What determines the number of auditory sensilla in the tympanal hearing organs of Tettigoniidae? Perspectives from comparative neuroanatomy and evolutionary forces

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Abstract

Insects have evolved complex receptor organs for the major sensory modalities. For the sense of hearing, the tympanal organ of Tettigoniidae (bush crickets or katydids) shows remarkable convergence to vertebrate hearing by impedance conversion and tonotopic frequency analysis. The main auditory receptors are scolopidial sensilla in the *crista acustica*. Morphological studies established that the numbers of auditory sensilla are species-specific. However, the factors determining the specific number of auditory sensilla are not well understood. This review provides an overview of the functional organization of the auditory organ in Tettigoniidae, including the diversification of the *crista acustica* sensilla, a list of species with the numbers of auditory sensilla, and a discussion of evolutionary forces affecting the number of sensilla in the *crista acustica* and their sensitivity. While all species of Tettigoniidae studied so far have a *crista acustica*, the number of sensilla varies on average from 15–116. While the relative differences or divergence in sensillum numbers may be explained by adaptive or regressive changes, it is more difficult to explain a specific number of sensilla in the *crista acustica* of a specific species (like for the model species *Ancistrura nigrovittata*, *Copiphora gorgonensis*, *Gampsocleis gratiosa*, *Mecopoda elongata*, *Requena verticalis*, or *Tettigonia viridissima*): sexual and natural selection as well as allometric relationships have been identified as key factors influencing the number of sensilla. Sexual selection affects the number of auditory sensilla in the *crista acustica* by the communication system and call patterns. Further, positive allometric relationships indicate positive selection for certain traits. Loss of selection leads to evolutionary regression of the auditory system and reduced number of auditory sensilla. This diversity in the auditory sensilla can be best addressed by comparative studies reconstructing adaptive or regressive changes in the *crista acustica*.

Keywords

acoustic communication, behavior, *crista acustica*, katydid, sexual selection

Acoustic communication and behavior of Tettigoniidae

The study of insect hearing is an interdisciplinary field of research that has highlighted the great diversity of tympanal organs in different taxa (Fullard and Yack 1993, Hoy and Robert 1996, Yager 1999, Stumpner and von Helversen 2001, Yack 2004, Yack and Dawson 2007, Römer 2018). The tympanal organs in insects usually consist of one or two tympanal membranes, a tracheal sack, and a scolopidial organ containing sensory neurons (Hoy 1998, Yager 1999, Yack 2004, Römer 2018). Tympanal hearing organs occur on almost all locations of the insect body and with a great variation in the number of sensory neurons (scolopidial sensilla) associated with the tympanal membranes. The sensilla numbers can vary between only one in notodontid moth and hawkmoth up to 2000 in cicadas and (atympanate) bladder grasshoppers (Yager 1999, Yack 2004, Strauß and Stumpner 2015). For several tympanal ears, sensillum numbers range between 20–100 auditory sensilla (Yager 1999), and within Orthoptera, locusts and crickets usually have 50–70 auditory sensilla. Differences in the set of sensilla have been discussed for adaptive modifications relating to specific hearing functions (e.g., Strauß and Stumpner 2015). In Tettigoniidae, the tympanal organs are located in the proximal tibia of the forelegs, with tympanal membranes at the anterior and posterior side (Fig. 1A). These hearing organs with auditory sensilla in the *crista acustica* (CA) are generally broadly tuned and cover frequency ranges from low sound into ultrasonic frequencies (e.g., Kalmring et al. 1990, Rössler and Kalmring 1994, Rössler et al. 1994, Schul and Patterson 2003).

With more than 6500 species (Ingrisch and Rentz 2009, Mugleston et al. 2013), Tettigoniidae are an ideal taxon to study proximate and ultimate aspects of acoustic signalling and the design and diversification of ears. Hearing in Ensifera in general and in tettigoniids in particular likely evolved for detection and localization of potential mates (Bailey 1991, Stumpner and von Helversen 2001, Robinson and Hall 2002, Greenfield 2016) by calls that are species-specific in temporal pattern (Gwynne 2001, Robinson and Hall 2002). Male tettigoniids usually produce acoustic signals by tegminal stridulation, and females perform phonotaxis towards the males (unidirectional communication system). However, this signalling system was expanded into duets with females producing a reply call in few tettigoniid taxa (bidirectional communication system) (Nickle and Carlysle 1975, Bailey 2003, Heller et al. 2015), and males or both sexes move towards the other signaller. Selection requires the sensitivity for conspecific call frequencies and the recognition of the temporal pattern in the conspecific signals over other species' signals. While highest auditory sensitivity

can match with the carrier frequency of the calls, there are also cases of mismatches between their call spectra and the frequency tuning of the ears known (e.g., Bailey and Römer 1991, Römer and Bailey 1998, see also Mason 1991 for a mismatch in the prophalangopsid *Cyphoderris monstrosa*). The transmission of sound signals is highly influenced by the environment, as vegetation filters particularly higher frequency components depending on the distance (Römer and Lewald 1992, Robinson and Hall 2002).

Hearing further allows predator detection and evasion, male aggressive behavior, and male spacing (Bailey 1985, 1991, Gwynne 2001, Robinson and Hall 2002). In particular, echolocating bats are important predators of tettigoniids (Belwood 1990, Kalka et al. 2008, Jones et al. 2014, ter Hofstede et al. 2017). Since bats evolved after the appearance of stridulatory structures in Tettigoniidae, the evolutionary sequence of hearing is likely to first involve intraspecific communication and then have expanded to higher ultrasonic ranges to include bat detection (Bailey 1991, Hoy 1992, Stumpner and von Helversen 2001, Greenfield 2016), while early insectivorous mammals likely also preyed upon stridulating insect (Hoy 1992). Tettigoniidae can hear bat echolocation calls and developed behavioral responses (Pollack 2015): certain species stop calling as it exposes the signaller (Faure and Hoy 2000, ter Hofstede et al. 2010), or animals in flight evade the sound source by dropping (Libersat and Hoy 1991) or changing flight orientation (Schulze and Schul 2001, Kilmer et al. 2010). In the tonotopically ordered CA (see below), the frequency contents of intraspecific calls or bat echolocation calls are processed by the adequately tuned sensilla. This tonotopic organization also allows intensity (distance) analysis (Hennig et al. 2004, Stumpner and Nowotny 2014, Römer 2016): further populations of sensilla will get recruited if the stimulus amplitudes increase to levels that also excite sensory neurons tuned to different best frequencies (Höbel and Schul 2007). The recruitment of sensilla for intensity discrimination is well documented for *Requena verticalis* with 22 auditory sensilla (Römer et al. 1998, Römer 2016). With the species-specific number of auditory sensilla and length of the auditory organ, the differences in thresholds extend the dynamic range of the hearing organ, and the number of sensilla can not only influence the accuracy of representing frequency resolution but also of amplitude differences (Römer 2016).

Selection and evolutionary adaptations of the tettigoniid hearing organ

Selection acts in a complex setting of acoustic signalling that includes the communication system, signal transmission, signalling distance (active space), and background noise. By the functions of hearing in mate detection and predator evasion, both sexual and natural selection affect the hearing organs in Tettigoniidae. Adaptations are notable in particular in the size differences of spiracles, which can be related to specific acoustic behaviors and selection pressures between sexes (e.g., Bailey and Römer 1991, Heller et al. 1997a, Mason and Bailey 1998, Strauß et al. 2017). In some circumstances, evolutionary forces may be difficult to identify by studying only the phenotypes, as selection pressures may overlap or even act in different directions (see Strauß and Stumpner 2015). After the loss of sexual selection, especially regressive evolution—in general, the decrease or reduction of a specific structure in some dimension like size, length, or number of elements—has been noted for spiracles and tympana, and this can also be analyzed for effects on the CA (the reduction of sensillum numbers) in a comparative approach. Drawing on the literature for several tettigoniid

groups, here the neuroanatomical and physiological evidence for adaptations in the number of auditory sensilla in the CA is summarized and discussed.

