Bulletin of Insectology **77** *(1): 113-118, 2024*
ISSN 1721-8861 eISSN 2283-0332

A membrane between chordotonal organs in the subgenual organ complex of the stick insect *Peruphasma schultei*

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Abstract

The subgenual organ complex in stick insects (Phasmatodea) consists of two mechanosensory chordotonal organs, the subgenual organ and distal organ, both located in the haemolymph channel in the tibia of the stick insects. The subgenual organ is a highly sensitive receptor organ for substrate vibrations, which are transferred in the haemolymph channel, while the distal organ has not yet been studied in detail physiologically. The neuroanatomy of the subgenual organ complex is unique to stick insects. A membrane between both organs occurs in different Phasmatodea - *Carausius morosus* (Sinety), *Sipyloidea sipylus* (Westwood) and *Oreophoetes peruana* (Saussure). Between the two sensory organs, the thin membrane is placed horizontally in the tibia. The present study investigates the species *Peruphasma schultei* (Conle et Hennemann) (Phasmatodea: Pseudophasmatidae: Pseudophasmatinae) from South America (Peru) as a representative of Pseudophasmatinae, a prominent group of neotropical stick insects, for the functional morphology of the chordotonal organs. The aim is to provide insights on the sensory complex from an additional stick insect species and on the similarity of the functional morphology. The present work revealed that in *P. schultei* the fine membrane occurs in both female and male individuals and in all leg pairs. The membrane was absent in a few leg preparations analysed, in which there was either a close contact or a gap between the subgenual organ and the distal organ. The presence of a membrane connection hints at a coupling between the sensory organs which is presumably also relevant for the mechanosensory functions, indicating that the distal organ may also respond to substrate vibrations.

Key words: functional morphology, mechanoreception, biotremology, sensory organ, biomechanics, distal organ.

Introduction

Mechanoreception in insects involves specialised sensilla of different types, and the mechanical coupling of these sensilla to other body elements is an important element to detect mechanical forces acting on the insect body (French, 1988). This mechanical coupling involves morphological structures linking the sites of energy uptake from the mechanical stimulus to the sensory neurons in sensilla, and leads to some deformation acting on the membranes of sensory neurons (French, 1988; Strauß and Stritih-Peljhan, 2022). Chordotonal organs are internal mechanoreceptors in insects and crustaceans, and consist of scolopidial sensilla (Howse, 1968; Field, 2005; French, 2008). The chordotonal organs detect different types of mechanical stimuli including body movements, substrate vibrations, or airborne sound, depending on the association with surrounding anatomical structures. As chordotonal organs are important in detecting both substrate vibrations and airborne sound (Hutchings and Lewis, 1983; Kalmring *et al.*, 1994; Yack, 2004; Nation, 2008), their structural coupling determines the specific stimuli which are most effective on a sensory organ. Their functional morphologies can be complex, and include further levels of organisation, such as the coupling to different elements of the body or the connection between sensory organs (French, 2008; Strauß *et al.*, 2024). Chordotonal organs include the subgenual organ (SGO) in the proximal tibia of insects, as well as associated organs forming the subgenual organ complex (SGOC) in Polyneoptera (Strauß *et al.*, 2021a). The chordotonal organs in the leg are well placed to detect vibrations transmitted in the substrate and taken up by the legs. However, SGOs in different insect taxa show different neuroanatomical organisations and also different types of attachments (Autrum and Schneider, 1948; Lakes-Harlan and Strauß, 2014; Strauß *et al.*, 2021a). In orthopteroid insects including stick insects, the SGO spans the tibia (Rössler, 1992; Shaw, 1994; Eberhard *et al.*, 2010; Strauß *et al.*, 2021b; Sansom *et al.*, 2022). It responds to vibrations transferred from the substrate through the tibia by haemolymph movements (Kilpinen and Storm, 1997). The presence of additional chordotonal organs in the SGOC of some taxa raises the question for the physiological adaptations and differences in the input pathways of the different organs (Strauß, 2017; Strauß and Stritih-Peljhan, 2022). The complexity of the mechanoreceptor system is also based on different structures to which they are linked.

