The tympanal precursor organ of insect auditory organs: Historical reconstruction of the comparative and conceptual formation

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Abstract: Tympanale Gehörorgane treten in großer Vielfalt bei Insekten in verschiedenen Taxa auf. Funktionsmorphologisch zeichnen sie sich generell durch Tympanalmembranen aus dünner Cuticula, einem chordotonalen Sinnesorgan und einem Tracheenraum aus. Zur Rekonstruktion der evolutiven Entstehung dieser Gehörsensillen ist das Konzept des sensorischen Vorläuferorgans wesentlich, nach welchem die skolopidialen Sensillen des Tympanalorgans vor der Entstehung der Tympanalmembranen als Sinnesorgane mit physiologischer Funktion z. B. in der Propriozeption oder Vibrationsdetektion vorhanden waren. Die Ableitung der Gehörsensillen von atympanalen sensorischen Strukturen wurde für Orthopteren und Lepidopteren bereits im späten 19. und frühen 20. Jahrhundert durch V. Graber, H. Friedrich und F. Eggers etabliert. Arbeiten von Graber, E. Rádl und Eggers generalisierten auch die Entstehung von tympanalen Gehörorganen aus atympanalen Sinnesorganen. Die empirische Basis hierfür war die neuroanatomische Analyse von Tympanalorganen und atympanaten Organen verwandter Taxa sowie seriell homologer Sinnesorgane in derselben Art. Diese neuroanatomischen Analysen sind weiterhin zentral für die Rekonstruktion der Gehörevolution, erweitert durch sinnesphysiologische Untersuchungen der ursprünglichen Organisationsformen und vergleichende Studien auf der Basis phylogenetischer Verwandtschaftsverhältnisse.

Key words: tympanal organ, hearing, neurobiology, sensory evolution, history of biology

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Tympanal hearing in insects: evolutionary diversity and the tympanal precursor concept

In insects, the sense of hearing is extensively studied for behavioural and sensory physiology (e. g. Hedwig 2014; Pollack & al. 2016). Tympanal hearing organs have evolved at least 20 times in different insect lineages (Yager 1999; Yack & Hoy 2009; Strauss & Lakes-Harlan 2014; Greenfield 2016). Despite differences in anatomical position and structure, the tympanal organs usually share some structural elements: a tympanum (ear drum) of thin cuticle, a tracheal sack, and a chordotonal sensory organ of scolopidial sensilla (Eggers 1928; Pumphrey 1940; Fullard & Yack 1993; Hoy & Robert 1996; Yager 1999; Strauss & Lakes-Harlan 2014). The scolopidial sensilla are internal mechanosensory sensilla that are found in more positions than in tympanal organs: they occur in sensory organs for proprioception (measuring body movements), or detection of substrate vibrations, gravity, and airborne sound. An important concept for the evolutionary origin of tympanal organs is that they are modified chordotonal organ which existed in the body plan before the tympanal membranes were elaborated (e. g. Boyan 1993; Fullard & Yack 1993; Yager 1999; Strauss & lakes-Harlan 2014). Such chordotonal organs have been termed tympanal precursor organs or precursors, and comparative studies have substantiated the mechano-receptor origin of auditory sensilla from sensory organs involved in e. g. proprioception. Here, historical roots and landmark studies in the early development of the tympanal precursor organ concept are summarised. Special emphasis is placed on the mechanosensory origin of tympanal hearing organs not only in specific taxa but for insect tympanal ears in general.

Historical roots of neuroanatomical studies and evolutionary considerations of chordotonal precursors

The neuroanatomical investigations of tympanal organs in the late 19th and early 20th century addressed Orthoptera, Lepidoptera and Cicadidae. Vitus Graber studied the tympanal organs in detail for Orthoptera, and published specific considerations on their evolutionary origin. He first suggested the development of complex tympanal membranes from simpler ones, which he inferred from the sequence of ontogenetic differentiations, and further discussed the homology of sensory organs in orthopteran ears (Graber 1876). He found chordotonal organs in most insects (not only associated with tympanal membranes), and also noted the serial organisation of subgenual organs in the legs (Graber 1881a, b). From that, he concluded that the atympanate form is more primitive, and that the tympanal organs in the foreleg's tibia of crickets and tettigoniids are specialisations of the sensory organs serially present also in atympanate form (Graber 1881a: 451, 1881b: 619) as well as in all pairs of atympanate cockroaches and locusts (Acrididae) (Graber 1881a: 452). In an extensive study, Graber covered the morphology and physiology of tympanal organs (Graber 1881b, 1882). Considering evolutionary origin of tympanal organs, he gave three criteria to support the hypothesis of tympanal organs as modified atympanal organs:

(1) the sensory organs differentiate earlier than tympanal membranes during ontogeny,
(2) not only tympanate organs but also homologous atympanate organs exist, and
(3) the subgenual organs associated with tympana are more elaborate than atympanate ones, indicating they are more derived than the atympanate sensory organs (Graber 1881b: 619).