Anatomical and neuronal structures of the tettigoniid tympanal hearing organ

The auditory organ in tettigoniids follows a ground plan of neuronal and anatomical elements, which can vary considerably in their morphology across different species (Bailey 1990, 1993, Lakes and Schikorski 1990, Rössler et al. 2006). These hearing organs show a remarkable evolutionary convergence to the vertebrate hearing organs for impedance conversion and frequency representation (Montealegre-Z et al. 2012, Palghat Udayashankar et al. 2012, Hildebrandt 2014).

The tympanal membranes are areas of thinned cuticle. The membranes can be openly exposed, but in other species can also be located behind tympanal covers or tympanal flaps (Bailey 1993). In the latter cases, sound enters to the tympana through thin tympanal slits (Fig. 1B, C). These flaps are supposed to contribute to the directionality of hearing (Bailey and Stephen 1978, Mason et al. 1991, Bailey 1993). In some species, so-called pinnae form around the tympana which leave a broader slit over the tympana (Bailey 1993). In some species like the Australian *Beiericolya tardipes* (Meconematinae), the Peruvian *Bufotettix auchenacophoroides* (Pseudophyllinae), and the Asian *Lacipoda immunda* (Pseudophyllinae), the proximal tibia is swollen so that it forms cups around the tympana and orients the opening dorsally on the tibia (Bailey 1990, Rentz 2001, Nickle 2006). The cup formation is described as most elaborated in *Phisis* and *Decolya* (Meconematinae) (Bailey 1990).

The neuronal responses to sound entering via the tympanal membranes are stronger for relatively lower frequencies (Hummel et al. 2011, Stumpner and Nowotny 2014), and low frequency sound travels relatively poor in the acoustic trachea (Jonsson et al. 2016). Rather than sound acting on the outer surface of the tympanal membranes, the major input to the hearing organ is via the acoustic spiracle in the prothorax, especially for higher sound frequencies (Lewis 1974, Nocke 1975, Michelsen et al. 1994, Bailey 1998, Hummel et al. 2011, Stumpner and Nowotny 2014, Jonsson et al. 2016). This enlarged acoustic spiracle is usually permanently open (for one exception see Römer and Bailey 1998), and continues into the acoustic bulla in the prothorax and the acoustic trachea that runs through the thorax into the foreleg and passively amplifies the sound input (Bailey 1993, Heinrich et al. 1993). The sizes of the spiracle and bulla differ between species (Mason et al. 1991, Stumpner and Heller 1992, Bailey 1993, Heinrich et al. 1993) and even between sexes of the same species (Bailey and Römer 1991, Heller et al. 1997a, Mason and Bailey 1998, Strauß et al. 2014). In addition, extensive differences in the sizes of bulla and spiracles occur between larger taxonomic groups, e.g., Phaneropterinae, Pseudophyllinae, and Tettigoniinae (Bailey 1990, 1993, Mason et al. 1991). In the proximal tibia, the acoustic trachea splits into an anterior and posterior branch at the level of the tympana (Fig. 1B; Schwabe 1906, Schumacher 1975a, Lin et al. 1994, Sickmann et al. 1997), forming a "bicompartmental receptor region" (Heinrich et al. 1993). The split into the two tracheal branches occurs only distally of the proximal sensilla of the CA (Rössler et al. 1994, Sickmann et al. 1997). The tracheal branches align laterally behind the anterior and posterior tympanum (Fig. 1B).

The principal sensory organ processing acoustic stimuli is the *crista acustica* (CA) located within the foreleg tibia between the
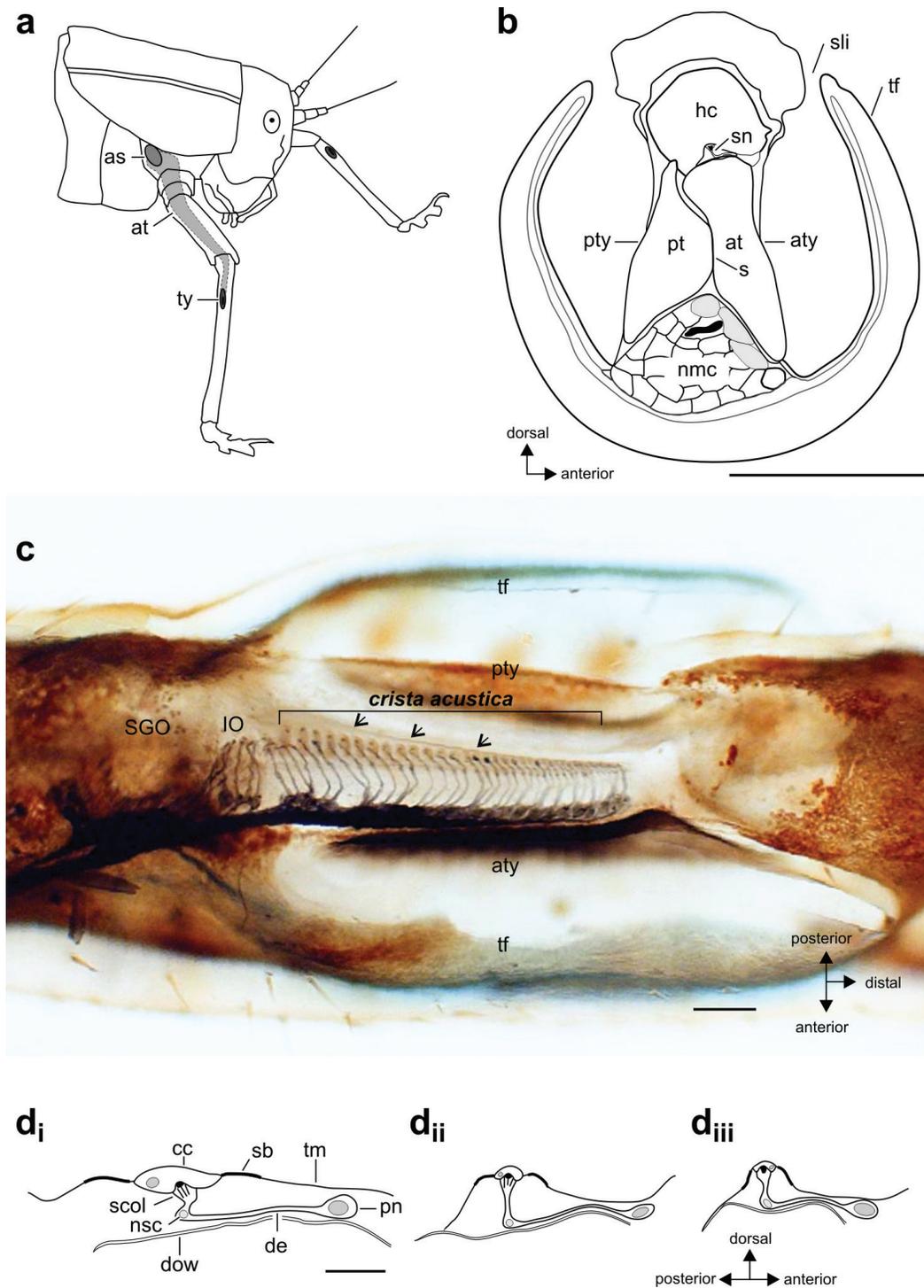
Fig. 1. The auditory system of bushcrickets. **A.** Schematic of the acoustic trachea (at) from the acoustic spiracle (as) in the thorax into the foreleg with tympanal membranes (ty) in the proximal tibia; **B.** Transverse section of the tibia at the level of the tympana and *crista acustica* in *Gampsocleis gratiosa*; in Gampsocleis gratiosa; **C.** The sensory organs in the proximal tibia of the male *Tettigonia viridissima*. The dorsal cuticle has been removed after axonal tracing of the tympanal nerve with cobalt solution to stain sensory neurons of the subgenual organ (SGO), intermediate organ (IO) and *crista acustica*. The *crista acustica* is placed between the anterior tympanum (aty) and posterior tympanum (pty). The tympanal flaps (tf) cover the tympanal membranes. Arrows indicate the tectorial membrane; **D.** Morphological differences of sensory neurons along the *crista acustica* from *G. gratiosa*, showing the (d_i) third-most proximal, (d_{ii}) middle, and (d_{iii}) third-most distal sensillum. Abbreviations: at, anterior trachea; aty, anterior tympanum; cc, cap cell; de, dendrite; dow, dorsal tracheal wall; hc, haemolymph channel; IO, intermediate organ; nmc, nerve muscle channel; nsc, nucleus of scolopale cell; pn, perikarya of sensory neurons; pt, posterior trachea; pty, posterior tympanum; s, septum; sb, supporting band; scol, scolopale cap and rods; SGO, subgenual organ; sli, slit; sn, sensory neuron; tf, tympanal flap; tm, tectorial membrane. Scales: 500 µm (**B**), 100 µm (**C**), 50 µm (**D**). Figure **A.** reprinted from Strauß et al. 2014, with permission from John Wiley and Sons. **B., D.** redrawn from Lin et al. 1994, with permission from John Wiley and Sons.