In stick insects (Phasmatodea), the SGOC consists of two chordotonal organs, the SGO and the distal organ (DO) present in all leg pairs (Strauß and Lakes-Harlan, 2017; Strauß *et al.*, 2021b). So far, the vibrational behaviour and possible intraspecific communication in Phasmatodea is rarely investigated, but the SGO common in insects could be involved in predator detection (Strauß *et al.*, 2021b). These organs are structurally linked by a fine membrane found in certain species, and the SGO shows a characteristic extension in the distal direction forming the origin of the membrane. The thin membrane is shaped like a broad sail spanning the tibia horizontally, between the anterior and the posterior side (Strauß *et al.*, 2021b; Strauß, 2022). The functional role of this connection is so far not established (Strauß, 2022). Here, the connection between both organs is documented in *Peruphasma schultei* (Conle et Hennemann). This species belongs to one of the most prominent group of neotropical stick insect, the Pseudophasmatinae (Phasmatodea Pseudophasmatidae) (Brock *et al*., 2024), with ca. 300 species described (Bradler and Buckley, 2018). Pseudophasmatinae are phylogenetically placed in the New World stick insects (Occidophasmata) (Simon *et al*., 2019; see also Tihelka *et al*., 2020). So far, only a few species of Occidophasmata have been investigated for (neuro-) physiological adaptations such as *Oreophoetes peruana* (Saussure) (Strauß, 2023a). *P. schultei* was analysed for the morphology and physiology of the digestive systems (Shelomi and Kimsey, 2013; Shelomi *et al*., 2014; 2015; Shelomi, 2022), cuticle structure (Maurer *et al*., 2017), tarsal attachment structures (Büscher *et al*., 2018), and the chemical defence glands (Dossey *et al*., 2006; McLeod *et al*., 2007; van de Kamp *et al*., 2015; Stolz *et al*., 2015; 2018). Recently, the innervation of the SGOC in *P. schultei* was studied, revealing a neuroanatomy similar to other stick insects (Strauß, 2023b; compare Strauß *et al*., 2021b; Strauß, 2023a). Here, the functional morphology of the sensory organs is analysed further for the presence of the connection between sensory organs. The aim of the present study is to broaden the range of stick insect species investigated for the functional morphology of the SGOC, and to provide data on the occurrence of the membrane between the sensory organs.

Materials and methods

Insects

This study investigated *P. schultei*. The species is described from the Cordillera del Condor in northern Peru, where it is found in a small area with dwarf forest (Conle and Hennemann, 2005). The insects (figure 1a) were obtained from a crowded laboratory culture at the Institute for Animal Physiology, Justus Liebig University Gießen. Females and males were reared under 12:12 light-dark conditions at temperatures between 21-23 °C. They were fed with leaves of *Ligustrum vulgare*, a plant they readily accept as food (Conle and Hennemann, 2005), and were sprayed on a daily basis with water (Stolz *et al*., 2015). For the experiments reported here, adult of both sexes were analysed.

The experiments reported here comply with the principles of animal care of the Justus-Liebig-Universitat Gießen and with the current law of the Federal Republic of Germany.

Neuroanatomy and morphology

The legs were processed for neuroanatomical studies with axonal tracing using 5% cobalt solution (Strauß, 2023b). They were treated as described previously for this method for intracellular staining (Strauß and Lakes-Harlan, 2013; Strauß *et al*., 2021b). Legs were incubated and cleared in methyl salicylate (Merck, Darmstadt, Germany), and the dark cuticle (Conle and Hennemann, 2005) was removed with a piece of blade and forceps prior to microscopy. The stained neuronal tissue and surrounding tissues were analysed by light microscopy (see below). Generally, the membrane is visible in lateral view of the leg / sensory complex. A specific staining of the membrane is so far not established. Overall, 36 legs were analysed here, with 6 preparations for each leg and from each sex. The 6 legs from one thoracic segment were always obtained from different insects, and legs from 9 female and 8 male were investigated. This histological analysis was used to obtain a larger sample size to determine the proportions of preparations with or without a membrane.

Statistical analysis

Statistics was analysed in Prism 4 (GraphPad, San Diego, CA). The proportions of leg preparations found with or without the membrane between the sensory organs was compared between *P. schultei* and data from *O. peruana* published before (Strauß, 2022) by using the two-sided Fisher's Exact test.