The last point is based on comparative studies including crickets, bushcrickets and cockroaches (*Blatta germanica*), with a higher number of scolopidial sensilla in the tympanate species (Graber 1881b: 544). Clearly, neuroanatomy was used at this point as the basis for evolutionary inferences that the auditory sensilla derived from atympanate conditions (also Graber 1882: 92). Problematically, Graber identified only the serially occuring subgenual organs, not the tettigoniid auditory organ (crista acustica) (1881b: 569-570; see Friedrich 1927). While Graber may have used the distinction between primitive atympanate organs and derived tympanal organs in a taxonomically restricted argument for Orthoptera and related insects, the evolutionary origins of tympanal organs from non-auditory sensory organs are unambiguously formulated. Graber explicitly states that the auditory sensilla "did not originate as such, but are to be derived from atympanal or primitive situations" (Graber 1881b: 619; transl. JS). The sequence of evolutionary auditory adaptations from pre-existing sensory organs is perfectly summarised as the "tympanalisation of the chordotonal organs" (Graber 1881b: 620).

Emanuel Rádl (1905) compared chordotonal organs in the legs, antenna, abdomen, and head. He found atympanate organs widely distributed, showing tympanal organs as derived, and suggested that the chordotonal organs are similar to muscle spindles. By that, he highlighted the common mechanosensory function; specified as "sense of movement and position" (Eggers 1928: 300; transl. JS), this concept is similar to a proprioceptive function of many chordotonal organs. However, Rádl also suggested the possibility that chordotonal organs originated from muscles. This proposal was taken up by Turner & Schwarz (1914) in their discussion of insect audition, and critically discussed by Eggers (1928).

Neuroanatomical studies of diverse tympanal organs and evolutionary considerations

Following the studies by Graber, further neuroanatomical descriptions improved the understanding of the sensory organs in Tettigoniidae (von Adelung 1892), and Schwabe (1906: 87) emphasised that the subgenual organ originated before tympana). The evolutionary development of tympanal organs from atympanate chordotonal organs was also proposed by Demoll (1917: 64) citing the serial homology in cricket and bushcricket legs. Neuroanatomical details on the serial homologues of tettigoniid auditory sensilla, the *crista acustica*, were documented in the mid- and hindlegs by Hermann Friedrich (1927, 1928) and Hans Knetsch (1939). Friedrich showed in bushcrickets that the sensory organ in the forelegs equipped with tympana has the highest number of sensilla, and concluded that the ancestral sensory organs were homogenous between legs ("In the ancestral forms of bushcrickets the mentioned differences were absent, the organs were identical." Friedrich, 1928: 93; transl. JS) and only became modified with the foreleg specialisation for tympanal hearing and the hindleg specialisation for jumping (Friedrich 1928).

His comparison of tibial sensory organs in orthopteroid insects saw the tympanal organs as the derived sensory adaptation (Friedrich 1929). Friedrich Eggers discussed if the gradient between legs indicates an elaboration of the sensory organs prior to development of tympana since the higher sensillum number in the midleg over the hindleg cannot be driven by the origin of tympana (Eggers, 1928: 191). Knetsch (1939) later argued that the atympanate sensory organs which contain fewer sensory neurons and have flattened cap cells are ancestral to the foreleg hearing organs with tympana, more sensory neurons ("increase in scolopidia"), and rounded cap cells.

Another important taxon for research on insect hearing are Lepidoptera with a great diversity of hearing organs (Yack & Hoy 2009). Forbes (1916) studied tympanal organs in several groups like Geometridae and Noctuidea including Notodontidae, Lymantriidae, and Arctiidae (see Richards 1933; Yack & al. 1999). He recognised these hearing organs as independently evolved, and declared the mechanosensory organ as a relevant factor allowing the development of tympana: "A brief examination shows that there are several analogous, but not homologous organs of this type in the various families, indicating parallel lines of descent from a form that presumably had neither, but may have possessed a wholly internal sense-organ, - which served as a stimulus to their formation, - in connection with the first spiracle." (Forbes 1916: 183-184) Richards (1933) also used a comparison of noctuid tympanal morphologies to reconstruct the differentiation and phylogeny of hearing organs in this group.

For cicadas, Vogel (1921, 1923) described the tympanal organ in the second abdominal segment and argued that it derived from abdominal chordotonal organs which occur metamerically in all segments (citing Graber's work) and which ancestrally monitored body movements (Vogel 1923). He derived the auditory organ from a mechanosensory precursor organ: "The most important step in transforming the chordotonal organ into a primitive auditory organ would thus be the development of a tympanum." (Vogel 1923: 227; transl. JS) This would also trigger the development of further scolopidial sensilla in the sensory organ, which in cicadas consists of ~15000 sensory neurons (Vogel 1923: 228).

