner and von Helversen (2001).

INSECT HEARING ORGANS: AN OVERVIEW

Auditory organs belong to a broader class of sensory organs known as mechanoreceptors, sensory neurons stimulated by mechanical deformations of the body. In insects, mechanoreceptors occur in several different forms, and are widely distributed throughout the body. Those sensitive to forces generated by the insect's own activity (e.g., wing vibration, breathing, limb movements) are proprioceptors, while those sensitive to external forces (e.g., touch, wind, sound), are exteroreceptors (for reviews on insect mechanoreception, see French, 1988; Keil, 1997; McIver, 1985). Auditory organs are those specialized for detecting sound, and sound, in turn, can be defined broadly to include various forms of vibrations transmitted through air, water, or solids. Although the distinction between some forms of sound and other mechanical stimuli is sometimes arbitrary (Michelsen and Larsen, 1985), it is convenient to begin with a few definitions when discussing hearing in insects. Airborne sounds may be categorized as being in the far- or near-field by their pressure and velocity components, respectively. When air particles are displaced close to a sound source, they transmit the disturbance to neighboring particles. This disturbance propagates as a fluctuating change in pressure that can travel a long distance from the source. Pressure waves are referred to as "far-field sounds." Closer to the sound source, the velocity of displaced air particles can be sufficient to move lightweight structures. These "near-field sounds" are most effective close to the sound source, typically within one wavelength and are restricted to lower frequencies ($<\sim$2 kHz).

In some insects, a sense of hearing is clearly defined by the presence of a highly visible hearing organ or marked behavioral or physiological responses to biologically relevant sounds. The tympanal ears of noctuoid moths, for example, are conspicuously located on the metathorax, and specifically tuned to ultrasonic cries of insectivorous bats, which evoke evasive flight maneuvers in the moth (Roeder, 1967). In other insects, a sense of hearing may not be so obvious. Some lacewings (Neuroptera) and mantids (Dictyoptera), for example, have anatomically cryptic, but functional hearing organs (Miller, 1983, 1984; Yager, 1999a,b). Other insects may exhibit a physiological response to sound, but an adaptive sense of hearing is unknown or lacking (Yack and Fullard, 1993). It is possible for a mechanoreceptor that does not normally function as a hearing organ to be stimulated by a sound stimulus of non-biological relevance. For example, chordotonal organs scattered throughout the body that normally function as proprioceptors may be positioned in relation to the external cuticle such that they respond physiologically to low-frequency, high-intensity air-borne sounds, but they may not necessarily elicit an adaptive behavioral response (Yack and Fullard, 1993). Alternatively, some auditory organs may also be sensitive to proprioceptive stimuli (e.g., Hedwig, 1988; van Staaden et al., 2003). Given the difficulties in defining an insect ear, for purposes of this review, I will follow the views of Haskell (1961) by defining a hearing organ as a receptor that mediates an adaptive behavioral response to sound. Ideally, an adaptive sense of hearing in an insect should be validated with behavioral experiments, in conjunction with anatomical and physiological evidence.

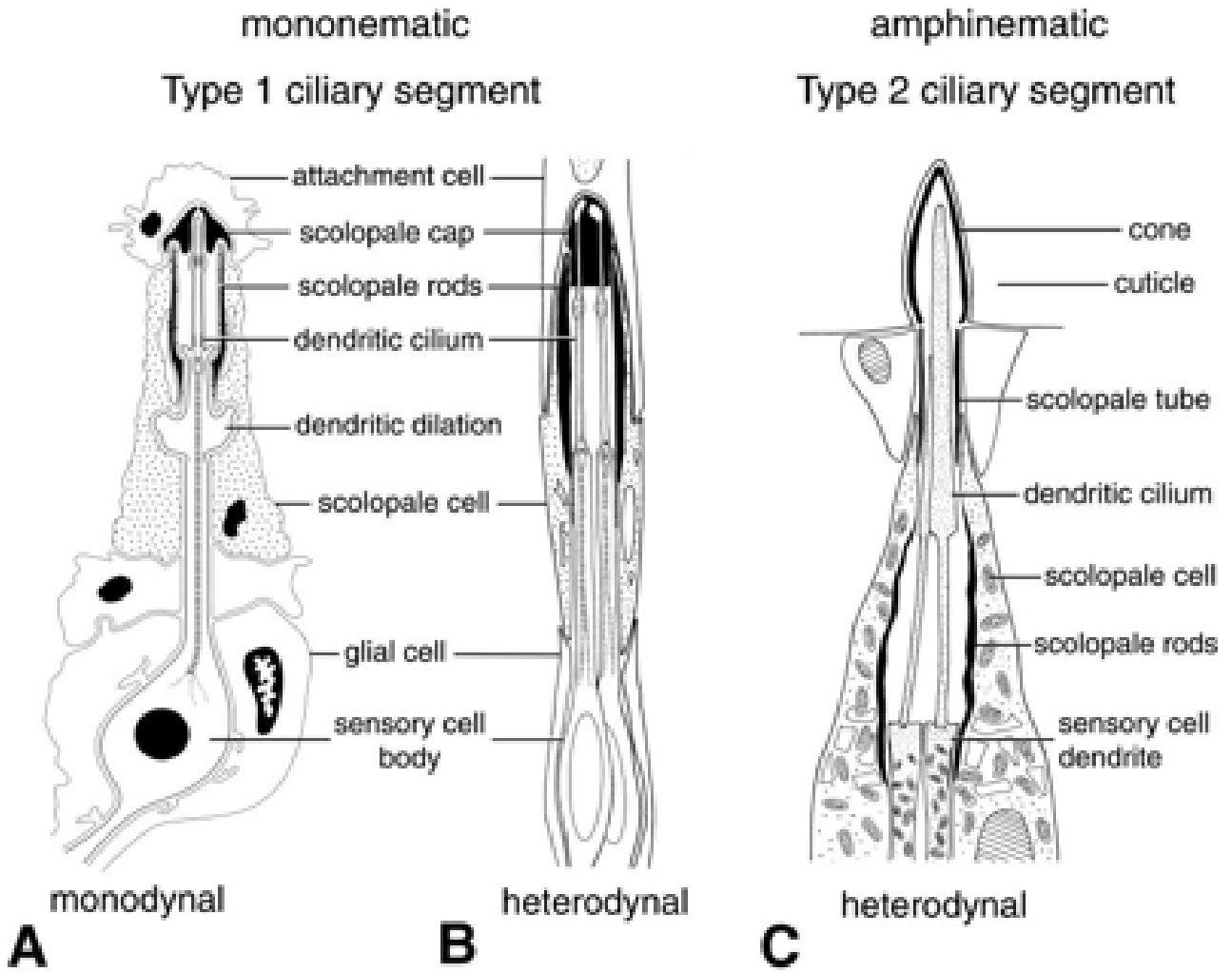


Fig. 2. Schematic representations of scolopidia from three different chordotonal organs to illustrate some of the structural differences between mononematic and amphinematic scolopidia, monodynal and heterodynal scolopidia, and scolopidia with Type 1 and 2 ciliary segments. **A:** A mononematic, monodynal scolopidium from the tympanal ear of *Locusta migratoria*. **B:** A mononematic, heterodynal scolopidium from the femoral chordotonal organ of an adult lacewing, *Chrysoperla carnea*. **C:** An amphinematic, heterodynal scolopidium from the mouthparts of a beetle larva, *Speophyes lucidulus*. A is reproduced from Yack and Hoy (2003; after Gray [1960]) with permission of the publisher. B and C are redrawn from Lipovsek et al. (1999) and Corbière-Tichané (1971), respectively.

Four main types of hearing organs have been described for insects: Trichoid sensilla, Johnston's organs, Subgenual organs, and Tympanal organs (Fig. 1).

Trichoid Sensilla

Trichoid sensilla are hair-like cuticular projections innervated at their bases by one or more bipolar nerve cells (Keil and Steinbrecht, 1984). In some species, the "hair" shaft is specialized to mediate responses to faint air currents, or near-field sounds. These sensilla are relatively long (up to 1.5 mm) and rest loosely in their sockets (Keil, 1997). Several species of lepidopterous caterpillars (Fig. 1A) have thoracic trichoid sensilla sensitive to the near-field sounds produced by flying wasps or flies (e.g., Markl and Tautz, 1975, 1978; White et al., 1983). Trichoid sensilla on the anal cerci of some crickets may function in detecting the near-field components of courtship songs (Kämper, 1984).

Antennae and Johnston's Organ

The antennae of many Diptera and some Hymenoptera are specialized for detecting near-field sounds generated by the wing-beats of conspecifics. The branched arista of female *Drosophila* (Fig. 1B) detect the species-specific courtship sounds of males (Bennet-Clark and Ewing, 1970), while the long, feathery antennae of male mosquitoes (Göpfert et al., 1999) (Fig. 9A) and chironomids vibrate in response to flight sounds of females (reviewed by McIver, 1985). In honeybees (*Apis mellifera*), the antennae are thought to respond to near-field sounds emitted by dancing conspecifics (Dreller and Kirchner, 1993). In all of these insects, the antennal flagella are specially adapted for capturing sound and fit loosely into specialized sockets, allowing them to vibrate. Located at the base of the flagellum, in the pedicel, is Johnson's organ, a large chordotonal

organ responsible for transducing antennal vibrations into neural impulses. The functional organization of Johnston's organ is discussed later in this report.

Subgenual Organs and Substrate Vibration Receptors

Substrate-borne vibratory communication is probably widespread in both larval and adult insects, but for the most part, the behaviors and receptor mechanisms associated with this form of communication are poorly understood (Cocroft, 2001; Hill, 2001; Markl, 1983). Trichoid sensilla, campaniform sensilla, and various scattered chordotonal organs have all been implicated as vibration detectors (Cokl and Virant-Doberlet, 2003; Kühne, 1982; Römer and Tautz, 1992), but the best known receptor specialized for receiving high-frequency vibrations (generally up to ~5 kHz) is the subgenual organ (Fig. 1C; see also Figs. 6, 10), a chordotonal organ located in the proximal tibia of the legs of most insects. Structural details of the subgenual organ are discussed later in this report.

Tympanal Ears

Tympanal ears are the best described, and most complex of all insect hearing organs (Fig. 1D; see also Figs. 4, 5B,D, 6–8). They have evolved numerous times in insects, and sometimes multiply within a given order or species (Hoy and Robert, 1996; Yack and Hoy, 2003; Yager, 1999a). Tympanal ears are capable of detecting far-field sounds at distances up to more than a kilometer, and over a broad range of sound frequencies (from ~300 to >100 kHz). Anatomically, tympanal ears are typically characterized by three sub-structures: (1) a tympanal membrane (=ear drum) consisting of a thinned region of exoskeleton; (2) an enlarged tracheal air chamber to which the internal face of the tympanal membrane is appressed; and (3) one or more chordotonal organs associated either directly or indirectly with the tympanal membrane. The structural characteristics of tympanal organs in various insect taxa are discussed in detail in this report.