Microscopy and documentation

Preparations were mounted in methyl salicylate and viewed with a microscope (Olympus BH-2 microscope; Olympus, Shinjuku, Japan). Documentation was by photography with a Leica DFC 7000 T camera (1920 × 1440 pixel) attached to the microscope via the Leica Application Software V4.9 (Leica Microsystems CMS GmbH, Wetzlar, Germany). Stacked photographs were generated from series of photographs using CombineZP. Figure panels were arranged in CorelDraw 11 (Corel, Ottawa, Canada). In addition, a schematic of the sensory organs was drawn on a Leitz microscope with a drawing attachment (Leitz, Wetzlar, Germany), and the neuronal structures were redrawn digitally using CorelDraw 11.

Results

Connection of chordotonal organs in the subgenual organ complex

In *P. schultei*, the SGOC contained the SGO and the DO (figure 1c-d). The SGO has dendrites of the sensory neurons extending distally, which insert into a tissue formed from accessory cells (figure 1c-d). This SGO tissue showed an extension towards the DO on the ventral side (figure 1d-f). A thin membrane occurred linking the SGO and DO (figure 1d, 1d_i), and this membrane was observed in all leg pairs (figure 1d-f). Neuronal structures (nerves, cell bodies and dendrites) in the sensory organs were stained by the axonal tracing (see figure 1c-d). However, no direct connection was observed for the neuronal structures in the two organs to the membrane, like a possible insertion of dendrites into the membrane (figure 1d_i-f).

Variability of the membrane structure and lack of the connection

Limited variation occurred in the morphology of the connection between organs: in one preparation of 36, there were two strands rather than one visible between the SGO and the DO surface (figure 2a). In one further preparation, the membrane contacted a strand of connective tissue and not the DO surface (figure 2d). Further, in few preparations, the membrane was completely lacking: one preparation showed a close contact between the chor-