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tympana (Fig. 1C). The sensory neurons are scolopidial sensilla located over the tracheal branches arranged in the proximo-distal axis of the tibia (Fig. 1B–D), covered by the tectorial membrane, which is triangular in shape with a curvilinear surface. The CA is part of the complex tibial organ together with other scolopidial organs: the subgenual organ, the intermediate organ and the accessory organ (Fig. 1C; Lakes and Schikorski 1990, Rössler et al. 2006, Strauß et al. 2016). The CA sensilla are attached to the tectorial membrane and the dorsal wall of the acoustic trachea but are not in direct contact with the tympana (Fig. 1B, D; Lakes and Schikorski 1990). The sensilla are placed dorsally of the acoustic trachea (the dorsal wall) and are mainly arranged linearly. Their dendrites run over the anterior tracheal branch from the anterior to the posterior tibia (Fig. 1B, C) and terminate in cap cells linked to the tectorial membrane (Fig. 1D). The sensilla are overall morphologically similar throughout the CA (Lin et al. 1994, Kalmring et al. 1995b) but decrease from proximal to distal in the size of cap cells, along with the width of the tectorial membrane and the width of the dorsal tracheal wall (Fig. 1D) (Rössler 1992a, Lin et al. 1994, Rössler and Kalmring 1994, Kalmring et al. 1995a, Sickmann et al. 1997, Hummel et al. 2017). This correlates to the physiological changes in sensory tuning of individual sensilla, with their best frequency increasing from lower to higher frequencies from the proximal to the distal end of the CA (Zhantiev and Korsunovskaya 1978, Oldfield 1982, Stölting and Stumpner 1998, Hummel et al. 2017), and forms a tonotopically arranged filter bank that allows frequency analysis (Stölting and Stumpner 1998, Hennig et al. 2004, Stumpner and Nowotny 2014, Montealegre-Z and Robert 2015). Anatomical variation between species is also expressed in the number of auditory sensilla in the CA.

Scolopidial sensilla are primary sensory neurons that send their axon into the corresponding segmental ganglion of the central nervous system to form synapses with first order interneurons. The tonotopic representation is maintained in the central projection of auditory afferents (Römer 1983, Stumpner 1996, Stölting and Stumpner 1998, Baden and Hedwig 2010). For the tonotopical organization, different physiological adaptations have been proposed (Hennig et al. 2004). Morphological changes in the organ size, organ height, dendrite length, and cap cell size correlate with the shift in frequency tuning (Hummel et al. 2017, Scherberich et al. 2017). The tonotopic frequency representation is formed by sound-induced travelling waves at the attachment/cap cells and in certain species also at the acoustic vesicle, a modified part of the haemolymph channel in the dorsal tibia (Montealegre-Z et al. 2012, Palghat Udayashankar et al. 2012, Stumpner and Nowotny 2014, Montealegre-Z and Robert 2015, Sarria-S et al. 2017). In such cases, the integrity of the acoustic vesicles and the lipidic fluid it contains are necessary for expressing travelling waves (Montealegre-Z et al. 2012).

The CA also occurs in the atympanate mid- and hind-legs with a gradual decrease in the number of sensilla (Friedrich 1927, 1928, Knetsch 1939, Schumacher 1975b, 1979), but lacks the auditory specializations such as tympanal membranes, an enlarged trachea and tectorial membrane, elaborate supporting bands, or smaller size of scolopale caps (e.g., Lin et al. 1994). The physiology of these atympanate organs remains unresolved (Rössler et al. 2006), but they lack the high sensitivity to airborne sound found in the forelegs (Rössler 1992b, Kalmring et al. 1994). Notably, some atympanate taxa of Ensifera have a sensory organ present in all leg pairs, the *crista acustica* homologue, that is homologous to the tettigoniid auditory sensilla, with a number of sensilla similar to the forelegs of tympanate bush crickets (Strauß and Lakes-Harlan 2008, 2010).

Physiological responses to airborne sound were noted also from the the subgenual organ (SGO) and the intermediate organ (IO), usually responding to relatively low frequency at high stimulus intensities (Kalmring et al. 1994, Stumpner 1996, Höbel and Schul 2007), though higher frequency responses were found in the distal IO (Stölting and Stumpner 1998). Both organs also respond with high sensitivity to substrate vibrations (Kalmring et al. 1994). Here, the focus is on the CA as the sensory organ mainly adapted to airborne sound detection.

Comparative neuroanatomy of the *crista acustica*

The CA has been investigated in several species of Tettigoniidae, and these comparative neuroanatomical studies showed that the number of auditory sensilla is species-specific (Knetsch 1939, Schumacher 1979, Lakes and Schikorski 1990). The sensillum numbers in closely related species are usually similar but not identical (Lakes and Schikorski 1990). Sensillum numbers for tettigoniid species are presented in Table 1, with numbers between a minimum of 12–14 sensilla (*Supersonus* and *Phlugis* spp., Meconematinae; F. Montealegre-Z, personal communication) and a maximum of 116 sensilla (male *Ancylecha fenestrata*, Phaneropterinae; Scherberich et al. 2017). In most species, the CA contains 25–35 sensilla. It could be assumed that well-developed hearing organs also tend to increase the number of sensory neurons if possible, e.g., for better signal detection against noise (Stumpner and Nowotny 2014). The number of auditory sensilla is thus an important indicator of the elaboration or regression of the hearing organ when compared within a specific taxon. Within Orthoptera, a higher number of auditory sensilla is found in both crickets and locusts in comparison to Tettigoniidae (crickets: Eibl 1978, Klose 1996; locusts: Michel and Petersen 1982).