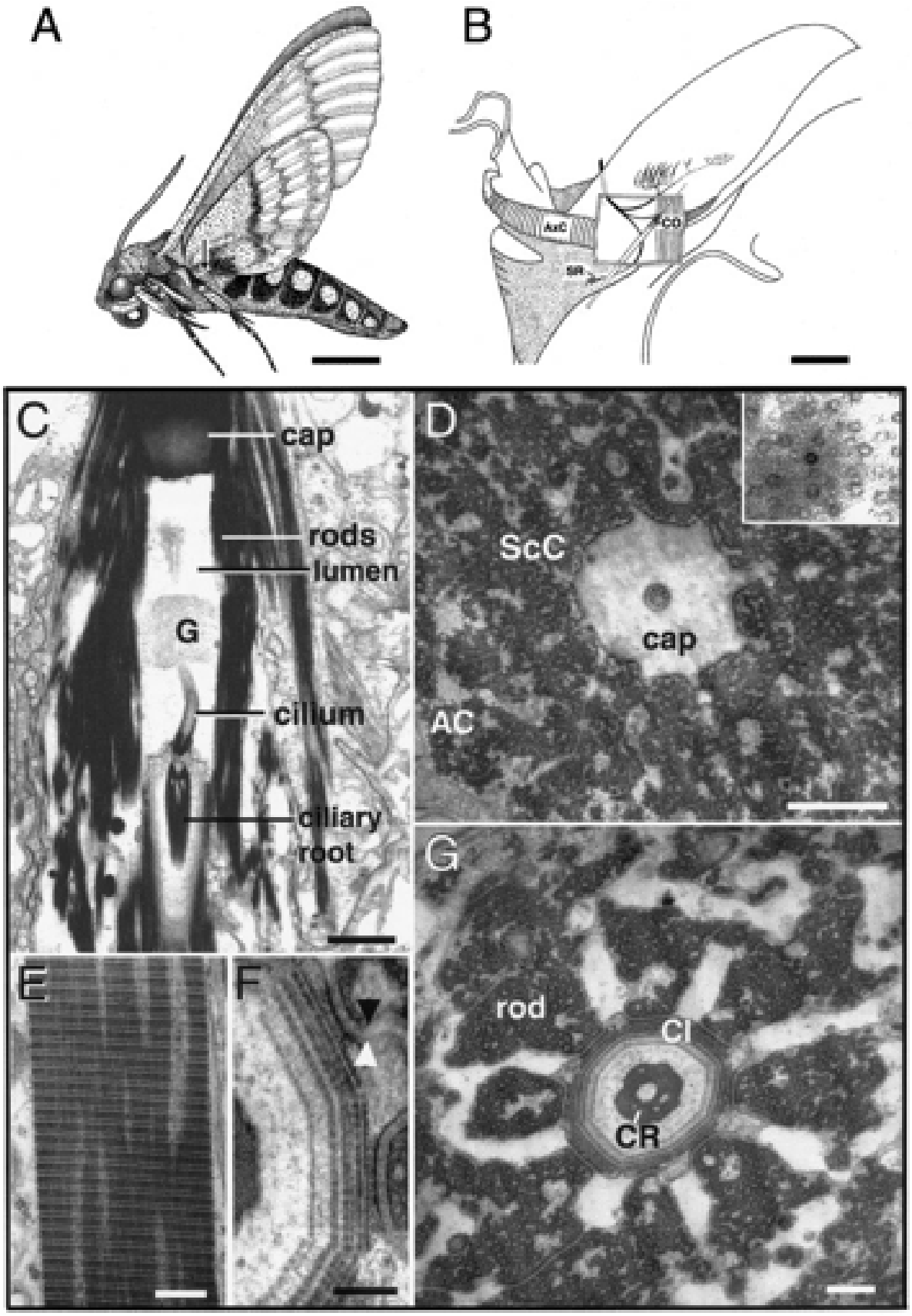
CHORDOTONAL ORGANS

Chordotonal organs are specialized mechanoreceptors unique to the Insecta and Crustacea (Field and Matheson, 1998). In insects, they are widely distributed throughout the body, where they function as proprioceptors, detecting self-induced movements of limbs and internal organs, or exteroreceptors, detecting gravitational forces or acoustic stimuli. Except for those innervating tympanal ears, there are typically no external manifestations of their presence. Chordotonal organs are particularly specialized for sensing rapidly alternating pressures, and, collectively, can detect cuticular displacements over seven orders of magnitude (Field and Matheson, 1998). Some tympanal organs are capable of registering displacements as small as 6×10^{-10} m (Michelsen and Larsen, 1985), while some proprioceptors, like the locust femoral chordotonal organ, are stimulated by much larger displacements of 1.3×10^{-3} m (Field and Burrows, 1982). These miniature "elaborate micromechanical transducers" (Field and Matheson, 1998) are characterized by their unique arrangement of constituent cells and subcellular structures. Each chordotonal organ comprises one or more special units called scolopidia. A single scolopidium consists of four cell types arranged in a linear manner: (1) one to four bipolar sensory neurons, each with a distal dendrite with the structure of a modified cilium [=a Type I mechanoreceptor (see McIver, 1985)]; (2) a scolopale cell that envelops the sensory cell dendrite; (3) one or more attachment cells associated with the distal region of the scolopale cell; and (4) one or more glial (=schwann, perineurium) cells surrounding the proximal region of the sensory neuron soma.

Chordotonal organs exist in several morphologically diverse forms. Reviews of their structure and distribution are provided by Eggers (1928), Howse (1968), Moulins (1976), McIver (1985), and Field and Matheson (1998). In accordance with the classification scheme summarized by Field and Matheson (1998), chordotonal scolopidia are categorized as being (1) Type 1 or Type 2, defined by the nature of the dendritic cilium; (2) mononematic or amphinematic, defined by the kind of extracellular structure associated with the scolopale cell; (3) monodynal or heterodynal, defined by the number of sensory neurons per scolopidium. The chordotonal organs may be connective or non-connective, depending on how they attach to the cuticle. Some general characteristics of these different types are outlined below, and illustrated in Figure 2.

Type 1 and Type 2 scolopidia are distinguished by the type of ciliary segment in the sensory cell dendritic segment (Moulins, 1976). In Type 1 (Fig. 2A,B), the cilium is of uniform diameter throughout, except for a distal dilation occurring about 2/3 along its length. With few exceptions, the axoneme is characteristic of what is believed to be a non-motile cilium (with a $9 \times 2 + 0$ microtubular configuration), and the cilium in-

Fig. 3. The wing-hinge chordotonal organ in atympanate moths, representing the evolutionary precursor to the metathoracic tympanal organ in Noctuoidea moths. **A:** Left lateral view of the atympanate *Manduca sexta*, with an arrow marking the location of the metathoracic wing-hinge chordotonal organ, illustrated in B. Scale bar = 1 cm. **B:** Posterior view of the left metathorax with parts of the cuticle, musculature, and tracheal tissue removed to reveal the wing-hinge receptor complex. The chordotonal organ (CO) attaches to sclerotized cuticle of the epimeron, slightly ventral to the multiterminal stretch receptor (SR). AxC, axillary cord. Scale bar = 500 μm. **C:** Longitudinal section (slightly oblique) through the distal region of a single scolopidium of the wing-hinge chordotonal organ in the atympanate *Actias luna*. A local ciliary bend can be seen between the dendritic apex and the granular material (G) within the scolopale lumen. **D:** Transverse section through the proximal third of the scolopale cap. The scolopale cell (ScC) wraps around the cap, joining at the mesaxon. The scolopale cell joins to the cap by hemidesmosomes. The dense fibrillar plaque (called rod material inside the scolopale cell) is located on either side of the apposed membranes of the scolopale cell and attachment cell (AC). Scale bar = 1 μm. **Inset**: High magnification (~80,000×) of cap material. **E:** Longitudinal section through a single ciliary root, showing the typical banding pattern. Scale bar = 0.25 μm. **F:** Transverse section through the dendritic collar. Inner membranes of the dendrite and scolopale cell are marked with black and white arrowheads, respectively. Scale bar = 0.20 μm. **G:** Transverse section through a single scolopidium at the level of the dendritic collar and ciliary root. The dendritic collar (Cl) is octagonally shaped. Adjacent to each side of the octagon, within the scolopale cell, is the scolopale rod material. This electron-dense material is organized into eight rods, separated from one another by proximal extensions of the lumen. The ciliary root (CR) is hollow, just proximal to where it branches into nine processes. Scale bar = 0.5 μm. A,B and C–G are reproduced from Yack (1992) and Yack and Roots (1992), respectively, with permission of the publishers.


A
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cap
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Cl
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Fig. 3.

serts into a scolopale cap as opposed to a tube. In Type 2 (Fig. 2C), the diameter of the ciliary segment increases into a distal dilation, which loses the typical ciliary axoneme, and can be densely packed with microtubules. This distal region is associated with a scolopale tube rather than a cap.

Mononematic and Amphinematic scolopidia are distinguished by the kind of extracellular structure associated with the scolopale cell and dendritic cilium. In mononematic scolopidia, the dendritic tip inserts firmly into an electron dense structure in the shape of a cap, which always occurs in the subepidermal region. In amphinematic scolopidia, the dendritic tip is surrounded by, but not firmly attached to, an extracellular, electron-dense tube that may terminate subepidermally, or be drawn out into a thread and insert into the epidermis (e.g., Fig. 9E).

Monodynal and Heterodynal scolopidia differ in the number of sensory neurons they possess. In earlier studies, scolopidia were classified as being isodynal (where all sensory neurons in one scolopidium are structurally similar), heterodynal (sensory neurons are structurally dissimilar), or monodynal (with a single sensory neuron per scolopidium). However, since it is now realized that all sensory neurons within a single scolopidium differ structurally to some degree, the term isodynal is no longer used. The terms monodynal and heterodynal now represent scolopidia with a single sensory cell (Figs. 2A, 3–8, 10) or more than one sensory cell (Figs. 2B,C, 9), respectively.

Connective and Non-Connective Chordotonal Organs differ by their association with the tegument. In connective chordotonal organs, the attachment cell(s) insert into a connective tissue strand that often forms a bridge between two moveable body parts. In non-connective chordotonal organs, the attachment cell(s) attach directly (or indirectly via an intermediate cell) to the hypodermis.

ULTRASTRUCTURE OF TYPE 1, MONONEMATIC, MONODYNAL SCOLOPIDIA

All insect chordotonal organs that respond to far-field sounds are non-connective, with monodynal, mononematic, Type 1 scolopidia. Although chordotonal organs with these particular features do not function exclusively as sound receptors, it is assumed that these specializations impart some functional advantage to the detection and transduction of acoustic signals. We can presently only speculate on the functional attributes of the several different structural variations of chordotonal organs, since we do not yet understand how chordotonal organs function, even in a general sense. A considerable number of studies have described the ultrastructure of chordotonal organs (reviewed by Field and Matheson, 1998; Howse, 1968; Moulins, 1976). Although insect auditory chordotonal organs have been included in these discussions, they have not been reviewed per se, and it is the purpose of this report to do so. First, it is useful to summarize the ultrastructural features of non-connective chordotonal organs, with monodynal, mononematic, Type 1 scolopidia. This information, drawn necessarily from both non-auditory and auditory chordotonal organs due to the limited number of studies on the latter, is used to discuss current theories on mechanical coupling and transduction in this type of chordotonal organ, followed by a specific look at auditory organs in various insect taxa.

Sensory Neuron

The sensory neuron comprises a peripheral cell body with a proximal axon projecting to the central nervous system, and a single distal, ciliated dendrite. The soma and axon hillock are typically enveloped by a perineurium (=schwann, glial) cell, while the dendrite is enveloped by the scolopale cell. The dendrite is divided into a proximal inner segment and a distal, ciliated outer segment (Fig. 2). The inner segment contains ciliary roots, microtubules, and, in some cases, a high proportion of mitochondria. A pronounced enlargement of the inner segment (=dendritic dilation) just proximal to the scolopale rods has been reported in several cases, and has been noted to be particularly common in chordotonal organs functioning in sound and vibration detection (Field and Matheson, 1998) (Figs. 2A, 6E). At the distal end of the inner segment, the dendritic membrane connects to the base of the scolopale rods by means of belt desmosomes, otherwise known as the dendritic collar (Fig. 3F,G). The outer dendritic segment is a long, modified cilium that extends through the center of the scolopale lumen, a fluid-filled cylindrical space formed by the surrounding scolopale cell. The diameter of the outer segment is uniform throughout, except for a small, distal, bulbous dilation (=ciliary dilation) (Figs. 2A,B, 4D,E, 6E). The distal tip of the outer segment inserts snugly into, and sometimes passes right through, the scolopale cap.

Dendritic Cilium

The cilium originates proximally within the dendritic inner segment as a number of ciliary rootlets, which appear cross-banded in longitudinal sections (Fig. 3E). As the inner dendritic segment narrows distally, the rootlets coalesce into a single, cylindrical, ciliary root that divides into nine processes that surround the proximal basal body, and continue distally where they converge to form the distal basal body (Figs. 3C, 4D,E, 5F). The proximal and distal basal bodies are two centriole-like structures that form the base of the dendritic cilium. The proximal basal body consists of nine triplets of microtubules connected to each other in a concentric ring. The distal basal body forms the base of the ciliary axoneme that extends distally into the dendritic outer segment. An "alar spoke" radiates outward from each set of triplets connecting the distal basal body to the cell membrane (Fig. 4E).