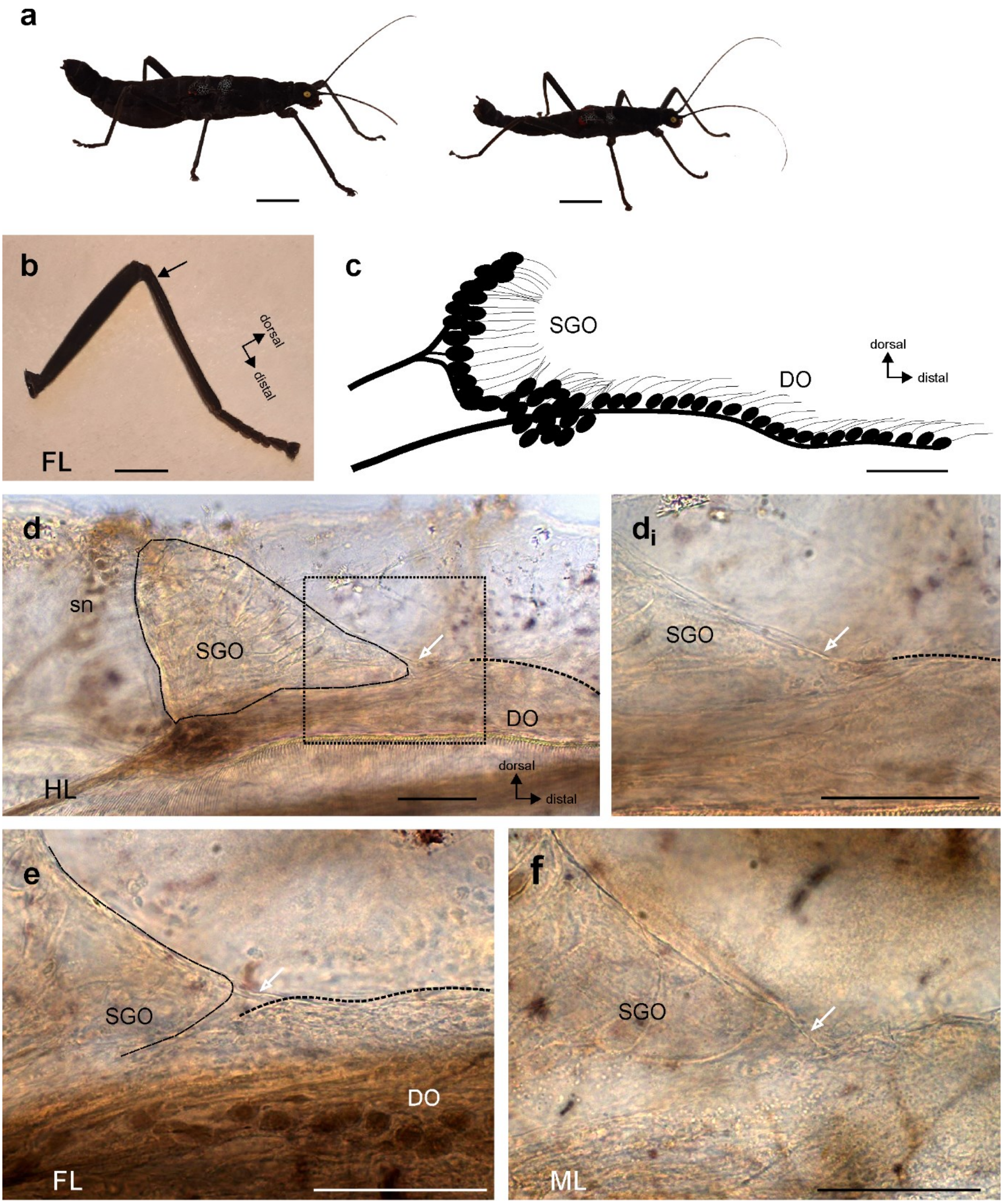

Figure 1. The subgenual organ complex in *Peruphasma schultei*. **(a)** *P. schultei*, adult female (left) and adult male (right). **(b)** Foreleg of *P. schultei*, viewed from anterior. The arrow indicates the position of the subgenual organ complex in the proximal tibia. Axis are indicated for the tibia. **(c)** Schematic of the neuroanatomy of the subgenual organ complex with subgenual organ and distal organ; the schematic shows the sensory neurons in both organs. Anterior view of a foreleg preparation. **(d)** The subgenual organ complex in a hindleg preparation. The subgenual organ tissue is outlined with a hatched line, the dorsal surface of the distal organ is indicated by a dotted line; detail in the boxed area shown in **(d$_i$)**. The thin membrane between the two organs is indicated by an open arrow. **(e-f)** The thin membrane is also present in **(e)** forelegs and **(f)** midleg (open arrows). **(d-f)** viewed from anterior. Axes for morphological photographs in **(d)** and **(e)** as indicated in **(c)**. Scales: (a) = 1 cm, (b) = 5 mm, (c-f) = 100 µm. Abbreviations: DO, distal organ; FL, foreleg; HL, hindleg ML, midleg; SGO, subgenual organ; sn, sensory neurons.