Within a genus, tettigoniid species usually have highly similar sensillum numbers, though larger differences occasionally occur (*Poecilimon*; Strauß et al. 2014). The variation in sensillum numbers between individuals from one species is usually very low (Lakes and Schikorski 1990, Rössler 1992b). Slight differences between individuals caused different averages as reported, for example, in *T. viridissima* (Schumacher 1973, Kalmring et al. 1995a, b, Strauß et al. 2012). Such ranges of differences have been reported for few species, e.g., in *Ancistrura nigrovittata* the mean number is 37, with rare extremes of 32, 33, and 40 CA sensilla found (Ostrowski and Stumpner 2010). Commonly, the sexes show no differences in the number of CA sensilla. A notable case of dimorphism exists in *Ancylecha fenestrata* where males have a significantly higher number of auditory sensilla and a longer CA than females (Scherberich et al. 2016, 2017; see below). In another case, males of *Ancistrura nigrovittata* have on average two sensilla more in the CA than females (Ostrowski and Stumpner 2010).

Notably, the number of auditory sensilla is not directly related to the CA length (Schumacher 1979, Lakes and Schikorski 1990, Strauß et al. 2017), and between species, fewer sensilla can be found in a longer CA (e.g., Rössler et al. 1994). The scolopidial sensilla can occur highly concentrated in the distal CA (Rössler et al. 1994, Kalmring et al. 1995a), leading to pairs or even triplets of somata at the same proximo-distal level (Sickmann et al. 1997, Strauß et al. 2012, Hummel et al. 2017). These findings raise the question of how differences in the number of auditory sensilla relate to the tonotopic frequency analysis, and what factors affect these changes in numbers.

For Tettigoniidae, a relatively high number of species have been investigated for the neuroanatomy of the hearing organs.

Table 1. Number of auditory sensilla in the *crista acustica* of Tettigoniidae. If one species is covered by several references, usually the number which includes mean and standard deviation is cited. Relatively large differences in sensillum numbers reported between studies based on different techniques or sample sizes are also referenced for a few species.

Species	CA sensilla	Tympana	Reference
Bradyporinae			
Deracantha onos	23	covered	O. S. Korsunovskaya, personal communication
Zichya baranovi	15	covered	Zhantiev et al. 1995
Conocephalinae: Conocephalini			
Conocephalus fuscus	26	covered	Knetsch 1939, Schumacher 1979
Conocephalus dorsalis	25	covered	Schumacher 1979
Conocephalus nigropleurum	28	covered	Fullard et al. 1989
Conocephalinae: Copiphorini			
Copiphora gorgonensis	28	covered	Montealegre-Z et al. 2012
Neoconocephalus robustus	35±1	covered	Strauß et al. 2017
Neoconocephalus bivocatus	Males: 34±1 Females: 34±2	covered	Strauß et al. 2017
Neoconocephalus exiliscanorus	35±1	covered	Strauß et al. 2017
Neoconocephalus nebrascensis	Males: 32±1 Females: 33±1	covered	Strauß et al. 2017
Neoconocephalus ensiger	32±1	covered	Strauß et al. 2017
Neoconocephalus triops	34±1	covered	Strauß et al. 2017
Neoconocephalus retusus	33	covered	Strauß et al. 2017
Neoconocephalus palustris	Males: 33±1 Females: 32	covered	Strauß et al. 2017
Neoconocephalus affinis	32±1	covered	Strauß et al. 2017
Mygalopsis marki	20	covered	Oldfield 1984
	24±1		Kalmring et al. 1995b
Ruspolia nitidula (syn. *Homorocoryphus nitidulus*)	31	covered	Knetsch 1939
	35		Schumacher 1979
Ephippigerinae			
Ephippiger ephippiger	28±1	covered	Rössler 1992b
Ephippiger perforatus	27	covered	Lakes and Schikorski 1990
Uromenus rugosicollis	30	covered	Lakes and Schikorski 1990
Hetrodinae			
Acanthoplus longipes	27±2	open	Kowalski and Lakes-Harlan 2013
Acanthoplus discoidalis	27±1	open	Kowalski and Lakes-Harlan 2013
Acanthoproctus diadematus	33±2	covered	Kowalski and Lakes-Harlan 2013
Enyaliopsis sp.	28±2	open	Kowalski and Lakes-Harlan 2013
Spalacomimus liberiana	26	covered	Kowalski and Lakes-Harlan 2013
Listroscelidinae: Requenini			
Requena verticalis	22	covered	Römer et al. 1998
Meconematinae			
Supersonus spp.	12–14	covered, tympanal slits asymmetrical	Sarria-S et al. 2014, F. Montealegre-Z, personal communication
Phlugis spp.	12–14	open tympana	F. Montealegre-Z, personal communication
Meconema thalassinum	21	open	Knetsch 1939
	16		Schumacher 1973
Meconema meridionale	15	open	Schumacher 1979
Mecopodinae			
Mecopoda elongata	48±2	open	Strauß et al. 2012
	45		Hummel et al. 2017
Phaneropterinae: Ephippithytae			
Caedicia simplex	35	open	Oldfield 1982
Polichne sp.	32	open	Oldfield 1984
Phaneropterinae: Barbitistini			
Ancistrura nigrovittata	37	open	Ostrowski and Stumpner 2010
Leptophyes punctatissima	28±1	open	Rössler et al. 1994
	24		Knetsch 1939
	22		Schumacher 1973
Leptophyes albovittata	22	open	Knetsch 1939
Isophya pyrenaea	27	open	Knetsch 1939
Isophya modestior	34±2	open	Strauß et al. 2014

Table 1. (Continued).

Species	CA sensilla	Tympana	Reference
Poecilimon ornatus	38±1	open	Strauß et al. 2014
Poecilimon gracilis	34±1	open	Strauß et al. 2014
Poecilimon elegans	32±1	open	Strauß et al. 2014
Poecilimon chopardi	30±1	open	Strauß et al. 2014
Poecilimon intermedius	17±1	open	Lehmann et al. 2007
Poecilimon ampliatus	21±1	open	Lehmann et al. 2007
Polysarcus denticauda	49±2	open	Sickmann et al. 1997
Phaneropterinae: Holochlorini			
Ancylecha fenestrata	Males: 116 (md)	anterior covered,	Scherberich et al. 2017
	Females: 86 (md)	posterior open	Kowalski 2010
Phaneropterinae: Phaneropterini			
Phaneroptera falcata	39	open	Schumacher 1973
Phaneropterinae: Steirodontini			
Stilpnochlora couloniana	45–55	open	Lakes-Harlan and Scherberich 2015
Phasmodinae			
Phasmodes ranatriformis	16–18	no tympanum	Lakes-Harlan et al. 1991
Pseudophyllinae			
Nastonotus foreli	22	covered	F. Montealegre-Z, personal communication
Tettigoniinae: Decticini			
Decticus verrucivorus	33±1	covered	Rössler and Kalmring 1994
Decticus albifrons	34±1	covered	Rössler and Kalmring 1994
Tettigoniinae: Gampsocleidini			
Gampsocleis gratiosa	33±1	covered	Lin et al. 1994
Tettigoniinae: Tettigoniini			
Tettigonia viridissima	37	covered	Schumacher 1973
	36±1		Kalmring et al. 1995a
Tettigonia cantans	35±1	covered	Kalmring et al. 1995a
Tettigoniinae: Platycleidini			
Bicolorana bicolor	23	covered	Schumacher 1973
Metrioptera roeselii	26		Kowalski 2010
Metrioptera brachyptera	24	covered	Knetsch 1939, Schumacher 1979
Platycleis albopunctata (syn. *denticulata*)	23	covered	Schumacher 1973
Psorodonotus illyricus	31±1	covered	Kalmring et al. 1995b
Tettigoniinae: Pholidopterini			
Pholidoptera griseoaptera	24±1	covered	Rössler et al. 1994
Zaprochilinae			
Kawanaphila nartee	18±1	open	Bailey and Römer 1991, Rentz 1993

This becomes apparent in comparison to the crickets, the other ensiferan group studied in detail for the neurobiological substrate for hearing (Pollack and Hedwig 2017), where the tympanal organ anatomy has been analysed mainly for a few selected model species (summary: Ball et al. 1989): *Gryllus bimaculatus*, *Gryllus campestris* (Michel 1974, Eibl 1978), *Achaeta domesticus* (Schwabe 1906), *Teleogryllus commodus* (Klose 1996), several Eneopterinae species (Schneider et al. 2017), and the mogoplistine *Cycloptiloides canariensis* with a unique hearing organ (Michel 1979). The research on diverse tettigoniid lineages not only addressed the neurophysiology of sound processing, but also led to the study of the effects of species divergence, the differences in the communication system, and the evolutionary regression of the hearing organs on the structure of the CA.