Within the dendritic outer segment, the ciliary component has the structural features of a modified cilium. The axoneme typically has a $9 \times 2 + 0$ configuration, with nine pairs of microtubules arranged in a concentric ring, but lacking the central pair of microtubules. At the base of the cilium, both microtubules are hollow, and each doublet is connected by radial extensions to the surrounding dendritic membrane. This is called the "ciliary necklace" region (Fig. 4E). Distal to the ciliary necklace, one of the microtubules of each pair is hollow, and the other has a dense core with arms (presumed to be dyenin arms). This pattern is maintained distally until reaching the ciliary dilation, at which point the

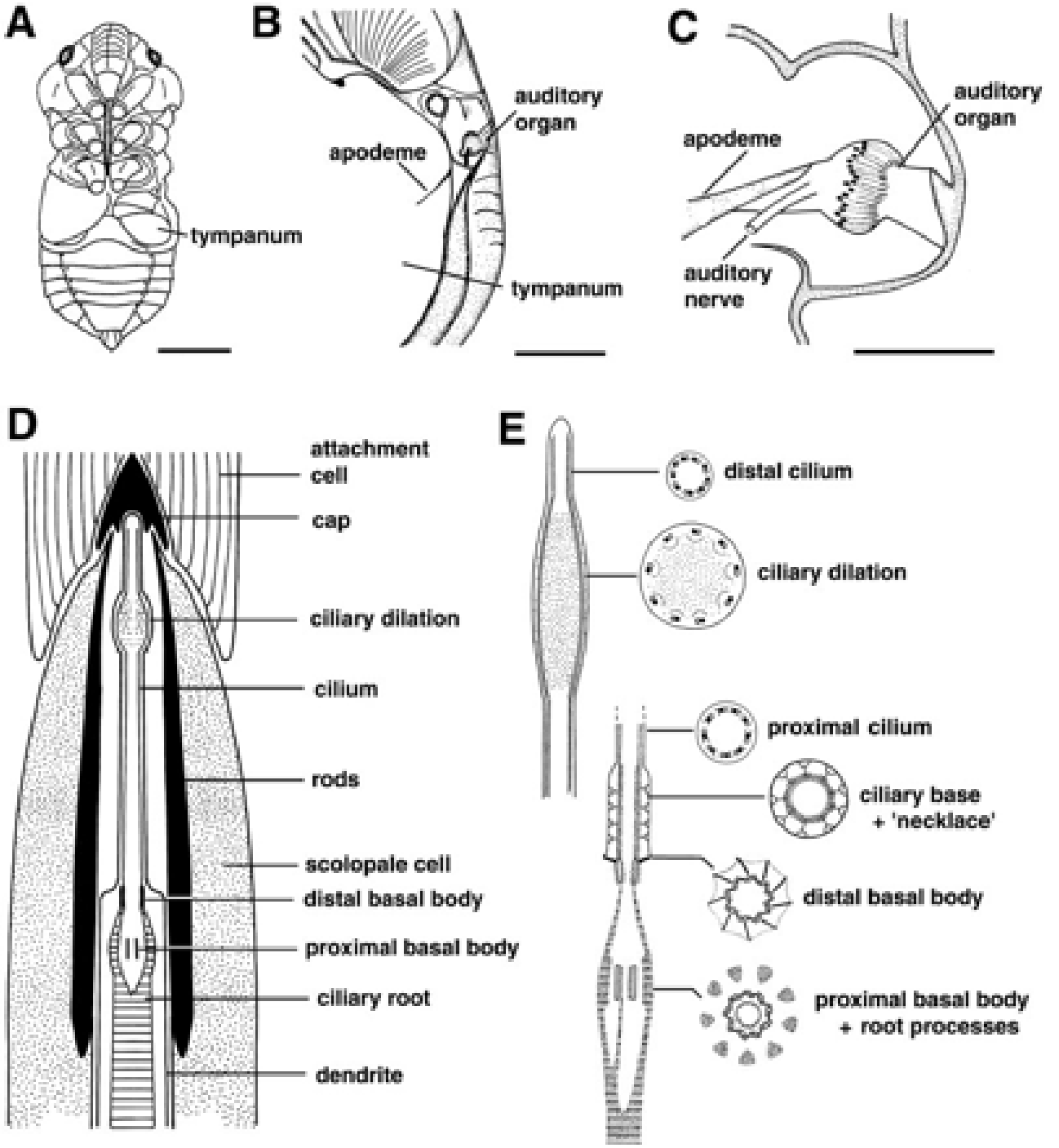

Fig. 4. Schematic diagram of the tympanal ear and auditory chordotonal organ of a cicada, *Cyclochila australasiae*. **A:** Ventral view of a male, showing the location of the tympanal membrane in the second abdominal segment. The wings, legs, and one operculum have been removed. Scale bar = 5 mm. **B:** Lateral portion of the left tympanal membrane viewed from the anterior, with the anterior cuticle of the auditory capsule removed to show the tympanal organ located within the auditory capsule. Scale bar = 2 mm. **C:** The auditory organ, showing the orientation of the scolopidia, facing away from the auditory nerve. Scale bar = 0.5 mm. **D:**. Diagramatic representation of the distal region of the dendrite and associated scolopale structures. **E:** Distal and proximal regions of the dendritic cilium. The longitudinal views are represented at half the magnification of the transverse views at left. A–C are redrawn from Daws and Hennig (1996). D,E are redrawn from Young (1973).

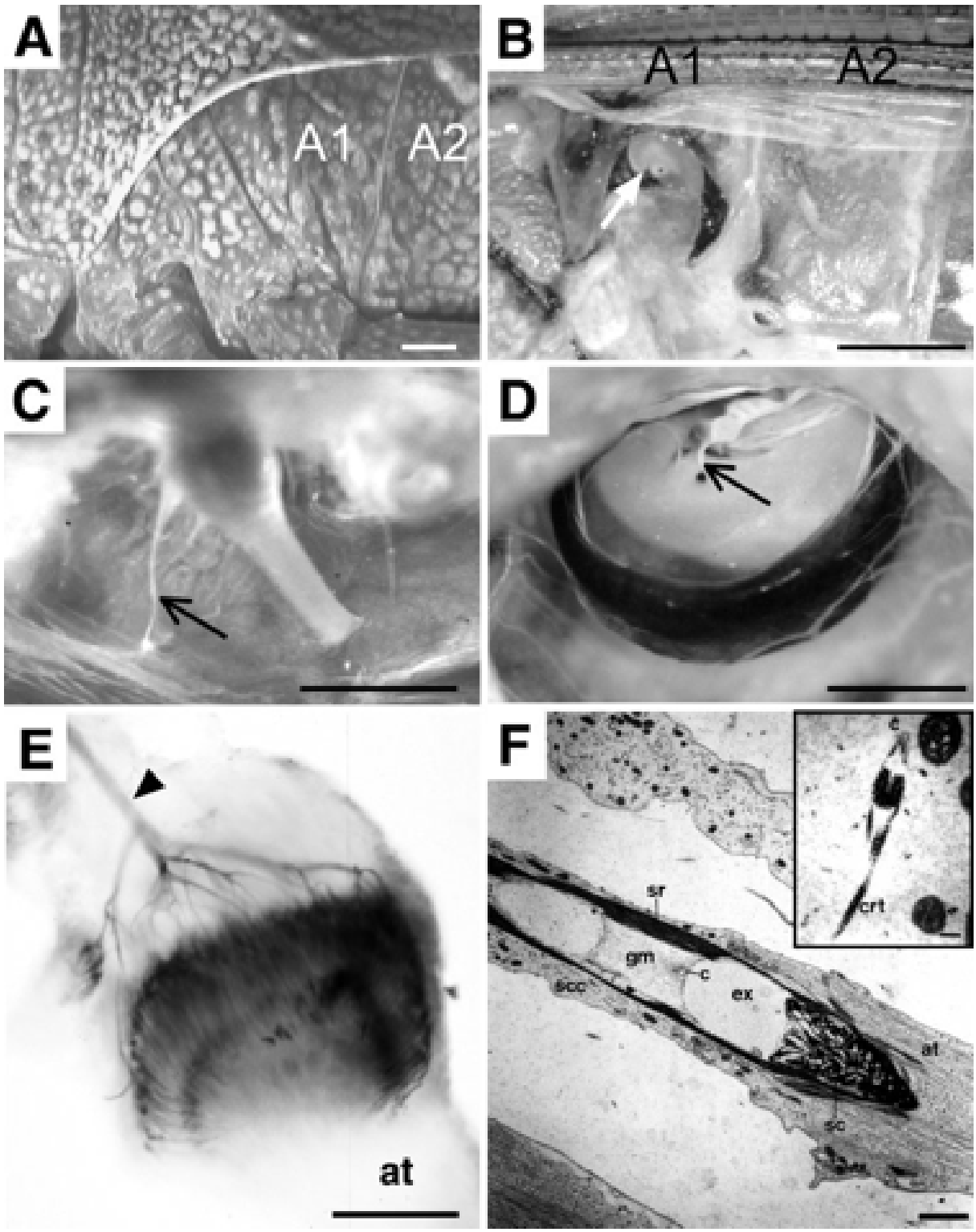

Fig. 5. Homologous hearing organs in the bladder grasshopper, *Bullacris membracioides* (A,C,E,F) and the locust, *Locusta migratoria* (B,D). **A,B:** External views of the left anterior abdominal segments (A1–A2) in the atympanate bladder grasshopper and tympanate locust (after removal of the forewing), respectively. A white arrow marks the location of the locust tympanal membrane. Scale bar = 2 mm. **C:** Internal view of the A1 auditory organ in *B. membracioides* showing two separate attachment sites to the membranous cuticle. A black arrow marks the smaller of the two. Scale bar = 1.2 mm. **D:** Internal view of the locust auditory chordotonal organ (=Müller's organ) showing one of the four attachment sites (black arrow) to the inner surface of a clearly defined tympanal membrane. Scale bar = 600 μm. **E:** Retrograde cobalt backfill of the A1 auditory organ in *B. membracioides*, showing staining of the auditory scolopidia. A black arrowhead marks the location of the auditory nerve. at, attachment cells. Scale bar = 200 μm. **F:** Longitudinal electron micrograph through a single A1 auditory scolopidia of *B. membracioides*. c, cilium; ex, extracellular space (=lumen); gm, granular material; sc, scolopale cap; scc, scolopale cell; sr, scolopale rod. Scale bar = 1.7 μm. **Inset:** longitudinal section of the basal body, between the ciliary root (crt) and the proximal end of the dendritic cilium. Scale bar = 0.25 μm. Reproduced from van Staaden et al. (2003) with permission of the publisher.

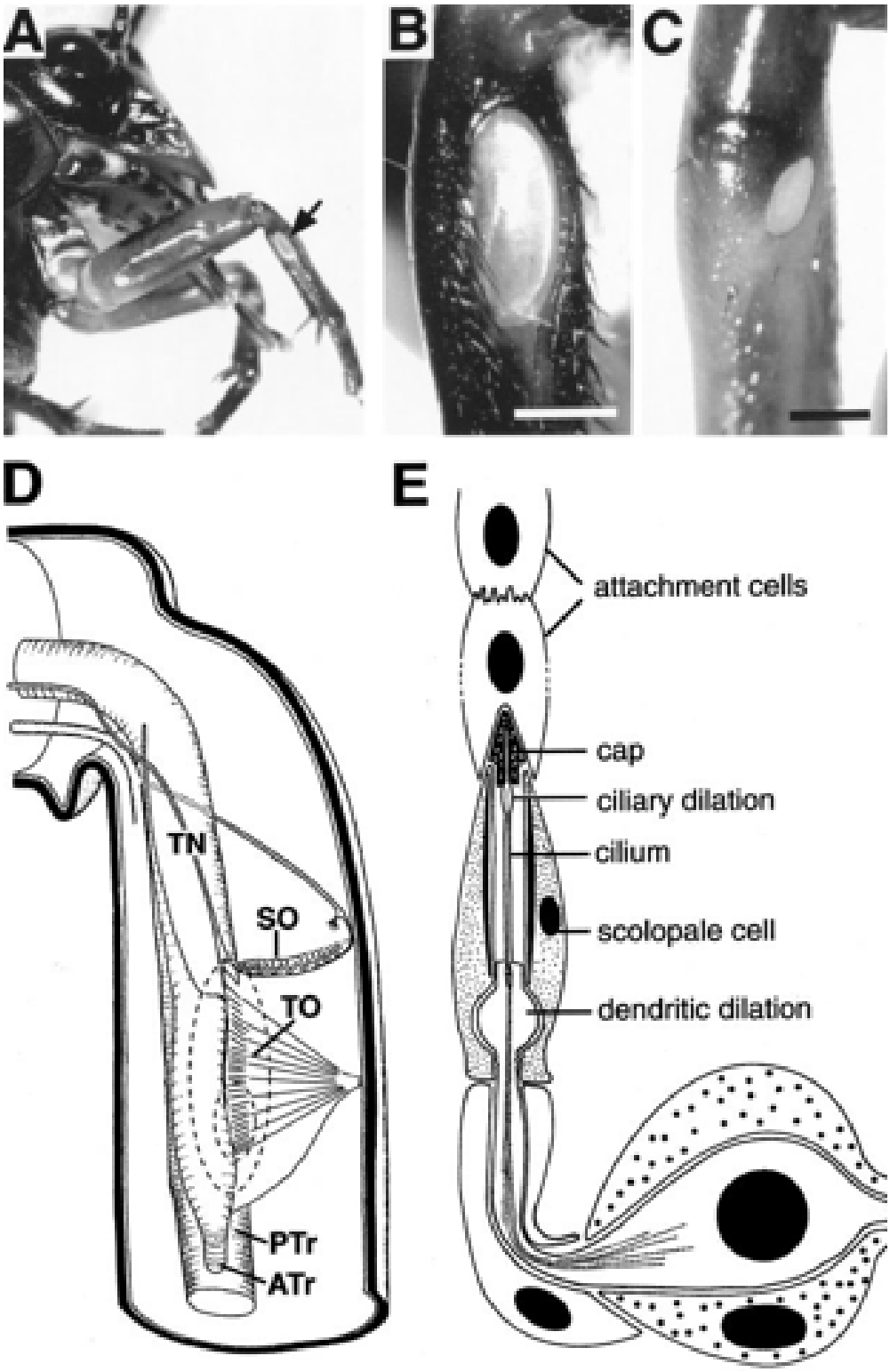

Fig. 6. Tympanal hearing organ of *Gryllus bimaculatus* (Gryllidae: Ensifera). **A:** Right lateral view of an adult male. An arrow points to the posterior tympanal membrane on the tibia of the foreleg. **B,C:** The posterior and anterior tympanal membranes, respectively. Scale bars = 0.5 and 0.4 mm. **D:** Schematic drawing of the of the complex tibial organ, including the tympanal organ (TO) and the subgenual organ (SO) in the prothoracic leg. Dashed lines indicate approximate location of the larger posterior and smaller anterior tympanal membranes. ATr, anterior trachea; PTr, posterior trachea; TN, tympanal nerve. **E:** Schematic representation of a single auditory scolopidium. A–C, Courtesy of A.C. Mason. D,E, redrawn and adapted from Michel (1974).

