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THIRTY YEARS OF THE CHAIR OF ANIMAL PHYSIOLOGY AND ETHOLOGY AT THE UNIVERSITY OF MARIBOR

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Abstract – A brief review is given of the history of the Chair of Animal Physiology and Ethology at the University of Maribor, which celebrates 30 years of teaching and research in 2022. The focus of the research group has been the integration of the structure and function of insect sensory organs, insect vision, and biophysical, ethological and ecophysiological aspects of prey capture in predatory insects.

Key words: Sensory physiology, predatory behaviour, substrate vibration, subgenual organ, insects, Neuroptera, antlions, *Euroleon nostras*, *Chrysoperla*

Izvleček – TRIDESETLETNICA KATEDRE ZA FIZIOLOGIJO ŽIVALI IN ETOLOGIJO UNIVERZE V MARIBORU

Podan je kratek pregled zgodovine Katedre za fiziologijo živali in etologijo Univerze v Mariboru, ki v letu 2022 obeležuje 30-letnico poučevanja in raziskovanja. Raziskovalna skupina katedre se osredotoča na integracijo zgradbe in delovanja čutilnih organov žuželk, gledanje pri žuželkah ter na biofizikalne, etološke in ekofiziološke vidike lova plena pri plenilskih žuželkah.

Ključne besede: Fiziologija čutil, plenilsko vedenje, vibracije podlage, subgenualni organ, žuželke, Neuroptera, volkci, *Euroleon nostras*, *Chrysoperla*

In 1986, the Pedagogical Academy of the University of Maribor evolved into the Faculty of Education. At this Faculty, an education-oriented study programme in Biology, defining the 4-year study of biology, was introduced in the late 1980s. Beginning in 1990, a course in Animal Physiology provided a solid foundation in basic physiological mechanisms. During the first year, the course was conducted by two colleagues from the University of Ljubljana: Kazimir Drašlar and Peter Stušek. A detailed review of the history of the study of Biology at the University of Maribor is presented by Devetak and Senčič (2008) and Devetak (2011a).

The year 1992 is recognised as the formal beginning of the Chair of Animal Physiology and Ethology, when Dušan Devetak, a former student of Academician Matija Gogala, began as a lecturer. At the beginning, behavioural topics were included in the physiology course, but these topics – i. e. Ethology, Behavioural Ecology and Predatory Behaviour – were later transferred to electives. By 1992, an electrophysiology laboratory was already operating at the then Faculty of Education. That laboratory had been established with the help of Tomaž Amon when the study of the insect subgenual organ began (Devetak 1992; Devetak and Amon 1997; Devetak 1998; Devetak et al. 2004).

Laboratory exercises initially used kymographs (Fig. 1) to visualise frog heart activity, muscle action, nervous activity and other physiological processes. The modestly equipped electrophysiology laboratory (Figs. 2, 3), with oscilloscopes and a Faraday cage, which they made themselves in the early years, enabled extracellular recordings of the activity in sensory neurons in selected invertebrates. Insects were favoured over mammals because of their relative simplicity for the experimental approach and for ethical reasons. The study of Neuropterid insects, particularly green lacewings (*Chrysoperla*), lance lacewings (*Osmylus*) and alderflies (*Sialis*), was con-

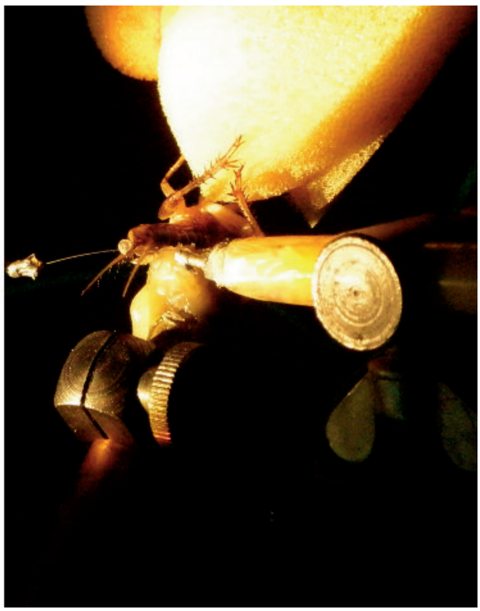

Fig. 1. (*left*). Laboratory exercises in the 1990s: a kymograph was used to study the respiratory movements of tracheal gills in May-fly larvae. Photo B. Mencinger Vračko. **Fig. 2.** (*right*). Extracellular recording of activity in sensory neurons of cricket hair sensilla. Photo DD.

