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OBITUARY

"The most beautiful profession in the world…" In memoriam Klaus Kalmring (1931–2015)

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Life and career

Klaus Kalmring was born as the eldest of three brothers in Erfurt, Thuringia. He attended high school in Erfurt, but due to the turmoil at the end of World War II, he had to leave school without graduation at age 14. His parents were farmers and gardeners. Most likely they nourished their son's interest in the natural world. Since his childhood, he also had a passion for geography and loved to spend hours studying maps and atlases. His talent was not overlooked, however, and he was accepted into the prestigious "Institut für Lehrerbildung" (teacher training) in Weimar (1951–1953). He passed the final examinations with excellent grades and could now be employed as a teacher for Russian language and Russian history. From 1953 to 1955 Klaus Kalmring taught both subjects in the central school in Unterpörlitz near Ilmenau, Thuringia, then in East Germany. In 1955 he relocated to Gelnhausen, then West Germany, to join his parents and worked as an assistant educator for youth in the children's sanatorium in Weilmünster/Taunus from July to December. He also enrolled again in a high school, the Goethe-Gymnasium in Frankfurt am Main, where he attended evening classes and graduated in 1959. Immediately thereafter he started his studies in geography, biology and chemistry at the Johann-Wolfgang-Goethe-University in Frankfurt am Main. It was during an excursion in 1963 that he first met his wife-to-be, Elke Bremm. Two years later they were married. To finance his studies, Klaus Kalmring took up a position as a teacher for biology and geography at a private high school in Königshofen/Taunus until 1966, when he cancelled his contract to focus on his studies (Fig. 1). The school's letter of reference explicitly acknowledges his extraordinary enthusiasm for his subject and for motivating and supporting the students—qualities, which he maintained throughout his life.

In 1969 Klaus Kalmring received his doctoral degree (Dr. phil. nat.) with a dissertation on the neurophysiology of muscles in cats, supervised by Prof. Rolf Hassler

On September 6, 2015, our dear colleague, teacher and mentor Klaus Kalmring, former professor of neurophysiology at Philipps-University in Marburg, Germany, passed away after a long illness at age 84. He is survived by his wife Elke and two sons, Stefan and Dirk, and their families.

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Fig. 1 Portrait of Klaus Kalmring from his "Studienbuch" at the Johann Wolfgang Goethe-University Frankfurt am Main, 1959

at the Max Planck Institute for Brain Research in Frankfurt am Main and supported by a research scholarship of the Max Planck Society. In 1969, Klaus Kalmring relocated to Bochum, where he joined the group of Prof. Johann Schwartzkopff, soon became junior (1971) and in 1976 senior assistant. He dedicated his years in Bochum to the study of the "Afferent auditory system in the ventral nerve cord in *Locusta migratoria*", for which he received his habilitation and *venia legendi* in 1975. In July 1978, Klaus Kalmring was appointed professor of neurophysiology at the Philipps-Universität Marburg. Here, he built a large and innovative team which included not only biologists, but also experts with different backgrounds like physics, who all brought their special expertise to the study of the auditory and vibratory sensory system of bush crickets. The vibrant atmosphere, the spirit of scientific curiosity and hard, but rewarding work were characteristics of the Kalmring lab and will be remembered fondly by all, who had the opportunity to visit (Fig. 2). Those were indeed many: students, doctoral students, post-docs, colleagues from all over the world, especially Slovenia, the United Kingdom, Russia, Australia, India and China. As a result of one of his collaborative efforts, Klaus Kalmring was appointed guest professor at Shandong Teachers University, China, in 1995 (Fig. 3).

Klaus Kalmring was both inspired by what he was doing and inspiring to others around him. His group was in fact like a family to him. He had extraordinary amounts of energy and a very good sense of humor. His good sense

Fig. 2 Always full of energy—Klaus Kalmring on a lab excursion to Bavaria (~1989)

of humor together with the high quality of his lectures and excellently organized courses attracted many students. He loved going out into the field, collecting bush crickets on sometimes long road trips to Southern Germany, Slovenia, Austria, France and Spain, for which he recruited students and family alike. These trips were always combined with visits to geological and/or cultural points of interest. Klaus Kalmring enjoyed lively discussions, even—or particularly—when they were controversial and was not afraid to speak out against authorities and influential colleagues, even if it meant risk.

He was aware that he had been lucky in his life, and he was happy to share and to support others, regardless of whether they were able to return his favors. He expected others to work hard when striving for knowledge and lived up to these postulates himself. Besides administrative work and teaching, he always found time for doing electrophysiological experiments himself until his retirement. All these attributes gained him the respect of students and colleagues. He used to claim that he had "the most beautiful profession in the world", a unique opportunity to live his greatest passions: research and teaching.