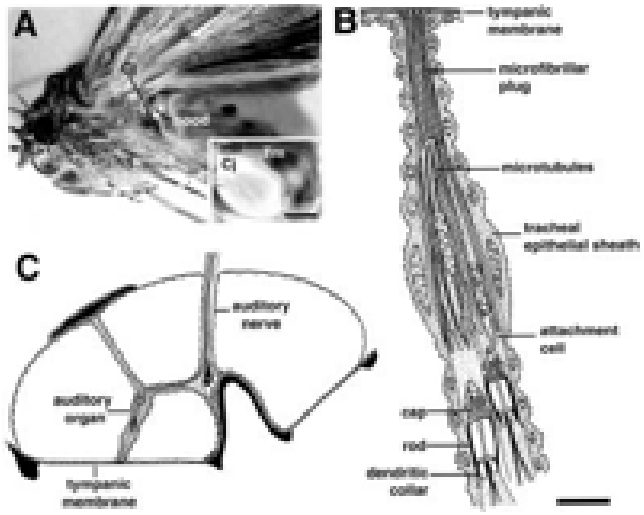

Fig. 7. The tympanal hearing organ of Noctuoidea moths. **A:** Left lateral view of a typical noctuoid moth, showing the location of the tympanal ear, within a cavity between the posterior metathorax and first abdominal segment. Inset: Light micrograph of the tympanal membrane (Tm) and adjacent conjunctivum (Cj). The attachment site of the tympanal organ can be seen as a white spot in the middle of the tympanal membrane. Scale bar = 500 μm. **B:** Schematic drawing based upon electron microscopical longitudinal sections through the distal tympanal scolopidium in *Feltia subgothica.* The two acoustic sensory cells are tightly apposed to one another, and attach to the tympanic membrane by a common attachment strand. The scolopale cell is omitted from the drawing. Scale bar = 10 μm. **C:** A schematic cross-section through the ear illustrating how the auditory sensilla are oriented within the tympanal cavity with respect to the tympanic membrane. B was redrawn from Ghiradella (1971) and C from Treat and Roeder (1959).

arms disappear, and the circle formed by the doublets expands and is filled with an electron dense material of unknown composition. There is evidence that the microtubules in the ciliary dilation are attached to the surrounding dendritic membrane. Distal to the ciliary dilation, the organization of the axoneme is widely variable.

Scolopale Cell, Rods, Lumen, and Cap

The scolopale cell envelops the sensory dendrite, forming a cylinder (=scolopale lumen, scolopale space, receptor lymph cavity) around the dendritic outer segment (Figs. 2, 3C, 4D, 5F, 6E, 7B). The scolopale cell cytoplasm is highly vacuolated, particularly near the circumference of the lumen. A labyrinth of extracellular cavities and vacuoles appears to communicate with the lumen, indicating that the scolopale cell has a secretory function. At the proximal end of the lumen, the scolopale cell attaches firmly to the dendritic inner segment by means of elaborate belt desmosomes (=dendritic "collar") (Fig. 3F,G). At the distal end of the lumen, the scolopale cell attaches firmly to the scolopale cap by means of hemidesmosomes (Fig. 3D). Thus, the scolopale lumen appears tightly sealed. The ionic composition of the lumen is unknown, but has been suggested to have a high concentration of potassium, analogous to the receptor lymph cavity of hair sensilla, and thus serves an ionic regulatory function (for discussion, see Field and Matheson, 1998). A "granular" region has been frequently noted midway up the scolopale lumen (Figs. 3C, 5F), and has been suggested to serve a role in restricting lateral movement of the cilium.

The scolopale rod material lines the inner surface of the scolopale cell membrane adjacent to the lumen (Figs. 2–7). The material is electron-dense, comprising longitudinally oriented microtubules surrounded by a fibrillar material containing filamentous actin (Wolfrum, 1990). The scolopale rod material is often organized into longitudinally oriented bundles (=rods) that attach distally to the base of the scolopale cap, and proximally to the distal region of the dendritic inner segment. The number and position of these bundles vary between different chordotonal organs. The scolopale cap is a bullet-shaped apical structure located at the distal end of the lumen. It is an extracellular structure, thought to be secreted by either the attachment cell or the scolopale cell. It is composed of an electron dense material of unknown composition, although it has been described as being "porous," "spongy," or "vacuolar" in different preparations (e.g., Figs. 3D, 5F). The distal tip of the dendritic cilium inserts into and is tightly coupled to the scolopale cap.

Attachment Cells

In mononematic scolopidia, the attachment cell connects the scolopale cell to the cuticle, either directly, or indirectly by one or more epidermal cells (Moulins, 1976). The latter form is the most common, and is found in tympanal, subgenual, and many other functional types. Attachment cells are typically elongate, and contain varying concentrations of longitudinally oriented microtubules and extracellular connective tissue. It is thought that different structural characteristics result in different viscoelastic properties, playing a critical role in the physiological responses of different chordotonal organs. To date, little is understood of the functional significance of variations in attachment cell structure.

MECHANICAL COUPLING AND SENSORY TRANSDUCTION

Despite our extensive knowledge of chordotonal organ ultrastructure, we know little about how these structurally unique sensory organs function as mechanotransducers. French (1992) outlined three steps in the mechanosensory process: (1) Coupling: How the external mechanical stimulus is linked to the sensory neuron. (2) Transduction: How mechanical displacement of the sensory neuron results in a variation of the receptor potential. (3) Coding: The formation of specific temporal patterns of electrical impulses. For chordotonal organs, all three steps are poorly understood at present. Several theories on the functional mechanisms of various components of the scolopidium have been proposed (for review see Eberl, 1999; Field and Matheson, 1998; French, 1988, 1992). Following is a brief outline of the current ideas on coupling and transduction in chordotonal organs with mononematic, Type 1 scolopidia.

Coupling

In current models of chordotonal organ function, the dendritic cilium has been implicated as being impor-

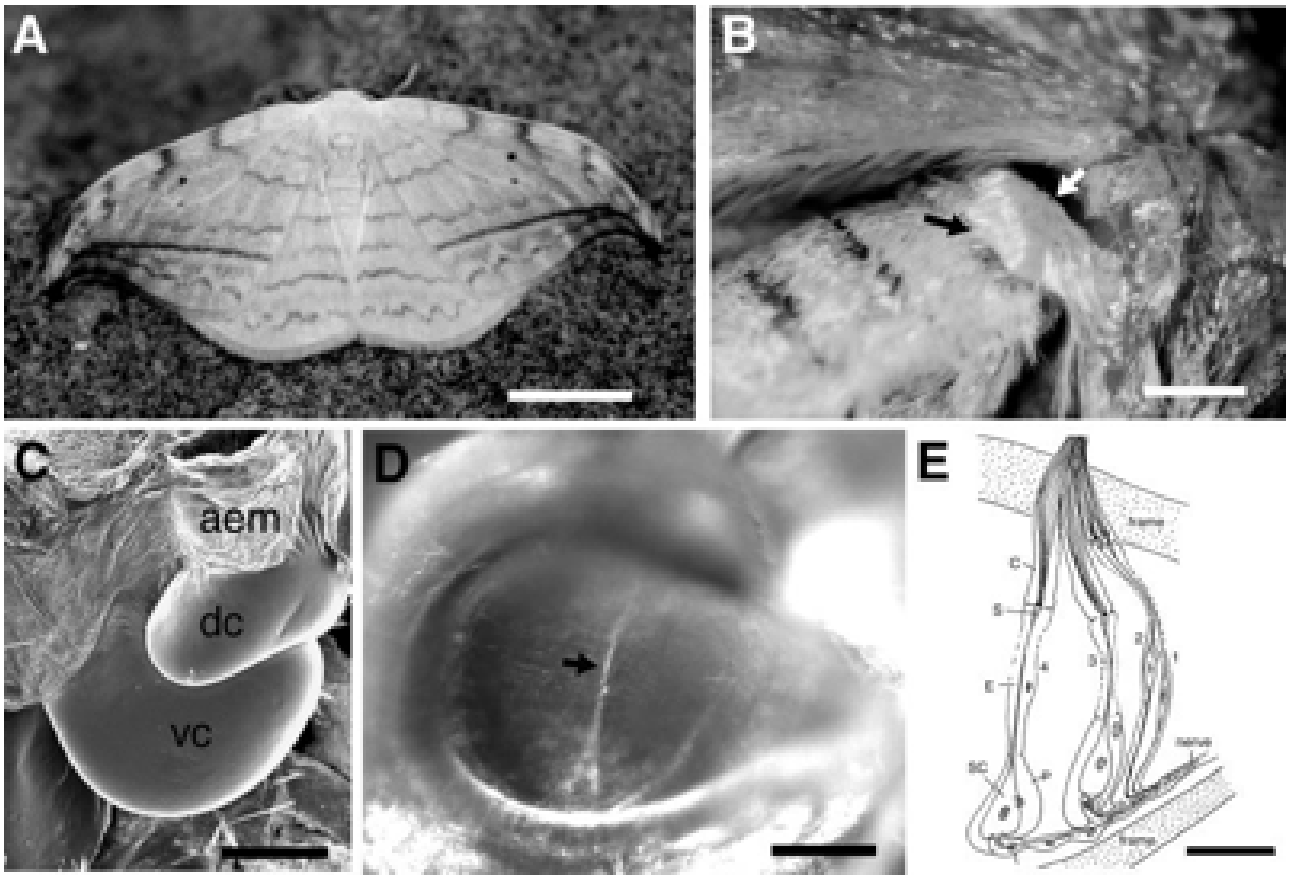

Fig. 8. Tympanal ears of a hook-tip moth, *Drepana arcuata* (Drepanoidea). **A:** A female *D. arcuata*. Scale bar = 6 mm. **B:** Right lateral view of the moth, showing the locations of the anterior (white arrow) and posterior (black arrow) external membranes. Scale bar = 750 μm. **C:** Scanning electron micrograph of the left first abdominal segment (anterior view of the ventral portion) in an adult male. The internal tympanal membrane is stretched between dorsal (dc) and ventral (vc) air chambers. Sound is thought to enter the dorsal chamber by means of the anterior external membrane (aem) and posterior external membrane (not shown). Scale bar: 250 μm. **D:** The left tympanal membrane as seen following removal of the dorsal chamber. Median is on the right. The four scolopidia are located between two appressed layers of trachea that form the tympanal membrane. The black arrow marks scolopidium 4. Scale bar = 80 μm. **E:** Diagrammatic representation of the four scolopidia innervating the left ear. Median is on the right, as in D. The tympanal nerve departs at the ventral and median edge of the tympanal frame. C, attachment or cup cell; E, enveloping cell (= scolopale cell); P, perineurium cell; S, Scolopidium; SC, Sensory cell body. Scale bar = 50 μm. A–E adapted from Surlykke et al. (2003).

tant in coupling the mechanical stimulus to the dendritic apex, the proposed site of transduction. The adequate stimulus for Type 1 cilia is thought to be longitudinal stretching of the dendritic segment (McIver, 1985; Moulins, 1976). There is some evidence that stimulation causes a proximal bend in the cilium, near the distal basal body (Moran et al., 1977; Yack and Roots, 1992) (Fig. 3C), although this needs to be validated, possibly by directly visualizing ciliary components during excitation. Whether or not the cilium is actively motile is a matter of current debate, and there are several models, based upon ultrastructural features of the cilium, that argue either for or against this idea (Field and Matheson, 1998). It has been argued that because the cilia lack the central microtubules characteristic of motile cilia, active ciliary movement is unlikely. However, recent evidence that cilia lacking central tubules can be motile and, that otoacoustic emissions have been recorded from the ears of some insects, supports the idea that dendritic ciliary segments are motile (see Eberl, 1999; Göpfert and Robert, 2003). New insights into the functional role of the cilium may be gained by studying *Drosophila* mutants with structurally altered chordotonal cilia (see Eberl, 1999; Eberl et al., 2000; Göpfert and Robert, 2003).