Functional and evolutionary factors influencing the sensillum numbers in the *crista acustica*

The sense of hearing provides important adaptations for mate recognition and localization as well as predator (bat) detection. Such positive selection for hearing will result in well-developed hearing organs with auditory receptors detecting frequency ranges of both intraspecific calls and ultrasonic frequencies of bats. How-

ever, additional factors could affect the structure of the hearing organs, like genetic drift, allometry, and phylogenetic constraints (structures preserving the ancestral state) as well as physical constraints (see Strauß and Stumpner 2015 for tympanal organs in general). From the comparative data, it can be concluded that CA under sexual and natural selection usually contain 22–50 sensilla, with most species having 25–40 auditory sensilla. These numbers thus appear to be adequate and adaptive to allow sound detection, frequency resolution, intensity discrimination, and input to the CNS for directional and temporal analysis, though smaller numbers do not necessarily exclude these physiological functions. For example, *Meconema thalassinum* does not use tegminal stridulation and has a low number of 16 auditory sensilla (Schumacher 1973, 1979), and in the tympanal hearing organ of this species, travelling waves were recorded over the CA that indicate frequency analysis (F. Montealegre-Z, personal communication). As both higher and lower numbers from the most common numbers are found, the evolutionary events behind the extreme values can be analyzed based on this comparative background. In addition, functional and physiological data are required to characterize the changes in the sensory organs further. Below, the different evolutionary forces are discussed for the CA, with expected outcomes of the effect of selection. Neutral evolution (drift) is difficult to support directly

by comparing anatomical traits or physiological features, as it is supported by the lack of evidence for explanations based on adaptions or constraints if detailed information on the genetic polymorphisms that encode a trait is not available (Schul et al. 2014). It likely contributes to the regression of auditory systems if a selection pressure ceases (e.g., Lakes-Harlan et al. 1991, Lehmann et al. 2007, Strauß and Stumpner 2015).

Evolutionary regression in the hearing organ.—Strong evidence for the role of selection pressures on the tympanal organs can be obtained from species where either natural or sexual selection have ceased. In these cases, often a regression is noted that can reduce the size of spiracles of the acoustic trachea, and potentially also the number of auditory sensilla. Such regression could be due to neutral evolution (drift) after selection ceases to maintain a certain structure, or auditory sensilla could be selected against, as they require energy to develop and maintain (see e.g., Laughlin et al. 1998). Case studies under which conditions and to what extent such regressions occur are discussed below.

Sexual dimorphism: Australian *Kawanaphila* show a notable sexual dimorphism in the auditory system, with a smaller auditory spiracle in males than in females and also smaller acoustic bulla in the prothorax (Bailey and Römer 1991, Mason and Bailey 1998). Three species in the genus have been studied, revealing a gradient in the reduction of the acoustic spiracle. While in *Kawanaphila yarraga* the auditory spiracle in males is significantly smaller than in females, in males of *K. nartee* and *K. mirla* no external auditory spiracle is developed, and males thus show decreased auditory sensitivity compared to females (Bailey and Römer 1991, Mason and Bailey 1998). Blocking the auditory spiracle in *K. nartee* females resulted in a reduced sensitivity similar to conspecific males (Bailey and Römer 1991). The number of CA sensilla in *K. nartee* males and females is not different between sexes, with 18 ± 1 sensory neurons (Bailey and Römer 1991). The CA of the other *Kawanaphila* species has not been studied for the number of sensilla, and such data might complement the evidence for gradual regression in these species. The auditory behavior of males also differs, with decreased male competition in *K. mirla* that is acoustically mediated between callers as indicated by lower distances between males (Mason and Bailey 1998) to the absence of any auditory behavior in male *K. nartee* (Bailey and Simmons 1991). This gradual decrease in the auditory function of males from different species and intraspecific dimorphism indicate that the male hearing organ is the result of an evolutionary regression from a well-developed auditory system. Since in *K. mirla* the regression is already anatomically and physiologically detectable, while auditory behavior of male-male competition still occurs, the decline in hearing function seems not to have triggered the regression (Mason and Bailey 1998).

Mimesis: A further reduction is found in the Australian stick katydid, *Phasmodes ranatriformis*. These mimetic animals remarkably resemble stick insects, and do not produce acoustic signals (Rentz 1993), resulting in a weakened selection pressure for hearing. Spiracles are small and tympana are only weakly expressed in males and females as depressions with thinner leg cuticle (Lakes-Harlan et al. 1991, Rentz 1993). The CA is present in the legs of females and males with 16–18 sensilla in the foreleg (Lakes-Harlan et al. 1991), also indicating a low elaboration of the auditory sense.

Parthenogenesis: In tettigoniids, parthenogenesis (loss of males) is rare but presents an interesting evolutionary scenario, since selection for intraspecific signal detection ceases without males producing acoustic signals. In *Poecilimon intermedius*, an obligate parthenogenetic species, only females occur (Lehmann et al. 2011) and the number of auditory sensilla is very low at 17 ± 1, even lower than in the sister species *P. ampliatus* (21 ± 1). This indicates an evolutionary regression of the hearing organ, while selection pressure from predators may have maintained some hearing function (Lehmann et al. 2007).

Change of signalling behavior: In two *Meconema* species, acoustic signals are not produced by tegminal stridulation as males of *M. thalassinum* and *M. meridionale* produce sound and likely vibration signals by tapping or drumming with the hind leg on the substrate (Sismondo 1980, Vahed 1996, Ingrisch and Rentz 2009). In these species with open tympana, the number of auditory sensilla is very low at 15 (*M. meridionale*) and 16 (*M. thalassinum*) sensilla (Schumacher 1979). However, the CA in *M. thalassinum* expresses travelling waves, indicating functional hearing (F. Montealegre-Z, personal communication). Female bush crickets of certain species can also use vibrational signals produced during wing stridulation for orientation toward males over shorter distances (*Ephippiger ephippiger*: Stiedl and Kalmring 1989). Since the most sensitive vibration receptor in the tibia is the subgenual organ (Fig. 1C), the tapping may also affect the signal detection by both auditory and vibratory sensilla, initiating a regressive process of the CA. However, since neuroanatomical data from related species with tegminal stridulation species are not available, the degree of regression is unclear in this case. Notably, even lower numbers of CA sensilla are also found in meconematine species with ultrasonic calls by tegminal stridulation (12–14 sensilla, Table 1; F. Montealegre-Z, personal communication).