Fig. 3 Klaus Kalmring with colleagues from Shandong Teachers University, China, 1995. All photographs are the private property of E. Bremm-Kalmring, Marburg

Klaus Kalmring was saddened when he came up for mandatory retirement in 1996, and thereafter dedicated his energy to voluntary work on the board of a home for the elderly, and to his interest in architecture. He will be remembered as an excellent scientist and dedicated teacher and also as an extraordinary human being with a very broad knowledge. He touched the lives of many, and in many ways. The scientific life and career of Klaus Kalmring were honored during the 1st Symposium on Biotremology in San Michele, Italy, September 5–7, 2016.

Scientific legacy

Klaus Kalmring became attracted to the processing of auditory information by different Orthopteran species as simple invertebrate examples for intraspecific auditory communication. He favored invertebrate species over mammalian species because of their relative simplicity for a physiological approach and for ethical reasons. The most important aspect of his group's research work was its integrative character, ranging from bioacoustics, electrophysiology, and neuroanatomy to behavior and ecology and including the application of a large spectrum of methods. One particular achievement was the development of equipment like precision amplifiers, apparatus needed for digital recording and playback techniques as well as versatile software with the support of highly motivated physicists. This development of technology was instrumental for many studies involving highly resolved sound recording, signal manipulation, single cell recording and others. Back then many of these techniques still were in an experimental stage, like the use of glass microelectrodes for single cell recordings, multi-unit recordings, the use of tracers for cell labeling or simply the use of computers.

To find out functional commonalities as well as species-specific adaptations for the reception and recognition of conspecific signals, Klaus Kalmring turned to *comparative neuroethological studies* of auditory/vibratory information processing in a wide range of Orthopteran species, especially in Tettigoniidae. He was among the first to describe the *convergence of auditory and vibratory information* in ventral nerve cord interneurons of acridids and tettigoniids (Čokl et al. 1977; Kalmring and Kühne 1980). His investigations on the *tonotopic organization of receptor cells and afferent projections* in the ventral cord of locusts and bush crickets (e.g., Kalmring et al. 1993) are still the basis for today's research on transduction mechanisms. He measured the tuning curves of individual auditory receptors in combination with the application of tracing techniques to establish the auditory threshold curves that are commonly tuned to conspecific song frequency parameters. Thereby, he identified a species-specific range of relatively low numbers of auditory receptors (~23 up to 50 *scolopidial cells* in the *crista acoustica* close to the tympanum) in tettigoniids (see Table 1), yet broad-banded hearing up to the ultrasonic range (>40 kHz). Morphological and physiological investigations on non-auditory but homologous organs complemented the investigations in Ensifera (Jeram et al. 1995). All these data are still important for concepts and hypotheses developed in regard to the evolution of auditory sense organs in insects. In addition, amplification functions of the acoustic trachea were identified and shown to enhance the sensitivity in the low frequency range as evolutionary adaptations in some species. Physiological and anatomical investigations revealed neuronal plasticity in the auditory system of insects, which was not self-evident by that time (Lakes et al. 1990). Studies on the *elytral sound production* identified a broad song spectrum range up to the ultrasonic range (Keuper et al. 1988). High temporal resolution of song features revealed individual sound impulses when the *plectrum* strikes along the teeth of the file (*pars stridens*) of the wings during sound production and age-related wear lowers this tooth impact rate (Stiedl et al. 1991). Thereby, the concept of *synchronized activity of ensemble populations of neurons* for parallel stimulus processing (that could

Table 1 Taxonomy and systematics of the Orthoptera species studied by Klaus Kalmring and his group and the main results of their experiments on auditory signals (A), behavior (B), ecology (E), morphology (M), neuroanatomy (N) and electrophysiology (P)