Immunohistochemical studies of both the ciliary roots and scolopale rods have led to hypotheses concerning their roles in the sensory process. Evidence for centrin-like proteins in the ciliary rootlets suggests that they may contract when exposed to raised Ca^{2+} levels, and that the resulting tension could enhance coupling by increasing tension in the cilium or enhancing the ciliary bend (Wolfrum, 1991a). Although it is generally agreed that the scolopale rods are primarily structural, Wolfrum's (1990, 1991b) demonstration that the scolopale rods contain actin, tropomyosin, and microtubule associated protein 2, suggests that they are somewhat elastic, and their flexibility may be regulated by Ca^{2+} levels, potentially playing a role in receptor sensitivity.

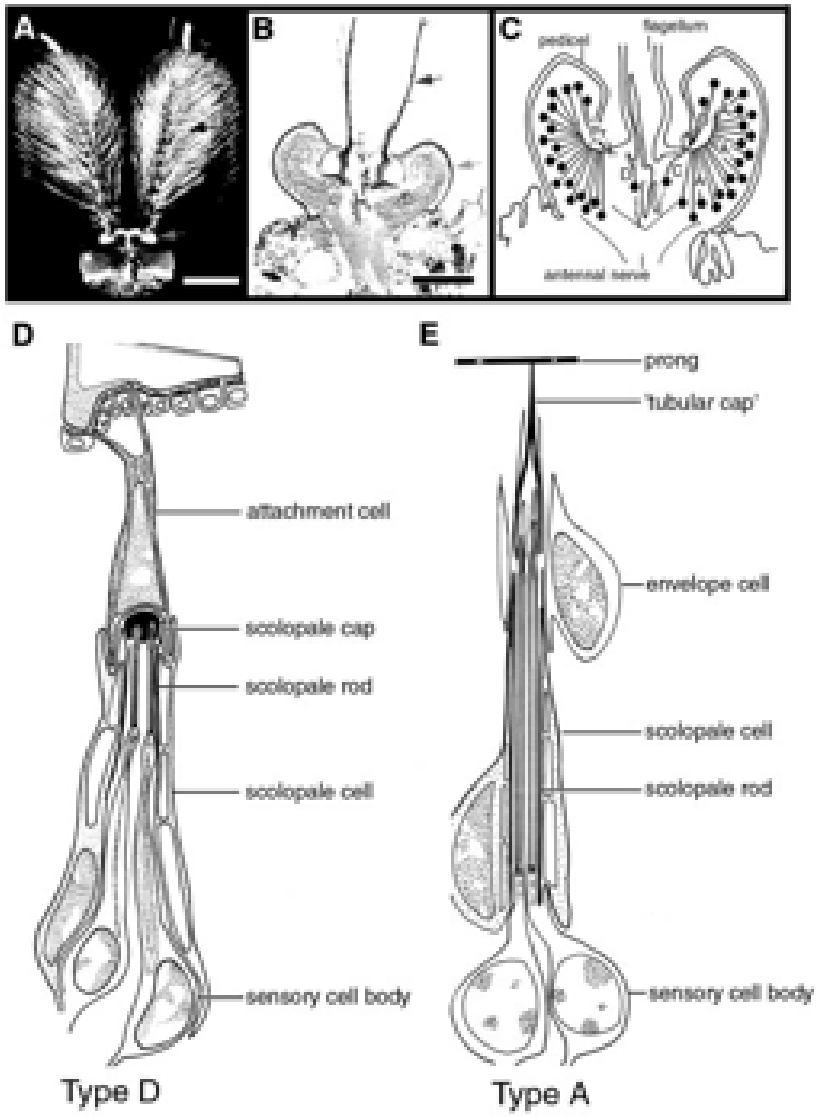

Fig. 9. Johnston's organ in male mosquitoes. **A:** The plumous flagella on the antenna (black arrow) of a male *Toxorhynchites brevipalpis*, resonates in response to the near-field sounds of flying females, stimulating receptors in the Johnston's organ located at the pedicel (gray arrow). Scale bar = 0.6 mm. **B:** Longitudinal section through the antennal base of *T. brevipalpis*, showing the location of Johnston's organ. Scale bar = 0.1 mm. **C:** Diagrammatic longitudinal section through Johnston's organ of a male *Aedes aegypti*. The positions of the four different scolopidia types (A–D) are indicated. Pr, prong to which the terminal filament of the "tubular cap" attaches. **D,E:** Diagrammatic longitudinal sections through Type D (mononematic) and Type A (amphinematic) scolopidia in *A. aegypti*. A, Courtesy of D. Huber; B, adapted from Göpfert and Robert (2001a); C–E, redrawn from Boo and Richards (1975a).

Transduction

In chordotonal organs, the site of transduction is generally believed to be at the apex of the dendritic inner segment, where mechanical distortion of the cell membrane is thought to affect the probability of channels being opened, resulting in a change of ionic conductance between the scolopale lumen and the dendrite. This model is based on extrapolations from other ciliated Type 1 mechanoreceptors in insects (trichoid and campaniform sensilla) that are developmentally related to chordotonal organs. In these cuticular mechanoreceptors, the receptor lymph space is rich in K^+ and poor in Cl^-, resulting in an ionic gradient between the lumen and dendritic apex that drives the receptor current upon opening of channels (for reviews, see Eberl, 1999; Field and Matheson, 1998; French, 1988; Kiel, 1997).

Little is known about the equivalent mechanisms in chordotonal sensilla at present. However, there is accumulating indirect evidence from both ultrastructural and physiological studies that the scolopale lumen is analogous to the receptor lymph space of cuticular mechanoreceptors. Evidence that the scolopale lumen maintains an ionic composition distinct from adjacent tissues comes from observations that (1) the lumen is tightly sealed at both ends, and (2) the scolopale cytoplasm surrounding the lumen contains a large number of vacuoles that appear connected to the lumen, suggesting a secretory function. Evidence of a "granular" material inside the lumen, localized at the dendritic apex, has been suggested to represent accumulations of acid mucopolysaccharides or other glycoproteins that function as ionic regulators at the site of transduction (Field and Matheson, 1998; Yack and Roots, 1992). Further evidence for involvement of the scolopale lumen in the process of transduction comes from a limited number of intracellular physiological recordings of auditory chordotonal organs. Non-propagating spikes recorded from the sensory neuron in locusts (*Locusta migratoria*), are thought to arise in the dendritic apex

as a result of a unique ionic concentration in the scolopale lumen (Hill, 1983). In the *crista acustica* of a katydid (*Caedicia simplex*), hyperpolarizations of the attachment cell recorded simultaneously with the depolarization of the sensory neuron were interpreted to mean that while ions flow out of the scolopale lumen into the neuron, they are replenished by an inflow of ions from the attachment cell, causing a hyperpolarization in the latter (Oldfield and Hill, 1986). Further investigations into the molecular and ionic composition of the scolopale lumen, dendritic apex, and surrounding tissues, using X-ray microprobe technology and immunohistochemistry, in conjunction with physiological recordings from various scolopidial components, are required to understand more clearly the nature of transduction in chordotonal organs. Additionally, exciting new developments with genetically manipulated auditory chordotonal organs in *Drosophila* (Caldwell and Eberl, 2002; Eberl, 1999), and the molecular basis of mechanosensory channels in *Drosophila* bristle organs (Gillespie and Walker, 2001; Walker et al., 2000), promise to lend insight into the underlying molecular machinery involved in transduction.

TYMPANAL CHORDOTONAL ORGANS

Insect tympanal ears vary considerably with respect to their location and complexity. They can occur on almost any part of the body, and range from having a single auditory sense cell (e.g., some moths: Göpfert and Wasserthal, 1999a,b; Surlykke, 1984), to well over a thousand (e.g., cicadas: Doolan and Young, 1981; Michel, 1975). One explanation for this remarkable diversity is that tympanal ears appear to be relatively easy to "construct." Evidence from comparative anatomical and developmental studies indicates that insect tympanal ears derive from pre-existing chordotonal organs that may have functioned as vibratory receptors or proprioceptors (Fullard and Yack, 1993; Robert and Hoy, 1998; Shaw, 1994; van Staaden et al., 2003; Yager, 1999a). Proposed modifications to peripheral structures associated with these "pre-tympanal" chordotonal organs include thinning of the cuticle, enlargement of tracheal sacs, and mechanical isolation from non-acoustic mechanical stimuli. Less is known about the changes to the chordotonal organs themselves that accompanied the evolution of tympanal hearing. There are several excellent reviews on the structure of insect tympanal ears, most focusing on external morphology and histology at the level of the light microscope (e.g., Haskell, 1961; Hoy and Robert, 1996; Michelsen and Larsen, 1985; Römer and Tautz, 1992; Yager, 1999a). In an effort to better understand the anatomical and functional specializations of auditory chordotonal organs, the following reviews insect tympanal ears, organized by taxa, with a particular focus on the structural organization of the auditory chordotonal organs.

Orthoptera

Tympanal ears of Orthoptera have been studied more extensively, both with respect to anatomy and physiology, than any other insect hearing organ. Hearing has evolved twice, independently in the suborders Caelifera (grasshoppers, locusts) and Ensifera (crickets, katydids, and wetas). Extant members of both taxa use their hearing primarily for conspecific communication.

Caelifera. The ears are best characterized in the Acrididae, for which various parts of the adult hearing organ have been described at the level of the light microscope for different species (e.g., Gray, 1960; Jacobs et al., 1999; Michel and Petersen, 1982; Michelsen, 1971a; Riede et al., 1990; Römer, 1976; Stephen and Bennet-Clark, 1982), and a single ultrastructural study has been performed on *Locusta* (Gray, 1960). The eardrums, located on each side of the first abdominal segment, are conspicuous, pear-shaped, opaque membranes supported by sclerotized rings (Fig. 5B,D). Each tympanum is backed by a large tracheal air sac that connects to both ears, providing the insect with a directional sense. The tympanal chordotonal organ (=Müller's organ) (Fig. 5D) contains between 60 and 100 monodynal, mononematic scolopidia, all tightly encased by the flattened epithelial layer of the tracheal air sac. The scolopidia are typically divided into four anatomical groups (a,b,c,d) according to their separate attachments to the tympanal membrane. The scolopidia of each group connect distally via attachment cells to four specialized outgrowths of the exoskeleton extending from the inner surface of the tympanal membrane (Gray, 1960).

Based on intracellular recordings, the scolopidia of Müller's organ have been placed into three (including anatomical types a+b, c,d; a,c,d) or four (types a,b,c,d) functional groups that differ in their frequency sensitivity (Inglis and Oldfield, 1988; Jacobs et al., 1999; Michelsen, 1971a; Römer, 1976). Pitch discrimination in the Acrididae has been explained by the "place principle" of frequency analysis, whereby the tuning of receptors is achieved by the unique resonant properties of the auditory organ, including the receptor cells, their respective attachment sclerites, and the specific regions of the tympanal membrane to which they attach (Breckow and Sippel, 1985; Michelsen, 1971b; Michelsen and Larsen, 1985; Stephen and Bennet-Clark, 1982). It is still conceivable that intrinsic properties of individual scolopidia forming different functional groups could be partially responsible for their respective tuning characteristics. Ultrastructural comparisons between the different functional types, particularly the high frequency d, and low frequency a–c groups, would be worthwhile investigating.

Meier and Reichert (1990) have convincingly demonstrated through developmental and comparative anatomical studies that the tympanal organ of *Schistocerca* is a specialization of the proprioceptive pleural chordotonal organs, thought to be involved in monitoring ventilatory movements (Hustert, 1975). The pleural chordotonal organ innervates the first abdominal segment of a primitively atympanate species *Heide amiculi* (Eumastacoidea: Morabinae), and serially abdominal segments of tympanate species.

Evidence for hearing in a primitively atympanate caeliferan family, the Pneumoridae, has recently been presented (van Staaden and Römer, 1998; van Staaden et al., 2003) (Fig. 5). The bladder grasshopper (*Bullacris membracioides*) of South Africa has six pairs of serially repeated abdominal ears: a complex anterior pair with around 2,000 scolopidia each, and homologous to the tympanal organs of acridids; and five sim-

pler posterior pairs with 11 scolopidia each, and homologous to the abdominal pleural organs of acridids. The auditory organs of *B. membracioides* are not associated with a differentiated tympanal membrane per se, but rather attach to a region of slightly thinned pleural cuticle, via unusually long attachment cells (1.4 mm compared to ~100 μm in the tympanal ears of other grasshoppers). Despite the absence of a tympanal membrane, the chordotonal organs are sufficiently sensitive to the sound frequencies and intensities (1.5–4 kHz; 60–98 dB SPL at 1 m) of conspecifics. These atympanate hearing organs are thought to represent the evolutionary transition from the earless to tympanate condition.