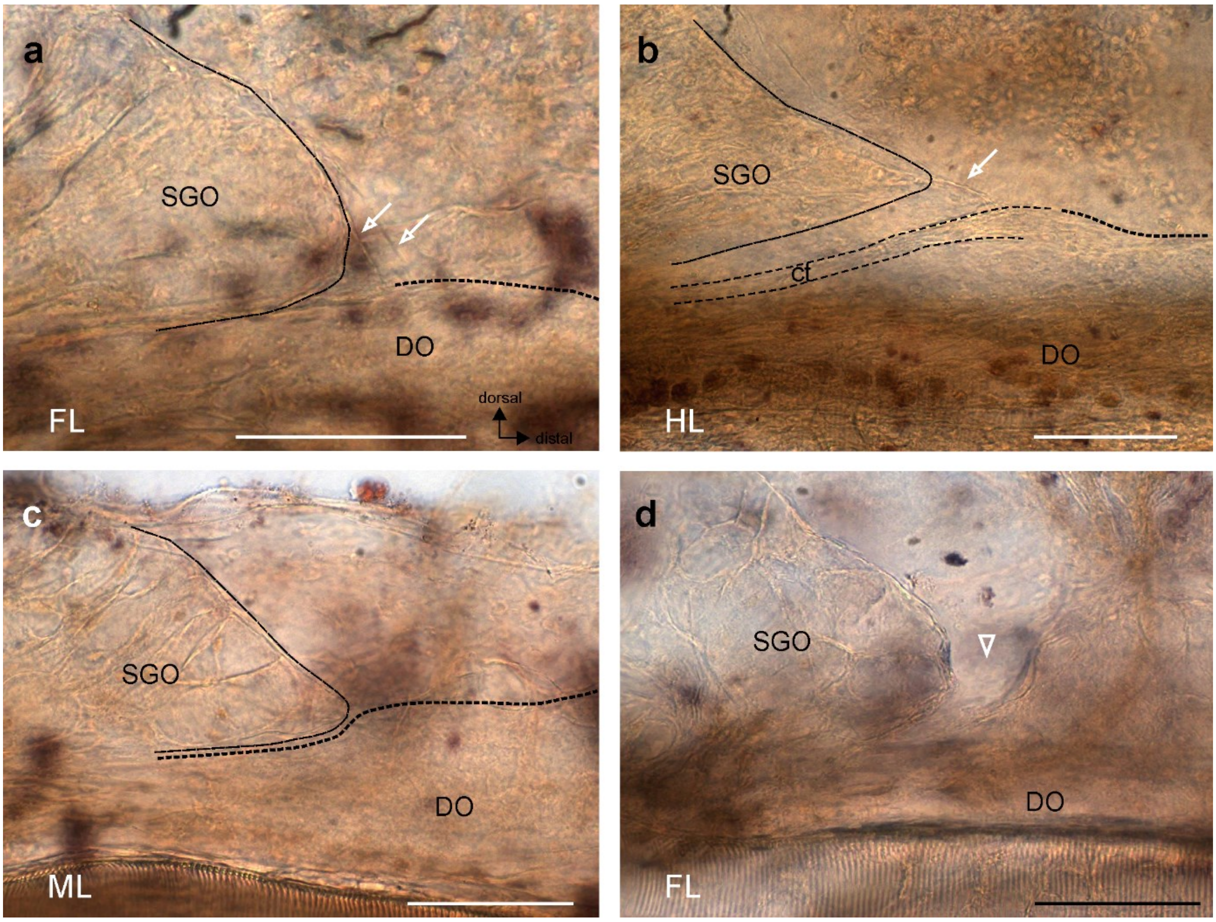

Figure 2. Variations in details of the thin membrane between the subgenual organ and distal organ, all viewed from anterior. **(a)** Two strands, **(b)** linked to connective tissue (ct; outlined) and not to the surface of the distal organ, **(c)** close contact, no membrane, **(d)** larger gap (open arrowhead) between two organs. Axes for photographs as indicated in (**a**). Scales = 100 µm. Abbreviations: ct, connective tissue; DO, distal organ; FL, foreleg; HL, hindleg ML, midleg; SGO, subgenual organ.

dotonal organs (figure 2c), while in three further preparations, a gap occurred between the sensory organs (figure 2d). In the sample inspected here from *P. schultei*, the membrane was found in 32 of 36 legs. Two of the four preparations without the membrane came each from female and male individuals, respectively (female: foreleg, hindleg; male: midleg, hindleg), without a clear tendency for absence in a specific sex or segment.

Only from *O. peruana* are so far similar data comparing the presence or absence of the membrane available (Strauß, 2022). In *P. schultei* is the proportion of preparations without a membrane higher (4 out of 36 leg preparations) than in the sample from *O. peruana* (2 out of 48 leg preparations examined; Strauß, 2022), although these differences were not statistically significant (Fisher's exact test, two-sided: $P > 0.05$).

Discussion

Connection of the sensory organs in *P. schultei* and other stick insects

The presence of the membrane between the SGO and the DO is shown here for both sexes of *P. schultei*. There was no difference between sexes in the sensory organs, and the adult legs show only slight sexual dimorphism in tibial length with longer tibiae in females than in males (Conle and Hennemann, 2005). The SGOC and the membrane are similar to the organisation found in other stick insects (Strauß, 2022). The findings in *P. schultei* show that the functional morphology of the SGOC including the membrane occurs across different taxa of Neophasmatodea. The membrane connection between SGO and DO is seen in different species of Neophasmatodea studied so far: *Carausius morosus* (Sinety), *Sipyloidea sipylus* (Westwood), *Ramulus artemis* (Westwood) and *O. peruana* (Strauß *et al*., 2021b; Strauß, 2022). Particularly notable is the shape of the SGO tissue which is extended distally towards the DO. The functional morphology of sensory organs includes several features (Strauß *et al*., 2024), and such a connection between two sensory organs could imply a physiological relation between the two organs. The SGO extension was also described in other stick insects (Strauß *et al*., 2021b; Strauß, 2022), and it was discussed that the mechanical properties of the SGO are likely influenced by the connection of the DO (Strauß, 2022). The material composition and the biomechanical properties of the membrane are so far not known.

