



## Lehr's fields of campaniform sensilla in beetles (Coleoptera): Functional morphology. I. General part and allometry



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### ABSTRACT

In this first of three articles we show the construction of the articular part of the elytron, the root. The root bears a conspicuous field of campaniform sensilla. This field was studied using light and scanning electron microscopes. The diversity of shape of the field among beetles, types of orientation of elongated sensilla within the field, individual variability of their number among conspecifics are demonstrated. Elongated sensilla point to the junction of the elytron with the second axillary plate. Presumably, they monitor twist movement in this junction, which is possible if the elytron is open. The goal of the whole project is to reveal the effect of both structure and function of the hind wings and elytra on the morphology of this mechanosensory field. Our data on allometric relationships between the animal size and quantitative characteristics of the field in normally flying beetles provide an important background for further functional analysis of this sensory organ.

We selected 14 series of several species belonging to the same taxon but differing in size from big to small. It is revealed that the area of the sensory field is directly proportional to the elytral area, whereas the number of sensilla is proportional to the square root of the elytral area. Despite the great range in the elytral area (1500 times) in series of selected species the area of an external pit or cap of a single sensillum varies only 25-fold. The density of sensilla per unit area of the sensory field increases with decrease of the elytral area.

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### 1. Introduction

A campaniform sensillum (CFS) is an elementary mechanosensory organ in the insect integument. It consists of a neuron and three accessory cells two of which penetrate the thick integument all the way through. The channel tapers toward the external face. The channel profile resembles a bell outline, the reason for the sensillum name. A process of one accessory cell, reaching the external surface, produces a flat cuticular cap. In turn, the external face of the integument around the cap is indented as a pit: round or elongated. The morphology of CFS in beetles was described by Lehr (1914) and by Pfau and Honomichl (1979).

Deformation of the cap, caused by strain in the integument, is transmitted to the dendrite of the neuron. A sensillum with an elongated pit is selectively sensitive to strain directed transversely to the long axis of the pit (Hößl et al., 2007). CFS are solitary or gather in sensory fields on various body parts (Hochreuter, 1912; Gnatzy et al., 1987). Fields of CFS are present on wing veins in various studied insects, some fields account for hundreds of CFS (Pringle, 1957). Hind wings in beetles also bear such fields (Lehr, 1914; Pfau and Honomichl, 1979). The latter authors supposed that fields on veins follow the sequence of the wing base twist and monitor temporal points of strain during pronation–supination in the hind wing.

A century ago, Richard Lehr (1914) described a field of CFS on the articular process of an elytron (the root) in the diving beetle, *Dytiscus marginalis*, and studied the histology of CFS. This field is referred to here as Lehr's field. Two years earlier, it was observed and depicted in a draft by Hochreuter (1912). Both articles contribute to treatises on anatomy and ontogenesis in *D. marginalis*

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### Nomenclature

$A_e$	area of the elytron
$A_f$	area of the sensory field
$A_s$	area of the sensillum
2Ax	second axillary plate
CFS	campaniform sensillum
e2	elytral process of 2Ax
ELM	epi-illuminated light microscopy
$f$	filling of the sensory field with sensilla
$L$	length of the elytron
LA	lateral apophyse of the elytral root
$L_s$	length of the campaniform sensillum
$m$	mass of the elytron
MA	medial apophyse of the root of the elytron
$N$	number of sensilla in the field
rd	internal ridge in the root
SEM	scanning electron microscopy
TLM	transmitting light microscopy
VA	ventral apophysis of the root of the elytron
$W$	width of the elytron
$\rho$	mean vector

(Korschelt, 1923), a part of a program on comparative morphology of the most common plants and animals, launched in several German universities. The First World War cut these studies short. Since Lehr, the elytral sensory field has not been inspected in any other beetle.

Forewings in beetles are transformed into hard plates which protect hind wings hidden under them during movement through hard or granular substrates. Prior to flight, a beetle opens its elytra and releases the hind wings. Opening-closing is the sole active movement of the elytra. The acquisition of elytra provided the enormous thrive of beetles: Coleoptera are the largest insect order of great diversity (Hammond, 1985). Many of beetles cope with the trade of their body resource investments: into ability to distant flight (with the aid of powerful wing muscles) or into enhanced reproduction in a favorable habitat at the cost of underdevelopment or extinction of the flight muscles, wings, and skeleton structures supporting these muscles. The loss of flight ability is a common phenomenon among beetles which affects the mobility of the elytra as well. One can find cases of restricted mobility of the elytra even among flying beetles, reduction of elytral size or loss of linkage between closed elytra. Numerous references concerning these topics are quoted in two following articles.