Ensifera. The tympanal ears of Ensifera occur on the proximal part of the tibia of each foreleg. There are some important anatomical differences between the ears of different taxa, particularly between the Grylloidea (crickets) and Tettigonoidea (katydids or bushcrickets), but all derive from a common ancestry and are innervated by homologous chordotonal organs. The anatomy of ensiferan ears has been studied extensively at the level of the light microscope (for reviews, see Bailey, 1990; Ball et al. 1989; Field and Matheson, 1998; Yager, 1999a), and ultrastructural studies exist for various parts of the ear in *Hemideina crassidens* (Stenopelmatidae) (Ball, 1981), *Gryllus assimilis* (Friedman, 1972), and *G. bimaculatus* (Michel, 1974); *Teleogryllus commodus* (Ball and Cowan, 1978) (Gryllidae). Crickets and katydids have two oval-shaped tympanal membranes on each leg, one on the anterior and one on the posterior side of the tibia. In crickets the tympanal membranes occur on the leg surface (Fig. 6), while in bushcrickets they are located within slits. Each tympanum is backed by a tracheal air sac that in turn connects to other sound input sources, including the spiracles and the contralateral ear. This system of tracheal tubes and air chambers is important for localizing sounds.

In most Ensifera, the auditory organ does not attach directly to the tympanal membrane, but to the anterior trachea lying directly beneath the tympanal membrane. The auditory scolopidia form part of the "complex tibial organ," comprising a subgenual organ and a tracheal organ. In crickets (Fig. 6), the tracheal organ functions as the tympanal organ, and typically has between 60–80 scolopidia. The scolopidia, enclosed within a tent-shaped covering membrane, attach proximally to the enlarged anterior trachea, and distally to a common attachment point on the leg epidermis by one or more attachment cells. In some Gryllidae, the auditory scolopidia have been divided into three or more groups based on the location and anatomical characteristics of their scolopidia (Ball et al., 1989; Young and Ball, 1974a).

In katydids, the complex tibial organ is typically divided into three distinct groups: the subgenual organ, intermediate organ, and crista acustica. The crista acustica has between 20 and 60 scolopidia, and is primarily responsible for sound reception, although some units of the intermediate organ also respond to low-frequency sounds (e.g., Lin et al., 1993; Stölting and Stumpner, 1998). The scolopidia are anchored proximally to the anterior trachea, and distally to the tegument of the tibia by one or more attachment cells. The attachment cells in turn connect to the tectorial membrane that is flanked by two strong supporting bands. The scolopidia are graded in their overall size, with the smallest occurring at the distal end of the organ (Lin et al., 1993; Oldfield, 1982; Rössler, 1992a). In a study of two species belonging to the Phaneropterinae and Decticinae, Rössler et al. (1994) observed that the distal scolopidia also have more slender scolopale caps. The width of both the tectorial membrane and the dorsal wall of the anterior trachea also decreases distally (Rössler, 1992a).

Like acridids, ensiferans are capable of pitch discrimination. In both crickets and katydids, the scolopidia are tonotopically arranged, with the more distal units responding to higher frequencies (Oldfield, 1982; Oldfield et al., 1986; Stölting and Stumpner, 1998; Stumpner, 1996). Unlike for acridids, the tuning characteristics of individual scolopidia in the ensiferan ear cannot be attributed to resonance properties of the tympanal membrane (Oldfield, 1985). At present, the mechanisms responsible for tuning are unknown. There are two competing hypotheses: (1) the mechanical properties of the whole ear structure, including various membranes and trachea, result in differential activation of the individual units; (2) intrinsic mechanoelectrical properties of the scolopidia are responsible for their different response patterns. There is currently support for both hypotheses (see discussions by Ball et al., 1989; Field and Matheson, 1998; Pollack and Imaizumi, 1999), and it is believed that a more extensive characterization of the ultrastructural, biomechanical, and neurophysiological properties of individual scolopidia will help to resolve this issue.

The ensiferan tympanal organ is thought to derive from leg mechanoreceptors that in some cases may have functioned as vibration receptors, and, therefore, were preadapted for sound reception (e.g., Meier and Reichert, 1990; Rössler, 1992a; Shaw, 1994). Based on comparisons between tympanate and atympanate homologues (e.g., Eibl, 1978; Houtermans and Schumacher, 1974; Jeram et al., 1995; Rössler, 1992a; Young and Ball, 1974b), the following adaptations to the foreleg and chordotonal organ are proposed to have accompanied the evolution of hearing in ensiferans: (1) development of tympanal membranes; (2) expansion of trachea; (3) enlarged spiracular openings; (4) enhanced coupling between the attachment cell and its membranous attachment, and better developed structural support of the attachment sites; (5) an increase in the number of scolopidia; and (6) an increase in the overall size of the scolopale, including a significant increase in the width of the scolopale caps.

Lepidoptera

In the Lepidoptera, tympanal ears have evolved independently no fewer than seven times. They occur on a variety of different body regions, including the mouthparts (Sphingoidea), wings (butterflies: Hedyloidea, Nymphalidae), thorax (Noctuoidea), and abdomen (Drepanoidea, Geometroidea, Pyraloidea, Tineoidea, Uraniidae). Moth ears are among the simplest of all insect hearing organs, with only one to four sensory cells per ear. All moth ears are ultrasound-sensitive, functioning primarily to detect echolocating bats (Miller and Surlykke, 2001), although some species

have secondarily evolved the ability to use their hearing for conspecific communication (Conner, 1999). To date, four studies report functional hearing organs in butterflies. Certain nocturnal species of the families Hedylidae (Hedyloidea) and Nymphalidae (Papilionoidea) have ultrasound-sensitive ears on their wings that presumably function as bat detectors (Rydell et al., 2003; Yack and Fullard, 2000), and some diurnal butterflies possess low-frequency (under 20 kHz) sensitive ears on their wings that appear to function in conspecific communication and/or predator detection (Ribaric and Gogala, 1996; Yack et al., 2000).

Numerous studies have described the gross morphological and histological features of lepidopteran ears at the level of the light microscope (reviewed in Hasenfuss, 2000; Minet and Surlykke, 2003; Scoble, 1995). Surprisingly, only one ultrastructural study has been performed, on the metathoracic ear of *Feltia subgothica* (Noctuoidea) (Ghiradella, 1971). With the exception of the hearing organs in Sphingoidea (hawkmoths) and Drepanoidea (hook tip moths), all other lepidopteran ears follow a standard tympanal ear morphology. They comprise a round or oval tympanal membrane, supported by a chitinous ring and backed by an enlarged tracheal air sac, with one or more chordotonal organs attached in a perpendicular or slightly oblique orientation to its inner surface (Fig. 7). The scolopidia are tightly enclosed within a tracheal sheath, and may be oriented such that their dendrites point toward (e.g., Noctuoidea, Nymphalidae), or away from the tympanal membrane (the "inverted" type, as in Pyraloidea and Geometroidea). No lepidopteran ears studied physiologically to date are capable of frequency discrimination, owing, presumably, to their singular attachments to the tympanal membrane (but see Yack and Fullard, 2000). Despite their common attachment sites, individual scolopidia typically have distinct differences in their threshold sensitivities (see Miller and Surlykke, 2001; Minet and Surlykke, 2003; Roeder, 1974). The A1 cell of the noctuoid moth ear, for example, is 20 dB more sensitive than that of A2, although the two units have similar tuning curves, and share a common attachment site. Ghiradella (1971) reported that one scolopidium was larger and more proximal than the other, and speculated that this may be A1. The tympanal organs of Noctuidae, Geometroidea, and Pyraloidea, with 2, 4, and 4 auditory scolopidia, respectively, would be ideal models for investigating possible structural/molecular basis for threshold differences, due to their having few cells with clear threshold differences and common attachments to the tympanic membrane.

The ears of some hawkmoths (Sphingoidea), and hook-tip moths (Drepanoidea) represent unconventional forms for insects. In the hawkmoth subtribes *Acherontia* and *Choerocampina*, the ears are composed of two disjointed mouthparts, the labial palp and labral pilifer, that work together to detect and transduce sounds (Göpfert and Wasserthal, 1999a,b; Göpfert et al., 2002; Roeder and Treat, 1970; Roeder et al., 1968, 1970). In the *Choerocampina*, the medial face of the enlarged, air-filled labral palp has a thin, smooth surface, and functions as a tympanum. The pilifer touches the outer surface of the tympanal membrane and picks up sound vibrations, which in turn are transmitted to a chordotonal organ with a single scolopidium at the base of the pilifer. In *Acherontia*, a tuft of scales extending from the labral palp vibrates in response to ultrasound, thus functioning in place of a tympanal membrane. The hinged pilifer rests upon the vibrating scales and transmits the vibrations to a single scolopidium in its base. Despite their different structures, both ears are innervated by a homologous chordotonal organ, containing a single, mononematic, monodynal scolopidium (Göpfert and Wasserthal, 1999b). In a primitively earless acherontiine species, *Panogena lingens*, Göpfert and Wasserthal (1999b) have identified the presumed non-auditory homologue, thought to function as a proprioceptor monitoring pilifer movements. In addition to structural modifications of the mouthparts that accompanied the transition from an earless to eared condition, the length of the chordotonal organ and the amount of tissue surrounding the chordotonal organ were reduced (Göpfert and Wasserthal, 1999a,b).

Drepanid ears represent another unique means by which insects have formed a high frequency ear (Fig. 8). The proposed tympanal membrane is not exposed directly to the moth's exterior, but rather, is internalized, comprising two thin tracheal walls stretched across an opening between two enlarged air-filled chambers. Four individual mononematic, monodynal scolopidia are "sandwiched" between the two tympanal layers, which bulge outward slightly into the dorsal chamber. A recent study on the functional morphology of this organ (Surlykke et al., 2003) suggests that sound reaches the internal tympanum through two external membranes that connect indirectly to the dorsal chamber, and that the curvature of the tympanic membrane is a biomechanical adaptation to enhance length changes of the scolopidia imposed by vibrations of the tympanal membrane. Only two of the four scolopidia identified anatomically were excited by sound stimuli and these two cells differ in threshold by around 20 dB. The morphology of the ear suggests that the two larger scolopidia function as auditory sensilla while the two smaller scolopidia, located closer to the tympanal frame, were not excited by sound, and may have retained their original proprioceptive function.

Moths lacking a metathoracic ear (i.e., all superfamilies except Noctuoidea) possess a homologous proprioceptive complex in the wing believed to represent the pleisiomorphic, atympanate condition (Yack, 1992; Yack and Fullard, 1990; Yack et al., 1999) (Fig. 3). This wing-hinge chordotonal organ is thought to be involved in monitoring wing movements during flight or preflight warm-up. In addition to registering wing movements, the tympanal organ precursor responds to low-frequency ($\sim$2 kHz), high-intensity ($>$70 dB SPL) sounds, although this is probably a non-adaptive response to unnaturally loud sounds causing cuticular vibrations (Yack and Fullard, 1990, 1993). Changes to peripheral structures proposed to have accompanied the evolution of hearing in noctuoid moths include the development of a tympanal membrane, enlarged tracheal air sacs, and a rigid cuticular structure to isolate the chordotonal organ from non-auditory mechanical stimuli. Proposed structural changes to the chordotonal organ itself include a decrease in the overall length of the distal attachment strand, and a loss of the elastic sheath surrounding the strand. These structural changes are proposed to have resulted in stiffen-

ing the connection between the tympanal membrane and scolopidium, resulting in lowered thresholds to rapid, small amplitude vibrations.

Hemiptera

Hearing in Cicadas (Cicadidae, Homoptera) functions primarily in conspecific communication. The tympanal ears, located ventrally on the second abdominal segment (Fig. 4), are among the most elaborate of insect hearing organs, with up to ~2,000 sensory cells per ear (Doolan and Young, 1981). Gross anatomical and light microscopic studies are available for a number of species (e.g., Daws and Hennig, 1996; Doolan and Young, 1981; Michel, 1975; Pringle, 1957; Vogel, 1923; Young and Hill, 1977), and ultrastructural details have been described for *Cyclochila australasiae* (Young, 1973) and *Cicada orni* (Michel, 1975). The main anatomical features are similar between species, and, typically, the ears of males and females differ somewhat, owing predominantly to the absence of sound production in the females. The auditory organ is contained within a sclerotized capsule at the lateral border of the large, oval-shaped tympanal membrane. In the male *C. australasiae*, the tympanal organ consists of a large bundle of around 1,000 scolopidia that attaches at one end to the tympanal membrane by a cuticular extension, the tympanal apodeme, and to the wall of the auditory capsule by the attachment horn (Daws and Hennig, 1996) (Fig. 4). The monodynal, mononematic scolopidia are inverted, with caps facing away from the tympanal membrane. The ear is sharply tuned to 3.5 kHz, as determined by whole nerve recordings of the tympanal nerve. Experimental manipulations of the tympanal membrane and accessory structures, as well as the chordotonal organ itself, do not affect the tuning characteristics of the scolopidia (Daws and Hennig, 1996). Interestingly, two other chordotonal organs associated with the auditory system, the tensor and tymbal organs, are similarly tuned to the auditory organ (Daws and Hennig, 1996) despite many differences in their modes of attachment to the cuticle (Young, 1975). Daws and Hennig (1996) argue that the similar tuning curves of the auditory, tymbal, and tensor chordotonal organs, noted to have structurally similar scolopidia (Young, 1975), are due to intrinsic properties of the scolopidia themselves, rather than to resonance properties of their attachment sites.