Influence of the communication system on the auditory system.—Depending on the communication system, different selective requirements can also differentially affect the auditory organs between the sexes. In Phaneropterinae, acoustic duets are most common (Heller et al. 2015), and the auditory behaviour has been studied in detail in the genus *Poecilimon* (Heller and von Helversen 1986, 1993, Heller 1990). The communication system in most species is bidirectional with male calls, and softer and short female replies (Heller and von Helversen 1986, Heller et al. 1997b, von Helversen et al. 2015). For the detection of the female replies, males should be selected for higher auditory sensitivity, morphologically reflected in larger spiracles to amplify the sound. In addition, males could benefit from summation of more sensilla to detect the soft and short female responses. In *Poecilimon*, the bidirectional communication system is also the evolutionary ancestral state for the group (see Heller 1990). However, in three distinct lineages the female reply was abolished (in the *P. ampliatus* group, the *P. propinquus* group, and in *P. jablanicensis* of the *P. ornatus* group), resulting in a secondary unidirectional communication system in which males should no longer be selected for higher auditory sensitivity. Testing for the possible correlation between the auditory system and the communication system showed the expected correlation of spiracle sizes with the communication system, with consistently larger spiracles in bidirectional signalling species. In addition, spiracles in males of these species are larger than in conspecific females, supporting the influence of sexual selection for higher male hearing sensitivity. Spiracle sizes in unidirectionally signalling species are smaller but show no sex-specific differences in spiracle size. The expected higher number of auditory sensilla was found in species with a bidirectional communication system (32–38 sensilla), with a strong relationship to body size (allome-

try, see also below). Notably, the sensillum numbers in *P. chopardi* (*P. propinquus* group) are only slightly lower (at 29 sensilla), while in species of the *P. ampliatus* group, they are ~30% lower than the correlation to body size would indicate (decreased to 17–21 sensilla) and with similar smaller spiracle sizes in both groups (Strauß et al. 2014). Thus, representatives in the groups with a secondary unidirectional signalling show evidence for an evolutionary regression in the auditory structures. These differences in *Poecilimon* auditory sensilla are the greatest variation between tettigoniid species from the same genus known so far, highlighting the evolutionary changes in the *Poecilimon* auditory system and the importance of sexual selection. It is uncertain why the degree of sensilla regression differs between members of the *P. ampliatus* and *propinquus* group. Further, it is difficult to identify the evolutionary starting point for the regression—if this started with the loss of the female reply reducing the selection for high sensitivity (larger spiracles) or if a reduced spiracle size led to a lower auditory sensitivity and the loss of female responses (Strauß et al. 2014). The evolutionary shift from bidirectional to unidirectional communication may depend on the mating success of females in relatively high population densities (*P. ampliatus*: von Helversen et al. 2012), the active distance between the mates, and the effective range of the acoustic signalling system (von Helversen et al. 2015). Here, the complexity of the acoustic environment is important as well, including the role of background noise (Römer and Bailey 1998), signal transmission (Römer 2016), and natural selection by predators that may maintain the hearing organs (Lehmann et al. 2007).

Does a correlation exist between carrier frequency of the communication signal and CA design?.—Tettigoniid tympanal organs are broadly tuned (Kalmring et al. 1990, Rössler and Kalmring 1994, Rössler et al. 1994). So far, a general correlation between spectral characteristics of the intraspecific signals and the number of auditory sensilla has been difficult to identify (Rössler et al. 2006): while the sensitivity of the auditory organ results from the summed activity of the CA sensilla and structures like the spiracles and bullae, similar tuning of receptors from different species or the absolute auditory sensitivity are not dependent on the overall number of CA sensilla (Rössler and Kalmring 1994, Scherberich et al. 2017). A change in carrier frequency of calls might affect the tuning of sensilla in the hearing organ, rather than the overall number of auditory sensilla. However, to detect extremely short female replies in duets, an increased number of auditory sensilla activated simultaneously could benefit the signal detection (see below for the auditory fovea).

Auditory sensilla with highly similar frequency tuning were found despite significant differences in the CA length and number of CA sensilla, both in related species (Kalmring et al. 1992) and also in more distantly related species (Kalmring et al. 1995b). Physiological data from some other species, however, showed specific hearing tuning for individual sensilla that adapt the frequency range to intraspecific call frequencies by broadening (*Neoconocephalus bivocatus*: Höbel and Schul 2007) or narrowing (*Ancylecha fenestrata*: Scherberich et al. 2016) the frequency response. The tonotopic organization of sensilla also contributes to intensity coding as stimuli at higher amplitudes activate both the sensilla tuned to the specific stimulus frequency together with sensilla tuned to other best frequencies that are also activated at increased amplitudes due to their broad tuning ranges (Römer et al. 1998, Hennig et al. 2004, Höbel and Schul 2007, Stumpner and Nowotny 2014). Whether such recruitment at higher amplitudes could affect the hearing organ to extend the set of auditory sensilla significantly is so far unclear.

Currently, the frequency representation over the CA is characterized only for a few species. The relative proportions of low vs. high frequency receptors differ along the CA, however, and are often adapted to the main frequency of calls by a relatively higher proportion of sensilla tuned to conspecific call frequencies (Kalmring et al. 1990, 1993, Rössler et al. 2006). This was shown by Current Source Density (CSD) analysis using a multiunit electrode system to record neuronal ensemble activities of sensory afferents in the auditory neuropile by their field potentials in relation to stimuli of different frequencies (Breckow et al. 1982, Rössler et al. 1990). However, this correlation so far provides no direct explanation for why a specific number of CA sensilla evolved in a given species. In *Neoconocephalus*, the number of CA sensilla from nine species was statistically negatively correlated to the species' call frequency (Strauß et al. 2017). Since this correlation was also found for the CA length and body size, it was assumed to indicate an allometric relationship (see below), because larger animals have larger stridulatory structures that produce calls in lower frequencies, and body size also influences the number of CA sensilla and CA length.

Frequency representation in an auditory fovea: The auditory fovea is an adaptation of frequency representation by highly similar tuning of multiple adjacent CA sensilla. In this case, frequency tuning is not linearly graded over the CA length. For the duetting phaneropterine *Ancylecha fenestrata*, a remarkable sexual dimorphism was shown where the ears of males contain 35% more auditory sensilla (median: 116) compared to females (86), and also a longer CA (Scherberich et al. 2016, 2017). Irrespective of the difference between sexes, this is the highest number of CA sensilla reported so far (Table 1). Physiologically, their CA shows an interrupted gradient in frequency tuning with a central region of 55 sensilla, where the change in characteristic frequency is less steep than at the proximal and distal CA ends. These sensilla in males are tuned to the dominant frequency of the female acoustic reply to male calls at about 10 kHz, and thus mediate the male phonotaxis. Females respond to male calls with a single, short sound of 42 ms duration (median; Scherberich et al. 2016). The auditory fovea can contribute to directional hearing of the very short and rare female response signals, as population coding from increased numbers of afferents improves the processing of temporal and intensity interaural differences at interneuron level to locate a sound source more reliably (Scherberich et al. 2017). The tuning of the auditory fovea also concurs in morphology with a CA region of similar organ height that does not follow the curvature of the CA surface (Scherberich et al. 2017). This organization is a sex-specific (male) adaptation relating to the specific duetting communication and indicates a strong sexual selection for detecting the signals of potential mates and shows most clearly an adaptive increase in auditory sensilla. Similar functional organizations with adjacent sensilla tuned to the same characteristic frequency are also found in CAs with less sensilla (< 30; Oldfield 1985, Montealegre-Z et al. 2012), but by far not as strong as in the case of *A. fenestrata*—this is the only case of a tettigoniid hearing organ with over 100 auditory sensilla known so far.