Generalisation of the chordotonal precursor organ and elaboration of the evolutionary atympanate-tympanate transition

Eggers studied tympanal organs particularly in Lepidoptera (e.g. Eggers 1919, 1923, 1925, 1937) and also summarised the knowledge on chordotonal organs across insects in an extensive review for the anatomy and physiology (Eggers 1928). From the comparative data, he stated: "The decisive difference between chordotonal organs and tympanal organs is thus only the absence or presence of a tympanal membrane." (Eggers 1928: 12) Repeatedly addressing the evolutionary origin of tympanal organs, he was very clear on the evolutionary modifications by which tympanal sensory organs originated from atympanal conditions (Eggers 1928: 12, 17; 1937: 292). Eggers also identifies the presence of a tracheal sack as a precondition (preadaptation) for the development of tympanal organs (Eggers, 1928: 302). Given this evolutionary background, Eggers dealt easily with cases were a tympanal function is more difficult to infer from the membrane structure: he declared such occurrences of intermediate sensory organs to be expected (Eggers, 1928: 12). With this, evolutionary series of morphological transformation between atympanate and tympanate chordotonal organs in specific lineages were the next logical step (see also Hoy & Yack 2009). Vogel stated for cicada ears that the evolutionary transition from a proprioceptor detecting body or muscle movements to responses to airborne sound implies intermediate stages with a bifunctional sensory organs that is activated by both stimuli (Vogel, 1923: 227). Eggers depicted such hypothetical reconstructions of intermediate forms for tympanal organs of Lepidoptera from an atympanal chordotonal organ for Pyralidae (von Kennel & Eggers 1933) and Uraniidae (Eggers 1937, but see Kristensen 2012). Studying orthopteroid insects, Friedrich (1929) compared tympanate and atympanate sensory organs in the tibia and discussed their homology and evolutionary modifications. Ander (1939: 225) suggested that the tettigoniid *crista acustica* and the gryllid tympanal organ derived from the subgenual organ. In the late 1920s, the evolutionary concept of the precursor organ was thus developed and generalised for different types of tympanal ears, although a strict phylogenetic framework was not yet applied. At this point the neuroanatomical research had also gone beyond statements of organ homology, and aimed at an evolutionary reconstruction of functional adaptations in insect sensory/hearing organs.

Insect hearing in neuroethology and comparative evolutionary studies

With the maturation of neuroethology and the development of physiological and anatomical tools to analyse sensory organs in more detail, the knowledge on tympanal organs has grown tremendously. In the last decades, an interdisciplinary research programme to identify and characterise precursor organs using neurophysiological, developmental, and neuroanatomical comparisons between tympanal and atympanal organs in a phylogenetic framework was established (Yack & Fullard 1990; Meier & Reichert 1990; Boyan 1993). It corroborated the evolutionary origin of auditory sensilla from mechanosensory chordotonal organs (Boyan 1993; Fullard & Yack 1993; Hoy & Robert 1996; Yager 1999). Particularly for lepidopteran ears, there is an intellectual lineage deriving tympanal organs from proprioceptor precursor organs leading from Forbes (1916) and von Kennel & Eggers (1933) to the topics of neuroethology (see e. g. references in Yack & Fullard 1990: 524). The term 'precursor' for sensory organs was used explicitly for Lepidoptera by Yack & Fullard (1990), Scoble (1992), and Hasenfuss (1997: 156) for "the scolopidia which are precursors of the sensory parts of tympanal organs", and more generalised for insect ears by Hoy & Robert (1996), Yager (1999), and Hoy & Yack (2009).. Serial homology and comparative studies of sensory organs in atympanate taxa are still crucial for investigations of insect ear evolution, enriched by the phylogenetic framework and physiological investigations of precursor organs. The notion of the precursor organ has given the evolutionary approach to insect ears a general concept as well as a neurobiological focus: Yager (1999) identified the chordotonal organs as limiting factor for the evolution of tympanal ears, since trachea and cuticle are more common on the insect body. A list of precursor organs identified so far was included recently in Strauss & Lakes-Harlan (2014). For some taxa, the precursor organ is not yet firmly established, e. g. for the tympanal organs in Ensifera (Jeram & al. 1995; Lin & al. 1995; Strauss & Lakes-Harlan 2009) or scarab beetles, and further research efforts will be directed at this topic. For sensory evolution, the precursor organ concept thus contributes to understanding functional changes of chordotonal organs. Certainly, this concept will continue to inspire studies on the origins and adaptations of insect hearing organs.

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