Several species of aquatic Heteroptera communicate acoustically (Aitken, 1985), although relatively little is known about the mechanisms of sound reception. The best described receptor organ is the proposed tympanal ear of the waterboatman *Corixa punctata* (Corixidae) (Prager, 1973, 1976; Prager and Larsen, 1981; Prager and Streng, 1982). The tympanal membrane occurs on the mesothorax between the forewing and leg. Much of the membrane is covered externally by the base of a club-shaped cuticular structure, which extends outward. When submerged, the tympanum is covered externally by an air bubble, allowing the membrane to vibrate under water. The auditory chordotonal organ, with two monodynal, mononematic scolopidia, attaches to the base of the cuticular club by a connective strand (see Michel, 1977). Both sensilla are tuned to the calling frequencies of conspecifics (~2 kHz), with one (A1) being the more sensitive. Interestingly, the A1 cells in either ear are asymmetrical in their thresholds and tuning (Prager, 1976), and these physiological differences can be at least partially ascribed to differences in vibrational qualities of the tympanal membrane and the clubbed process (Prager and Larsen, 1981). Ultrastructural details of the A1 receptors are not available to rule out the possibility that intrinsic properties of the scolopidia may also contribute to the physiological asymmetry.

Diptera

Certain species of parasitoid flies belonging to the taxa Ominii (Tachinidae) and Emblemasomatini (Sarcophagidae) have independently evolved paired tympanal ears on the anterior prosternum, just behind the fly's head capsule. Hearing is best developed in females that use their ears to detect and localize singing crickets, katydids, and cicadas (Köhler and Lakes-Harlan, 2001; Lakes-Harlan and Heller, 1992; Lakes-Harlan et al., 1999; Robert and Hoy, 1998; Robert et al., 1992, 1994). The ear anatomy is best known for *Ormia ochracea* (Orminii) (Robert et al., 1994; Robert and Willi, 2000). The eardrums are 1-μm-thick, transparent, corrugated membranes that fuse at the midline, and unlike for other insect tympanal ears, both tympana are backed by a single tracheal air chamber. Attached to the inner surface of each tympanum, via a stiff "cuticular thorn" (=auditory apodeme) is a single, non-connective chordotonal organ (=bulba acustica) with around 100 Type 1, mononematic, monodynal scolopidia. All scolopidia are oriented in the same direction, with each attaching apically to the tympanal apodeme by a single attachment cell. Basally, the chordotonal organ attaches to the posterior wall of the prosternal chamber by a short ligament. The scolopidia within a single bulba acustica vary considerably in their size and shape (Robert and Willi, 2000), but the functional significance of these structural differences is unknown.

The ears of female *O. ochracea* are most sensitive between 4–6 kHz, corresponding to the dominant frequencies of their host's call. Males do not exhibit phonotactic behavior to cricket sounds, and their ears are significantly less sensitive than females to lower frequencies. Their sensitivity to ultrasound (15 to 50 kHz), however, is equivalent to that of females, and it is thought that both sexes use ultrasound for bat avoidance, although this hypothesis remains untested (Robert and Hoy, 1998). There is a strong sexual dimorphism in the ear structure. Most notably, the size of the tympanal membranes, tracheal air sacs, and mesothoracic spiracles are reduced in males (Robert et al., 1994, 1996). Robert and Willi (2000) speculated that the observed sexual dimorphism in frequency sensitivity might be reflected in different structural characteristics of the scolopidia, but this hypothesis was not supported in a detailed morphometric comparison between the hearing organs of both sexes.

Comparative anatomical studies indicate that the fly tympanal organ derives from a prosternal chordotonal organ, thought to function in primitively atympanate species as a proprioceptor or vibration receptor (Edgecomb et al., 1995; Lakes-Harlan and Heller, 1992; Lakes-Harlan et al., 1999). Comparisons between *O. ochracea* and the closely related but primitively atympanate species *Myiopharus doryphorae* revealed sev-

eral structural modifications to the ventral prothorax, as well as the chordotonal organ itself that accompanied the evolution of hearing (Edgecomb et al., 1995; Robert et al., 1996). Modifications to peripheral structures included the enlargement of trachea and mesothoracic spiracles, the isolation of the chordotonal organ from surrounding hemolymph by a tracheal fold wrapping, and the expansion and thinning of the prosternal cuticle to form a tympanum. Proposed structural changes to the chordotonal organ itself included: (1) an increase in the number of scolopidia; (2) an increase in the overall size of the scolopidia; (3) increased variance in the size and spatial organization of individual scolopidia within the bulba acustica; (4) shortening of the apical attachment to the presternum from a long flexible ligament to a rigid apodeme, and (5) increased reinforcement between the basal end of the bulba acustica and the prosternal apophysis.

Dictyoptera

Although hearing was once considered to be absent in praying mantids, it is now estimated that up to 65% of all species possess tympanal hearing organs. All metathoracic ears studied to date are ultrasound-sensitive, responding to frequencies between 25 and 50 kHz, and thought to function primarily as bat detectors (Yager, 1999b). Hearing is typically best developed in males, and the degree of sexual dimorphism in different species is correlated with wing length dimorphism and, hence, flight ability (Yager, 1990). Some species of Hymenopodidae have an additional pair of tympanal ears on the mesothorax that are serial homologues to the metathoracic ears. These are sensitive to lower frequency sounds (2–4 kHz), and, to date, their function remains unknown (Yager, 1996b).

The gross anatomy and histology of the metathoracic ear have been described in detail (Yager, 1990,1996a,b, 1999b; Yager and Hoy, 1986, 1987). Inconspicuously located inside a narrow groove between the metathoracic legs, two tympanal membranes, formed by thinned walls of the sternum, face each other, separated by a short distance of 100 to 200 μm. Compared to other ultrasound-sensitive insect ears, the tympana are unusually thick (15 to 20 μm), and stiff. The auditory chordotonal organ is an oval structure comprising 35–45 monodynal, mononematic scolopidia. These are organized into three groups, one of which attaches directly to the anterior edge of the tympanum by a long, narrow process, with the scolopale caps facing the tympanum. The other two groups are anchored to the ventral cuticle of the metathorax by ligamentous processes, with the scolopale caps oriented away from the tympanum. Whether or not there are physiological differences between the three cell groups, or even if all cells within the group function in audition, remains to be determined.

Insights into the evolutionary origin of hearing in mantids have been gained from developmental studies, and comparative anatomical and physiological investigations of atympanate homologues in cockroaches and primitively earless mantids (Yager, 1996a,b; Yager and Scaffidi, 1993). In cockroaches, the tympanal organ homologue contains between 35 to 45 scolopidia, and has been proposed to function as a vibration receptor involved in predator avoidance (Yager, 1999b; Yager and Tola, 1994). Yager (1996, 1999b) argues that the transition from the atympanate to tympanate condition involved primarily changes to peripheral sound-transducing structures, such as cuticular thinning and tracheal sac enlargement. To date, comparative ultrastructural studies have revealed no obvious differences between tympanate and atympanate scolopidia (Yager, personal communication).

Coleoptera

Tympanal ears have evolved independently in tiger beetles (Cicindelidae) (Spangler, 1988; Yager and Spangler, 1995; Yager et al., 2000), and scarabs (Scarabidae) (Forrest et al., 1995, 1997). In tiger beetles, several species of *Cicindela* have ears on the dorsal surface of the first abdominal segment, beneath the wings. The eardrums are thin, transparent membranes, resembling the ultrasound-sensitive ears of other insects, and behavioral and physiological evidence indicates that these ears function as bat detectors. The auditory chordotonal organ has not yet been described in tiger beetles. Some scarabs belonging to the subfamily Dynastinae have ultrasound-sensitive ears located under the pronotal shield. The paired tympanal membranes are 3–5 μm thick, and backed by enlarged tracheal air sacs. The tympanal organ, identified in one species, *Euetheola humilis*, has between 3–8 scolopidia and attaches to the dorsomedial apex of each tympanal membrane by attachment cells. Behavioral and physiological evidence indicates that these ears also function as bat detectors.

Neuroptera

Green lacewings (Chrysopidae) have tympanal ears that respond to sounds between 40–60 kHz, and are sufficiently sensitive to detect echolocating bats at close distances (reviewed in Miller, 1984). The ear anatomy has been described in one species to date, *Chrysoperla carnea* (Miller, 1970). Each ear occurs at the base of the forewing, in a location similar to the ears of butterflies, and consists of a swelling of the radial vein, with a region of very thin (1 μm) cuticle on the ventral side that functions as a tympanal membrane. With the exception of a small trachea running through the swelling, the tympanal chamber is predominantly fluid filled. Two groups of scolopidia, a distal group with 5–7 units, and a proximal group, with 18–20 units, attach by their apical ends to the inner surface of the tympanum. It is surmised that only six of the 25+ scolopidia, probably belonging to the distal group, are acoustically active, although this requires confirmation (Miller, 1984; Miller and Surlykke, 2001; Miller, personal communication).

ANTENNAL NEAR-FIELD SOUND RECEPTORS (=JOHNSTON'S ORGAN)

Johnston's organ is a non-connective chordotonal organ situated at the base of the antenna, in the second segment (=pedicel). Although present in most insects, it differs widely in both size and function between groups (McIver, 1985). Johnston's organ reaches its highest degree of complexity in the Diptera, particularly in Culicidae (mosquitoes), Chironomidae (midges), and Drosophilidae (fruit flies), where it functions to

detect near-field sounds produced by the wing beats of conspecifics.

In male mosquitoes, the pedicel is greatly enlarged, containing up to 30,000 sensory neurons and an extensive arrangement of apodemes (=prongs), arranged radially, to which the scolopidia attach. In male *Aedes aegypti*, four types of scolopidia (A–D) occur in the antennal base (Boo and Richards, 1975a; McIver, 1985) (Fig. 9). Type A account for more than 97% of the scolopidia in the pedicel. They are Type 1, amphinematic and heterodynal, with two anatomically similar sensory neurons. The scolopidia attach in a coronal array to the undersides of the prongs (Fig. 9E). Type B account for most of the remaining 3% of the scolopidia in the pedicel. They are also amphinematic and heterodynal, but with three sensory neurons each, and attach to the upper sides of the prongs. The three sensory neurons are structurally dissimilar, with two bearing Type 1 cilia, and the other a Type 2 cilium. In both Types A and B, the tips of the sensory dendrites are only loosely associated with the "tubular cap," which, in turn, extends its terminal filament to the prong. Types C and D are isolated scolopidia, both Type 1, mononematic and heterodynal, with two sensory neurons each that attach to the epidermis under the basal plate by an attachment cell (Fig. 9C,D). Type D appears to be absent in females (Boo and Richards, 1975b).

There have been conflicting opinions concerning which scolopidia are involved in sound reception, but more recent consensus is that Types A and B are most important, and that the mononematic scolopidia (Types C and D) are not considered part of Johnston's organ (see Field and Matheson, 1998). Eberl et al. (2000), Caldwell and Eberl (2002), and Göpfert and Robert (2001b, 2002) have described acoustic stimulation of the arista and Johnston's organ in *Drosophila*. Briefly, conspecific sounds stimulate the arista and the third antennal segment (=funiculus) to oscillate as a unit, which causes stretching and relaxation of scolopidial units in the pedicel. Precisely how stretching of the amphinematic scolopidia leads to sensory transduction is not yet clear, nor is the functional significance of the different types of scolopidia in Johnston's organ. The neural and mechanical basis for hearing in a mosquito, *Toxorhychites brevipalpis* (Göpfert and Robert, 2000, 2001a), and the mechanical and physiological basis of active audition in Diptera (Göpfert and Robert, 2001b, 2003) are currently being investigated.