Adaptive significance for CA changes as a result of temporal call pattern.—The recognition of call patterns is carried out by the central nervous system, while the auditory sensilla code the temporal/syllable pattern (Schul and Rössler 1993, Pollack 1998). Hence, differences in call patterns are not expected to be a major influ-

ence on CA sensilla. One possible exception is the signal duration, which in cases of short acoustic signals would benefit from more sensilla that provide stronger input to the CNS (see the above discussion on the auditory fovea).

The North American genus *Neoconocephalus* is a study model for the evolutionary diversification of call patterns and their recognition mechanisms (Schul et al. 2014). Among tettigoniids, the male *Neoconocephalus* calls have notably narrow frequency bands with center frequencies mainly at 10–15 kHz (Schul and Patterson 2003). The ancestral call pattern in *Neoconocephalus* is characterized by continuous calls with single pulses at fast repetition rates (Schul et al. 2014). During the evolutionary radiation of the group, the call patterns diversified repeatedly into discontinuous calls, slow repetition rates, and/or double pulses (Schul et al. 2014). The evolutionary diversification is highlighted e.g., by the repeated evolution of double-pulsed calls (Schul et al. 2014, Frederick and Schul 2016). Studying the CA anatomy of nine species representing different taxonomic groups, life histories, call patterns, and call center frequencies, similar averages from 32–35 sensilla between the species were documented (Strauß et al. 2017). A similar number of 35 sensilla is found in the most closely related *Ruspolia* (*R. nitidula*, Schumacher 1979), suggesting that the ancestral *Neoconocephalus* already had a number of auditory sensilla in these ranges. The variation between *Neoconocephalus* species was influenced by the species specificity as well as body size (allometry), but not by phylogenetic relationships.

Statistical analysis for standardized effects of the call pattern also revealed correlations with CA sensillum numbers and CA length (Fig. 2). Male calls with slow pulse rates correlated with significantly more CA sensilla and longer CA (Fig. 2A), continuous calls with the increased number of CA sensilla (Fig. 2B), and double pulses with a longer CA (Fig. 2C). In the latter case, double pulsed calls also correlate with a higher number of sensilla, though the increase was not statistically significant. These correlations indicate a clear influence of sexual selection on the CA.

The findings are notable since the analysis of temporal call patterns is not carried out by the sensilla but in the central nervous system. The increased number of sensilla in species with slow-calling rates may be most easy to explain, as they could be an adaptation to shorter signals by providing a relatively stronger input to the CNS by additional sensilla. In addition, indirect effects of acoustic signalling on the CA are likely (Strauß et al. 2017). The correlation of discontinuous calls with lower sensillum numbers may depend on the behavioral ecology of signallers since discontinuously calling species have higher population densities (Greenfield 1990), which in turn may relax the selection on the auditory system. A continuously calling species (*N. affinis*) occurring in relatively high population densities (Greenfield 1983) also had relatively low CA sensilla (Strauß et al. 2017). Notably, not all evolutionary-derived call patterns in *Neoconocephalus* correlate to the increased number of CA sensilla (Fig. 2). While the differences in CA sensilla between *Neoconocephalus* species are small compared to those found in *Poecilimon*, the evolution of call patterns and call recognition mechanisms triggered the recent radiation of the group (Schul et al. 2014) and the hearing organs might diverge further in response.

Allometry.—Allometry refers to the relation of a structure to body size. It can highlight the influence of selection between body size and a morphological character under investigation, inferred from positive allometry and low morphological variation in the character (see also Bailey and Kamien 2001 for sound transmitting structures and Anichini et al. 2017 for stridulatory structures). Hence, a
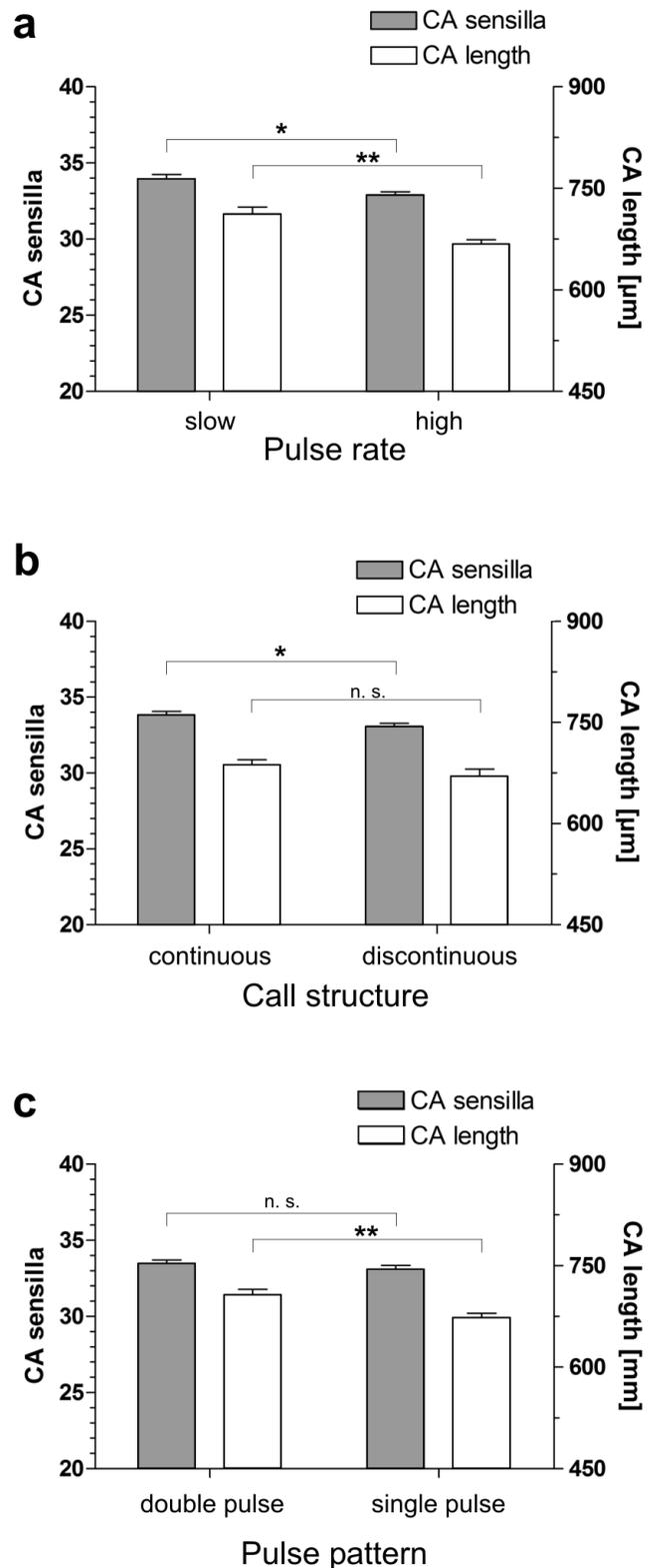

Fig. 2. Standardized effects of call patterns in *Neoconocephalus* on the number of CA sensilla and CA length for **A**. Pulse rate; **B**. Structure of continuous or discontinuous calls; and **C**. Pulse pattern. The evolutionary derived call characters are a slow pulse rate, discontinuous calls, and double pulses. Significance levels: * 0.05 > p > 0.01; ** 0.01 > p > 0.001. Adapted from Strauß et al. 2017, with permission from John Wiley and Sons.

larger body size would predict a longer CA and/or a higher number of auditory sensilla. Different features in the tettigoniid auditory system, like the spiracle and tracheal bulla size, were shown to be determined by allometry (Bailey 1998, Bailey and Kamien 2001). If larger individuals have larger spiracles they are more sensitive, that sensitivity can be determined by allometric relationships (*Requena verticalis*: Bailey 1998, but see also Römer et al. 2008 with a broader species sampling). The correlation of auditory sensillum numbers to body size was first suggested by Knetsch (1939), albeit with limited data from nine species and diverse genera. Closely related species were analyzed for *Poecilimon* (Strauß et al. 2014) and *Neoconocephalus* (Strauß et al. 2017) with a substantial influence of body size found on the CA for both groups, but evolutionary changes were also detected that affected the sensillum numbers more strongly: the reduction of acoustic signalling as well as adaptations to temporal call features such as the pulse rate, pulse pattern, and call structure can override the allometric relationship (see above). Allometry is thus one among several factors influencing the CA.