This study is the first attempt to show structural characters of the sensory organ at the elytral articulation, to deduce the function of Lehr's field from its structure, and to find possible correlations between the morphology of the sensory field at the forewing base and structural and functional properties of both wing pairs. As the amount of data was rather large, we divided our results into three parts. They share similar methods but differ in questions asked and in author teams.

The first article describes the general construction of the elytral articulation, the position of the sensory field, the arrangement of sensilla, and the allometric relationships between quantitative characteristics of the Lehr's field and the size of the elytron in flying beetles. The possible functional significance of the CFS field is discussed. The size of surveyed species spanned from the giant rhinoceros beetle *Megasoma elephas* (body length of the hornless female over 70 mm) to dwarfs, such as the lady bird *Stethorus punctillum*, staphylinid *Eusphalerium alpinum*, weevil *Sitophilus*

*oryzae* (1–2 mm) and, lastly, one of the smallest insects, the featherwing beetle *Primorskiella anodonta* (0.5 mm). For this study we selected beetles representing some narrow taxonomic groups (family, subfamily or tribe). This provided a background for analyzing the impact of functional restrictions of both hind and fore wings on the elytral sensory field.

The next two articles are dedicated to the analysis of the impact of the hind wing reduction occurring independently among many coleopteran families; on the other hand, we have studied the effect of restricted elytral mobility, brachyelytry or stenoelytry in particular flying beetles. However, we did not consider the following problems: (1) application of our observations for taxonomy or phylogeny; (2) effect of wing polymorphism on the variability of Lehr's field within the same species; (3) internal structure of CFS; (4) electrophysiology of CFS.

## 2. Materials and methods

### 2.1. Insects

Different methods of preservation do not disturb hard cuticular structures and visibility of CFS. Therefore, we used dry specimens from collections, alcohol-fixed or freshly frozen and thawed specimens.

Specimens originated from our own field samples, as well as from comparative collections of the Department of Ethology and Social Biology of Insects (Schmalhausen Institute of Zoology, Kiev, Ukraine), Department of Functional Morphology and Biomechanics (Christian-Albrechts-University, Kiel, Germany), Institute of Biology of South Seas (Odessa, Ukraine) and Chairs of Zoology in the National Shevchenko-University and National Dragomanov-Pedagogical University (both in Kiev), fundamental collection of the Schmalhausen Institute of Zoology (Kiev), Zoological Institute (St.-Petersburg, Russia), State Museum of Natural History (Lviv, Ukraine), Australian National Museum (Canberra, Australia).

The taxonomic rank or specific names of some beetles studied by us may be disputed. The list of investigated species with full scientific names is attached in the Supplementary materials as Table S1. Synonyms are quoted in some cases. The order of families is given according to Lawrence et al. (2011). We also refer to relevant monographs treating particular families. We hope that readers in spite of rapidly changing taxonomy will recognize the organisms reported in this study.

### 2.2. Dissection and preparation

Dry specimens were placed in water for 1–2 h, the prothorax was cut off, elytra parted and carefully excised together with axillary plates. If necessary, hind wings were excised as well.

Elytra and wings were photographed using a photcamera Canon EOS 550D (Canon Inc., Tokyo, Japan) either with a macrolens or attached to a stereomicroscope MBS-9 or light microscope MBI-3 (both: Soviet Union).

Pieces of elytra containing the root were excised in a drop of distilled water with a sliver of a razor blade. The dust was removed with a fine brush in a drop of ethyl alcohol. Some pieces were processed in an ultrasonic bath Bandelin Sonorex RK 52 (Bandelin Electronic GmbH, Berlin, Germany). However, the cleanest whole mounts were obtained from specimens macerated in 10% KOH. They were placed on specimen mounts for epi-illuminated light microscopy (ELM) or for scanning electron microscopy (SEM). In the latter case they were coated with gold–palladium (thickness 10 nm).

Specimens for transmission light microscopy (TLM) were macerated in 10% KOH until they became soft. They were then

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