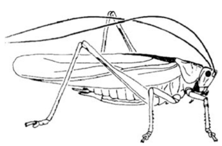
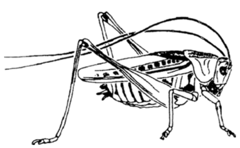
Family	Subfamily	Tribe	Species	Highlights of results in specific scientific fields	References
Suborder Caelifera					
Acrididae (MacLeay, 1821)	Oedipodinae (Walker, 1871)		*Locusta migratoria* (Linné, 1758)	P: Bimodal suboesophageal and higher order ventral cord neurons processing simultaneously sensory input from auditory and vibratory receptor neurons; modulation of responses by different parameters of signals of both modalities; acoustic neurons in the suboesophagial ganglion and ventral nerve cord; auditory–vibratory convergence in large ventral cord neurons with vibration frequency-specific modulation	[4, 5, 7, 9–14, 16, 17, 19, 20, 23, 25–27, 31, 32, 35, 38, 39, 41, 49, 55, 57, 61, 75]
	Cyrtacanthacridinae (Kirby, 1910)		*Schistocerca gregaria* (Forskål, 1775)	P, N: Comparison of vibratory receptor neurons, their central projections and physiology in larvae and adults; comparative physiology of bimodal auditory–vibratory interneurons with tettigoniids and locusts	[38, 39, 41, 49, 75]
Suborder Ensifera					
Gryllidae (Laicharting, 1781)			*Gryllus (Gryllus) bimaculatus* (De Geer, 1773)	M: Projections of high (HF) and low frequency (LF) ventral cord interneurons in the supraesophageal ganglion; P: Characterization of two LF and two HF neuron types	[15]
Tettigoniidae (Krauss, 1902)	Tettigoniinae (Krauss, 1902)	Tettigoniini (Krauss, 1902)	*Tettigonia viridissima* (Linné, 1758)	A: Song consists of a continuous series of syllables; B: Effect of song parameters for female preference: syllable pattern is decisive for female species discrimination; N: ~37 scolopidia in the crista acustica; P: Acoustic neurons in the ventral nerve cord; most sensitive auditory range is 6–25 kHz	[6, 42, 43, 50, 67, 72, 81]
			*Tettigonia cantans* (Fuessly, 1775)	A: Song consists of a continuous series of syllables; B: Role of song production for dispersal; N: ~36 scolopidia in the crista acustica; P: Co-processing of auditory–vibratory information in ventral cord interneurons	[22, 25, 30, 35, 36, 39, 42, 43, 50, 67, 72, 84]
		Decticini (Herman, 1874)	*Decticus albifrons* (Fabricius, 1775)	A: Song consists of repetitions of a single syllable; N: ~34 scolopidia in the crista acustica; P: Co-processing of auditory–vibratory information in ventral cord interneurons; most sensitive auditory range is 6–25 kHz	[6, 39, 42, 43, 50, 56, 58–60, 67, 69]
			Decticus verrucivorus (Linné, 1758)	A: Song consists of groups of syllables; E: Habitat distribution reflects oviposition sites in larvae, adult male distribution biased by male acoustic interaction; N: ~33 scolopidia in the crista acustica; P: Characterization of auditory receptors and ventral cord interneurons; co-processing of auditory–vibratory information in ventral cord interneurons; E: High mobility of singing males in the habitat to increase mating success (female phonotaxis)	[8, 9, 18, 21, 24, 25, 36, 39–43, 46–48, 50, 51, 56, 58–60, 67, 69]
		Pholidopterini (Beier, 1954)	*Eupholidoptera chabrieri* (Charpentier, 1825)	P: Characterization of acoustic neurons in the ventral nerve cord	[6]

Table 1 continued

Suborder Ensifera				
		Pholidoptera littoralis (Fieber, 1853)	P: Co-processing of vibratory and auditory information in the ventral cord system and comparison with different tettigoniid and locust species	[39]
		Pholidoptera griseoaptera (De Geer, 1773)	M: Protected very thin (min 0.7 µm) tympana in forelegs; N: ~24 scolopidia in the crista acustica; P: Most sensitive auditory range 6–25 kHz	[69, 70]
	Gampsocleidini (Brunner von Wattenwyl, 1893)	*Gampsocleis gratiosa* (Brunner von Wattenwyl, 1862)	A: Low frequency component of conspecific sound; 'passive' filtered amplification of the frequency of airborne sound by subalar airpocket. N: ~33 scolopidia in the crista acustica; adaptations in auditory and vibratory receptor organs; P: Increased low frequent auditory sensitivity due to amplification properties of the acoustic trachea as adaptation	[63–65, 68, 73, 82]
	Platycleidini (Brunner von Wattenwyl, 1893)	*Platycleis albopunctata* (Goeze, 1778)	A: Variable (increased) impulse repetition rate within a syllable from the first to the forth syllable	[67]
		Psorodonotus illyricus (Ebner, 1923)	N: Comparative neuroanatomy of the auditory-vibratory receptor organs. P: Comparative physiology of low frequency sound processing; E: High mobility of singing males in the habitat to increase mating success (female phonotaxis)	[40, 42, 43, 50, 56–60, 66, 67]
Bradyporinae (Burmeister, 1838)		*Ephippiger* (spec.)	P: Acoustic neurons in the ventral nerve cord	[6]
		*Ephippiger discoidalis* (Fieber, 1853)	A, M: Comparative study of sound production and emission; correlation of song parameters of bush cricket with wing morphology	[42, 43]
		Ephippiger ephippiger (Fiebig, 1784)	A: High frequency (10–30 kHz) calling song generally composed of two syllables; M: Age-related wear of the files' teeth on the wings lowering the tooth impact rate within syllables; B: Female discrimination of syllables with tooth impact rates below the temporal resolution of single receptor cells; female phonotaxis influenced by vibratory signals (tremulation) on bushes; N: ~25 scolopidia in the crista acustica, E: Female preference for song of 'young' males	[42, 43, 45–47, 50, 51, 54, 67, 84]
		Ephippiger perforatus (Rossius, 1790)	A: Calling song consists of groups of syllables with the main sound emitted during the closing movement of wings	[67]