Rare preparations lacking the membrane connection between sensory organs

The thin membrane was seen in the majority of leg preparations analysed here. Likely, the absence of the membrane in these preparations does not indicate an adaptation of the sensory physiology of the chordotonal organs, but the membrane was not formed during embryonic development when the sensory organs differentiate (see Jägers-Röhr, 1968 on the embryonic differentiation of chordotonal leg organs in *C. morosus*; Strauß, 2020 on the postembryonic presence of the SGOC in *S. sipylus*). So far, the development of the membrane during the embryonic and postembryonic stages of stick insects is not documented. Presumably, the membrane also develops in embryogenesis when the SGO and the DO differentiate, and both organs are present in the first larval instars after hatching (Strauß, 2020).

The role of vibration detection for the behaviour of *P. schultei* is so far not studied. To gain an insight into the sensory physiology of the SGOC, a first experiment could analyse the vibration sensitivity in insects without the membrane compared to those with the regular morphology. A possible correlation between functional morphology and physiology could be analysed by extracellular recordings of response thresholds to vibrational stimuli (see Strauß and Lakes-Harlan 2017) with consecutive axonal tracing and / or histological analysis. The latter would allow to identify the sensory organs lacking the membrane, which were present in the current sample of legs at a proportion of 11%, and test for any differences in vibrational thresholds to preparations with a membrane.

Functional morphology and relevance for vibration detection

Of the sensory organs in the SGOC, the SGO has been studied in most detail for the vibration detection in different insects including Polyneoptera (Shaw, 1994; Kilpinen and Storm, 1997; review: Strauß and Stritih-Peljhan, 2022). The SGO in the haemolymph channel acts as an overdamped system in bees (Kilpinen and Storm, 1997). The physiology of the additional organs occurring in the sensory complex, if not adapted to the detection of airborne sounds as seen in the tympanal organs in the Ensifera, is less well understood. These organs can show bimodal responses to both airborne sound and vibration (e.g., Kalmring *et al.*, 1994). Especially the biomechanical features of the DO in different insect taxa (locusts, cockroaches, heelwalkers and stick insects) are not investigated. For vibrosensitive chordotonal organs, the attachment to other body elements, like linking to the leg cuticle or suspension in the haemolymph, is particularly important (Strauß and Stritih-Peljhan, 2022). Despite the lack of a direct contact to sensory neurons, the connection between sensory organs - SGO and DO - by the thin membrane could be expected to affect the mechanical properties of the SGO but also of the DO (Strauß, 2022). The position of the DO in the haemolymph channel and the orientation of dendrites in distal direction (Strauß *et al.*, 2021b) is consistent with a role in vibration detection, and the physiological response is possibly similar to the SGO by the membrane connection (Strauß, 2022).

Conclusions

The present study extends the species of stick insects for which the functional morphology of the SGOC is investigated. The data on *P. schultei* document the second example investigated for the SGOC from the Occidophasmata, the New World stick insects (Simon *et al.*, 2019). Notably, the neuroanatomy and also the connection between the two chordotonal organs appears conserved in Neophasmatodea analysed so far. They may thus occur also in different species from other groups of Neophasmatodea. The occurrence of the membrane between the two chordotonal organs in the major lineages of Neophasmatodea also suggests an important physiological role of this functional morphology. Further physiological and biomechanical analysis could clarify the role of the DO in mechanosensation. The DO in stick insects shows an elaborate neuroanatomy and functional morphology not seen in other taxa (Strauß and Lakes-Harlan, 2013), making this taxon unique to investigate the morphological diversity present in the SGOC of orthopteroid insects.

Acknowledgements

Funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) - STR 1329/2-1.

The funding agency did not play a role in the design of the study, the data collection and analysis, or the writing of the manuscript, and the decision to submit the study for publication.

The author declares no conflict of interest.

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Received January 14, 2024. Accepted March 15, 2024.