Different traits have been used as a measure for body size, such as the body length (Knetsch 1939), pronotum length (Bailey 1998, Bailey and Kamien 2001), hind femur length (Lehmann 1998, Bailey and Kamien 2001, Schul and Patterson 2003, Strauß et al. 2014, Anichini et al. 2017), or foreleg tibia length (Knetsch 1939). As shown for *R. verticalis*, hind femur and pronotum length are not isometrically related (Bailey and Kamien 2001), and the choice of anatomical parameter(s) to measure allometry is important.

Phylogenetic ancestral states.—Phylogenetic constraints result in a retained character state in successively evolving species. Constraints would set limits on the evolutionary changes in a character and counter the influence of selection pressures, retaining an ancestral situation. For the CA, the studies including outgroups found both cases were specific adaptations (*Neoconocephalus*: Strauß et al. 2017) and regressive changes (*Poecilimon*: Strauß et al. 2014) indicate the importance of sexual selection for elaborate CAs and argue against a phylogenetic constraint on sensillum numbers in these taxa. Certainly, further comparative studies including multiple species and outgroup species will give more insights on the adaptive significance of sensillum numbers.

A neuroanatomical feature that was discussed as a possible ancestral state are the distally concentrated sensilla in the CA of *Polysarcus denticauda*, leading to pairs or triplets of somata (Sickmann et al. 1997) and a loss of frequency resolution for frequencies above 20 kHz in these sensilla (Kalmring et al. 1996). Such a crowded organization of somata and dendrites was also found in several species of Phaneropterinae with thin tympana and a variable number of sensilla (Strauß et al. 2012), which makes an ancestral situation in *P. denticauda* less likely.

Relation to tympanum structure.—It has been noted that species with open tympana often have higher numbers of auditory sensilla (Lakes and Schikorski 1990). For example, *Mecopoda elongata* and *Polysarcus denticauda* have close to 50 CA sensilla and open tympana. *P. denticauda* is also exceptional as it has very thick tympana (Sickmann et al. 1997). *Supersonus* spp. have narrow asymmetric slits (Sarria-S et al. 2014) and exceptionally few CA sensilla with 12–14 (F. Montealegre-Z, personal communication). However, notable exceptions for this relationship between CA sensilla and tympanum morphology exist, as one of the species with the lowest known sensillum numbers has open tympana (*Phlugis* spp.) and the species with the highest known sensillum number (*Ancylecha fenestrata*) has a cover at the anterior tympanum. Specific evolu-

tionary scenarios for increasing or decreasing sensillum numbers obviously override a possible relation with the tympanum morphology in these cases.

Diversity of tettigoniid auditory organs and evolutionary causes

With respect to the number of CA sensilla, only a small fraction of the tettigoniid species has been studied so far. Neuroanatomical and physiological studies have revealed a diversity in the number of auditory sensilla among tettigoniid species that is species-specific. To characterize the auditory system of any species, the number of CA sensilla is an important parameter, together with tympanal and tracheal dimensions and the hearing threshold curve. So far, the tonotopic organization of the CA has been studied in even fewer species, and it remains to be analyzed how the changes in neuron numbers affect frequency representation and the accuracy of frequency discrimination (Rössler and Kalmring 1994). Obviously, the auditory system consists of successive levels of signal analysis in the central nervous system, and further processing in the auditory pathway may increase or decrease the relevance of specific cues for the receiver (e.g., Stumpner and Nowotny 2014).

While comparative studies indicate divergences in the number of CA sensilla between species, it is so far easier to explain such divergence in adding or reducing sensilla than to explain the functional requirements which determine a certain number of sensilla in a specific species. Such cases of divergence indicate the importance of multiple determinants. The elaborate auditory system of Tettigoniidae is formed by several selective forces: natural and sexual selection as well as allometry (Stumpner and von Helversen 2001, Robinson and Hall 2002, Strauß and Stumpner 2015), which makes it more difficult to analyze the contribution of specific influences. For a tympanal organ that is shaped by sexual and natural selection, it is somewhat difficult to determine the lower end of sensillum numbers since some species which show no regressive elements have numbers such as 24 sensilla (*Mygalopsis*, *Pholidoptera*) or 22 sensilla (*Requena verticalis*, *Nastonotus foreli*). *Poecilimon ampliatus* with 21 sensilla, compared to related species from the genus, shows evidence for regression both for the spiracles and the CA sensilla. This highlights the importance of a comparative approach covering several species. However, the strong influence of sexual selection even at the level of the CA sensilla can be detected for several model groups (Lehmann et al. 2007, Strauß et al. 2017).

Based on the currently available knowledge, some groups of tettigoniids are promising candidates for further studies of neuroanatomy and the functional morphology of the CA: For the large group of Pseudophyllinae with over 1000 species, important physiological experiments have shown ultrasonic call frequencies and directional hearing mediated by tympanal slits rather than sound input via the small spiracles (Mason et al. 1991), but the CA is so far only rarely studied (see *Nastonotus foreli*, Table 1).

A detailed analysis of the CA for such species with ultrasonic carrier frequencies of calls (Morris et al. 1994, Montealegre-Z et al. 2006) will be important to study the CA frequency representation. For the Australian *K. nartee*, which produces narrow ultrasonic calls, the number of sensilla is rather low at 18 CA sensilla (Gwynne and Bailey 1988, Bailey and Römer 1991). Remarkably, species calling at ultrasonic frequency ranges can have an even lower number of CA sensilla (*Supersonus*: 12–14 sensilla; F. Montealegre-Z, personal communication), inviting further investigations and functional comparisons.

Biomechanical analysis in *Onomarchus uninotatus* (Pseudo-phyllinae) showed fascinating adaptations for the two tympanal membranes with differential tympanal tuning (acoustic partitioning) of the anterior tympanum as a low-pass filter and the posterior tympanum as a high-pass filter (Rajaraman et al. 2013). The structure and mechanics of the CA and associated elements would be interesting for their organization in this case.

Further work on already researched groups will extend the understanding of evolutionary changes in the CA. For example, in the genus *Poecilimon*, the CA anatomy of relatively few species is known. Additional data are relevant from those species already studied with respect to auditory physiology (*P. laevis-simus*, *P. thessalicus*: Stumpner and Heller 1992), hearing organ embryology (*P. affinis*: Meier and Reichert 1990), or the acoustic communication system (unidirectional signalling in the *P. pro-pinquus* group, and further bidirectional species of the *P. ornatus* group and the unidicrectional *P. jablanicensis*: Chobanov and Heller 2010) to better understand auditory adaptations and diversification in the CA.

Finally, allometry in the CA is worth exploring in more detail, both within and between species. For tettigoniids, the influence of allometry on CA sensilla is not studied in detail for intraspecific variation, which would be interesting to address for different communication systems and the influence of selection. For studies on the auditory system of additional tettigoniid species, the question of what determines the number of auditory sensilla can guide the analysis of the hearing organ and can also be expected to give insights relevant to sensory evolution.

Acknowledgements

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