Table 1 continued

Suborder Ensifera				
		Sabaterpia taeniata [before *Ephippigerida taeniata*] (Saussure, 1898)	A: Calling song consists of a single syllable of high-frequent sound with the predominant energy produced during the closing movement of wings by males; B: Temperature-dependent syllable alternation rate to a simulated male ranges from 0.2 to 1.2 Hz, from 19 to 35 °C, respectively	[71]
	Conocephalinae (Burmeister, 1838)	*Mygalopsis marki* (Bailey, 1980)	A: Sound transmission in acoustic tracheae. N: ~23 scolopidia in the crista acustica; comparative neuroanatomy of auditory receptor organs. P: Multi-unit recording of temporal processing via synchronization of parallel receptor activation	[46, 47, 50, 65, 67, 73, 81]
		Ruspolia nitidula (Scopoli, 1786)	A: 'Active' filtered amplification of the frequency of airborne sound by subalar airpocket	[82]
	Phaneropterinae (Burmeister, 1838)	*Polysarcus denticauda* (Charpentier, 1825)	A: Complex song with 10–20 kHz main frequency range; M: Unprotected very thick tympani (anterior: 10–15 µm, the posterior 20–25 µm) in forelegs; N: ~49 scolopidia (concentrated distally) in the crista acustica; P: High auditory sensitivity from 3 to 20 kHz; ventral cord interneurons responding to sound, vibration or both as in other bush cricket species	[77, 78, 80, 81]
		Leptophyes punctatissima (Bosc, 1792)	M: Unprotected thick (min 3 µm) tympana in forelegs; N: ~28 scolopidia (concentrated distally) in the crista acustica; P: dimensions of spiracles, acoustic trachea and tympana determine the sensitivity, arrangement of scolopidia and dimensions of structures in the crista acustica affect the frequency tuning of the auditory threshold	[70]
Rhaphidophoridae (Walker, 1869)		*Troglophilus* (*Paratroglophilus*) *neglectus* (Krauss, 1879)	N: Neuroanatomy of atympanate tibial organs in the legs; P: Atympanate tibial organs with 11 functional receptor types (higher sensitivity to substrate- than to airborne sound at 200–2000 Hz)	[74, 76]

The numbers of the references refer to the publication list provided as supplementary material. Source of taxonomic information: Eades DC, Otte D, Cigliano MM, Braun H (retrieved September 16, 2016) Orthoptera species file. Version 5.0/5.0. Drawings by Alfred Mücke not be explained by single response properties) emerged (Rössler et al. 1990, 2006). Female bush crickets demonstrated behavioral (*phonotactic*) discrimination between songs composed of song syllables with different sound impulse rates (Stiedl et al. 1991). These naturally occurring differences in sound impulse rates within syllables were not reflected in the temporal action potential discharge patterns of individual auditory receptor neurons, but they resulted in distinct patterns of synchronization in the ensemble activities of auditory receptor neurons. This discovery was made years before the concept of *synchronized activation* was described and globally accepted in olfactory information processing. Behavioral (*phono- and vibrotactic*) experiments addressed the importance of *auditory and vibratory communication* signals as an important basis for the survival of species for mate localization (Stiedl and Kalmring 1989). Finally, ecological studies on the distribution patterns of individuals in the habitat suggested that oviposition sites influence larval distribution, whereas adult males show clumped distribution due to auditory interaction. Main research findings from different Orthopteran species are highlighted in Table 1.

The bibliography of Klaus Kalmring lists 85 publications in total (see supplementary information) from 1967 to 2006. However, the output of his group is even larger, because he did not insist on honorary authorships as head of the group. The publication of the book *Acoustic and Vibrational Communication in Insects*, co-edited with Norbert Elsner in 1985 and based on two symposia held at the 17th International Congress of Entomology in Hamburg, is a milestone in the developing field of what we now call ‘biotremology’. The comprehensive analysis of the “auditory–vibratory sensory system” in bush crickets (reviewed by Rössler et al. 2006) is Klaus Kalmring’s scientific legacy.

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