SUBGENUAL ORGANS

Subgenual organs are located in the proximal tibia of each leg in most insects. The size and overall shape of the organ can vary between legs of an individual, and between different insect groups (for reviews, see Field and Matheson, 1998; Howse, 1968; McIver, 1985). In species that are particularly sensitive to solid-borne vibrations, and for which the ultrastructure of the organ has been studied, including some ants (Menzel and Tautz, 1994), cockroaches (Moran and Rowley, 1975), crickets (Friedman, 1972), wasps (Vilhelmsen et al., 2001), and lacewings (Devetak and Pabst, 1994), the scolopidia are monodynal, mononematic, Type 1, and typically attach in a perpendicular orientation to a fan-shaped septum that spans the leg cavity. For example, many species of green lacewings (Chrysopidae: Neuroptera) use complex substrate-borne vibrations for the purposes of mating and species recognition (Henry, 1980), and the subgenual organ is thought to play an important role in vibration reception (Devetak, 1998). In *Chrysoperla carnea*, the attachment (=cap) cells of three scolopidia form a septum (=velum) that divides the leg hemolymph by attaching loosely to the integument and trachea of the leg. Each scolopidium attaches separately in a perpendicular orientation to the velum (Devetak and Pabst, 1994) (Fig. 10). Vibrations of the leg are thought to cause acceleration of the hemolymph against the septum, resulting in the stretching and stimulation of the attached scolopidia. Relatively little is known about the structural and functional characteristics of subgenual organs. Considering the purported widespread occurrence of vibrational communication in insects (Cocroft, 2001; Hill, 2001), these structures are worthy of further investigation.

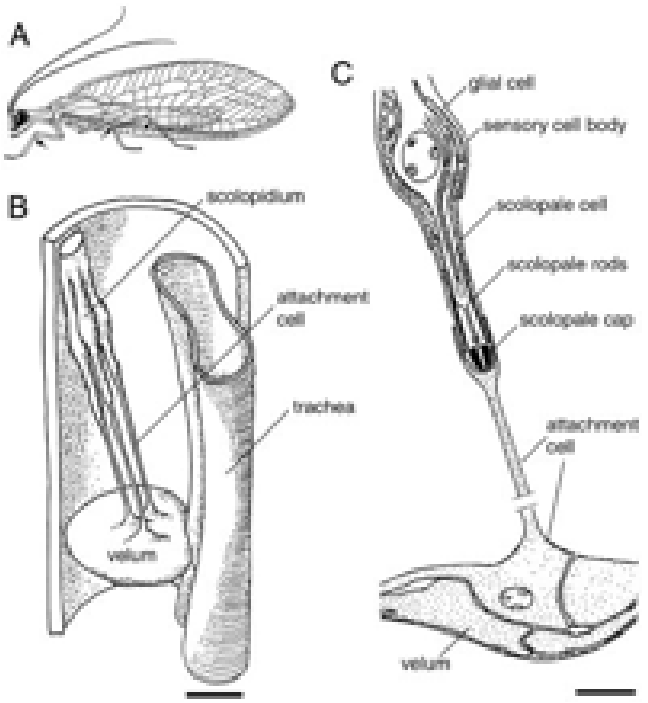

Fig. 10. Subgenual organ of the green lacewing, *Chrysoperla carnea*. **A:** An adult male with arrows pointing to the general location of the subgenual organs in the pro, meso, and metathoracic legs. **B:** Schematic reconstruction of the subgenual organ of the left mesothoracic tibia. Scale bar = 20 μm. **C:** Schematic of a longitudinal section through a single scolopidium. Scale bar = 5 μm. A, courtesy of C. Henry; B,C, redrawn from Devetak and Pabst (1994).

DISCUSSION

It is now more apparent than ever that insect hearing organs exist in great morphological and functional diversity, ranging from single hairs that vibrate in response to low-frequency, near-field sounds, to tympanal ears that may be associated with elaborate sound-receiving structures and are capable of deciphering complex songs of conspecifics. Tympanal ears alone

have evolved independently at least 20 times in seven insect orders (Yack and Hoy, 2003; Yager, 1999a), and there is little doubt that additional taxa will be added to this list in the future. The most recently described ears include those of Diptera, Dictyoptera, and Coleoptera, all previously considered to lack a sense of hearing. Perhaps most relevant to the future discovery of novel hearing organs are recent descriptions of functional ears that are anatomically discrete in the sense that they are not associated with a differentiated tympanal membrane exposed to the body's exterior. Included among these are the multiple abdominal ears of bladder grasshoppers (van Staaden et al., 2003), the "internal ears" of drepanid moths (Surlykke et al., 2003), and chordotonal organs of cicadas and some orthopterans that lie in the body cavity outside the conventional tympanal organ, but nevertheless respond to biologically relevant sounds (e.g., Daws and Hennig, 1996; Pflüger and Field, 1999; Stölting and Stumpner, 1998). Evidently, not all hearing organs sensitive to far-field sounds are necessarily recognizable as tympanal ears. This may be particularly relevant with respect to aquatic insects that use sound and vibrational communication extensively (Aitken, 1985), but for the most part lack recognizable tympanal organs, and may not require them, due to the high degree of coupling offered by the aqueous medium (Haskell, 1961). Furthermore, there is increasing evidence that communication using substrate-borne vibrations is widespread throughout many insect orders (Cocroft, 2001; Hill, 2001; Markl, 1983), although the receptor mechanisms for the most part remain unidentified. As we broaden our search image for what morphologically constitutes a functional auditory organ, and employ new methodologies that allow us to "eavesdrop" on acoustic signals beyond our own sensory experience, the number of "auditive" insects may very well be in the majority.

Despite their many anatomical forms, most insect hearing organs are innervated by chordotonal organs, and herein lies the secret to their diversity. Proprioceptive chordotonal organs are widely dispersed throughout the body, representing a ubiquitous pool of candidates that could potentially be converted into sound receivers. The factors influencing the "selection" of one chordotonal organ over another may be many, including the existence of appropriate central projections, the proximity to tracheal or cuticular structures, or the degree of protection offered by surrounding structures (for a discussion, see Yack and Roots, 1992; Yager, 1999a). As discussed previously, comparative studies between tympanate and atympanate homologues have provided the opportunity to learn about the structural specializations that accompanied the evolution of hearing. Adaptations to peripheral, non-neural structures typically have included: (1) thinning of cuticle associated with the chordotonal organ to the extreme thinness of a tympanal membrane; (2) enlargement of tracheal air sacs and spiracles; (3) mechanical isolation of the chordotonal organ from body movements; and (4) isolation of the chordotonal organ from surrounding hemolymph. Collectively, these adaptations serve to enhance the reception and transmission of sound to the sensory neuron.

Less is known about how the chordotonal organs themselves and their constituent scolopidia may be specially adapted for sound reception. Again, comparisons between tympanate and atympanate homologues, as well as between scolopidia within a single ear with different physiological characteristics, can provide insight into this question. It is possible that auditory chordotonal organs are not specialized for sound reception compared to their atympanate counterparts, and that differences in sensitivity are due entirely to modifications of peripheral structures. However, it also seems quite probable that various components of the coupling and transduction mechanism, such as the viscoelastic properties of attachment cells, and mechanical and/or electrical properties of the various intra- and extracellular components of the scolopale and sensory cells, impart special response characteristics to the sensory neuron. Although to date a few studies have examined the ultrastructure of physiologically characterized scolopidia, or compared auditory scolopidia with various homologues, there is still inadequate information to establish meaningful generalizations linking structure to function. More pointedly, we still do not understand how chordotonal organs function in general, so interpreting any such differences would be speculative. The following discussion summarizes some proposed structural specializations of auditory chordotonal organs.

1. As previously indicated, all insect auditory organs sensitive to far-field sounds are innervated by chordotonal organs with monodynal, mononematic, Type 1 scolopidia. These scolopidia are characterized by having tight junctions between various cellular and subcellular components, including a firm attachment between the single dendritic outer segment and scolopale cap, and highly reinforced intercellular junctions between the scolopale rods and attachment cell. These features are thought to promote a high degree of coupling between the vibrating structure and the sensory cell, a necessary requirement for the detection of minute, rapid sound vibrations.
2. Structural variations between entire scolopidia, or their components, including the scolopale rods, caps, and attachment cells, may be correlated with differences in their sensitivity and tuning characteristics. The dimensions of one or more of these structures can vary considerably between scolopidia within a single hearing organ (e.g., Robert and Willi, 2000; Rössler et al., 1994; Young and Ball, 1974a), between various developmental stages of a given hearing organ (e.g., Ball and Young, 1974; Rössler, 1992b), between different species within a given taxon (e.g., Rössler et al., 1994), and between various tympanate and atympanate homologues (e.g., Robert et al., 1996; Rössler, 1992a; Yack and Roots, 1992; Young and Ball, 1974b). However, the functional implications of these differences are not clearly understood.

   In all tympanal organs studied to date, the sensory and scolopale cells attach indirectly to the integument by one or more attachment cells (Field and Matheson, 1998; Moulins, 1976). Given that attachment cells are presumably involved in relaying rapid vibrations from the primary vibrating

structure (usually the tympanum) to the transducing structures, one might expect them to possess structural features that enhance coupling. Various comparative studies have demonstrated that the apical attachment in auditory organs is typically shorter, less flexible, and more tightly coupled to the vibrating structure than in atympanate homologues (e.g., Edgecomb et al., 1995; Robert et al., 1996; Rössler, 1992a; Yack and Roots, 1992; Young and Ball, 1974b). In addition to their mechanical role in sound reception, there is some evidence that attachment cells serve a physiological function (Oldfield and Hill, 1986). Clearly, the ultrastructural, mechanical, and physiological properties of attachment cells require further investigation.

Certain anatomical features of auditory scolopidia in Ensifera have been correlated to their tuning characteristics. In katydids, the more distal scolopidia of the crista acustica, those more sensitive to high-frequency sounds, are smaller in general, with more slender scolopales and smaller attachment cells than those sensitive to lower frequencies (see Rössler, 1992a,b; Rössler et al., 1994; Stumpner, 1996). This trend was not supported in a morphometric study of fly ears, however, where the tympanal scolopidia of female flies, which are more sensitive to low frequencies than males, were not significantly different than those of males (Robert and Willi, 2000).

3. It was recognized by Field and Matheson (1998) that the bulbous enlargement of the inner dendritic segment may be particularly prominent in scolopidia associated with sound and vibration reception. Although the function of this enlargement is unknown, it is proposed to provide additional surface area for ion exchange at the dendritic apex, thus enhancing the rapid regeneration of spikes necessary for relaying rapid vibrations. These particular scolopidia were also noted to have a thickening midway along the scolopale rod region (see Fig. 5F), which may offer structural stability to the scolopale rods.
4. Although there are exceptions, most tympanal chordotonal organs attach to the inner surface of the tympanum at an angle directly perpendicular or slightly oblique to the plane of the membrane. Whether or not the scolopidia are oriented with their dendrites pointing toward or away from the tympanum does not appear to be important, since both types occur in both high- and low-frequency-sensitive ears. The orientation of the scolopidia, together with the tight coupling between all links in the chain from membrane to dendritic apex, indicates that the adequate stimulus must be apical stretching of the dendritic cilium in response to tympanal vibration.
5. The number of scolopidia may increase (grasshoppers: Edgecomb et al., 1995; Lakes-Harlan and Heller, 1992; Meier and Reichert, 1990; flies: Robert et al., 1996; Ensifera: Houtermans and Schumacher, 1974; Rössler, 1992a; Young and Ball, 1974b), decrease (moths: Hasenfuss, 1997; Yack et al., 1999), or remain about the same (mantids: Yager and Scaffidi, 1993) between the preauditory and auditory condition. Although the number of comparisons are limited, the pattern suggests that ears functioning as bat detectors become simplified, with fewer cells, while those used for communicative purposes, with a presumably more complicated function, become more elaborate, with an increasing number of cells (for discussion, see Yack et al., 1999).

CONCLUDING REMARKS

Many questions remain concerning the functional organization of insect auditory chordotonal organs. How are they specialized, if at all, for receiving and transducing small, rapid vibrations? What is the basis for frequency discrimination between different scolopidia, and what mechanisms allow scolopidia that share a common tympanal attachment point to discriminate between sound intensities? Are different functional characteristics related more to differences in the mechanical properties of peripheral sound receiving structures, or to intrinsic properties of the chordotonal organs themselves? In this report, I have reviewed the anatomy of auditory chordotonal organs, and, based on inferential evidence from the existing literature, proposed some structural features that may be linked to functional specializations. These hypotheses, however, need to be tested directly through careful documentation of the ultrastructural and physiological characteristics of identified scolopidia. To date, only the auditory organs of Orthoptera and some Diptera have been examined in any detail, and future endeavor should extend these kinds of studies to other insect orders.

Most critical to the advancement of research on insect hearing organs will be further developments in understanding how chordotonal organs in general function as mechanotransducers. Numerous ultrastructural studies of chordotonal organs have led to several testable hypotheses about the roles of various cellular and subcellular components in mechanical coupling and transduction. In the future, it is expected that the functional organization of chordotonal organs will be elucidated by combining traditional ultrastructural and neurophysiological studies with novel genetic, immunohistochemical, and biophysical techniques.

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