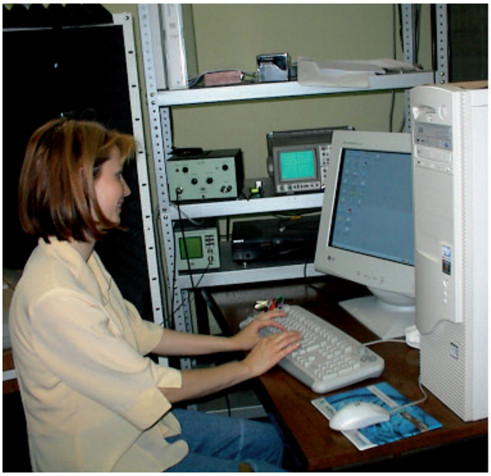

Fig. 3. (*left*). Bojana Mencinger Vračko in the accelerometry laboratory. Photo DD. **Fig. 4.** (*right*). Maria Anna Pabst (right) and Saška Lipovšek. Photo DD.

ducted by both students and researchers and focused on the morphology, ultrastructure and mode of action of the sensory systems, especially the chordotonal organs (Kolar 1991; Čavka 1995; Devetak et al. 1996; Devetak 1998; Božič 1999).

From the very beginning, a link was established between the Chair and two Austrian universities—the University of Graz and the Medical University of Graz. Cooperation with Maria Anna Pabst (Fig. 4), the head of the Institute of Cell Biology, Histology and Embryology in Graz, has lasted more than two decades and resulted in electron microscopy studies of the chordotonal organs, starting with detailed analysis of the ultrastructure of the green lacewing subgenual organ (Devetak and Pabst 1994; Fig. 5). In her doctoral dissertation, Saška Lipovšek (Fig. 4) studied another insect mechanoreceptor – the femoral chordotonal organ (FCO) (Lipovšek et al. 1999; Devetak et al. 2004). Confocal laser scanning microscopy and immunohistochemical methods revealed that sensory cells in the green lacewing FCO show immunoreaction with antiserotonin (Lipovšek et al. 2003). Furthermore, contrary to the FCO in the locust, acetylcholine does not occur as a neurotransmitter in the FCO of green lacewings (*Chrysoperla*). In addition to the study of sensory systems (e. g., Lipovšek Delakorda et al. 2009; Devetak et al. 2013), special attention was devoted to investigation of the ultrastructure of insect larval digestive system and the feeding strategies in neuropterid insects (e. g., Lipovšek et al. 2012a, 2012b; Devetak and Klokočovnik 2016). Because neuropterid insects are considered beneficial fauna, all the data obtained are important in the concept of biological pest control. In cooperation with Austrian colleagues, the Chair presented the most comprehensive review of sensilla in larval antlions by 2020 (see Acevedo Ramos et al. 2020).

On the initiative of Karl Kral (Fig. 6) from the former Institute of Zoology (now Institute of Biology) of the University of Graz, common research began into the role

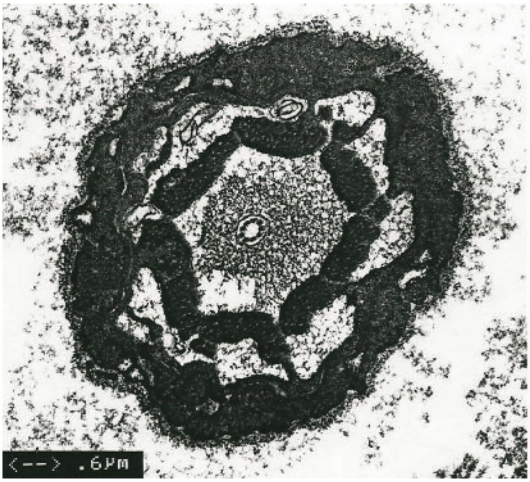

Fig. 5. (*left*). The axoneme of a cilium in the subgenual organ in *Chrysoperla* has a ring of 9 outer microtubule doublets (9+0 axoneme). The cilium is surrounded by an extracellular space which is delimited with dark scolopale rods. Photo DD and M. A. Pabst. **Fig. 6.** (*right*). Karl Kral. Photo DD.

of compound eyes in two convergent insect groups – mantids (order Dictyoptera, suborder Mantodea) and mantidflies (order Neuroptera, fam. Mantispidae). Different orientation principles were studied in two mantid species: *Mantis religiosa* uses motion parallax, and *Empusa fasciata* uses a combination of motion parallax and forward and backward movements to detect object distances (Kral and Devetak 1999). When studying another insect, the mantidfly *Mantispa styriaca*, an earlier assumption that prey-capture behaviour was based on a triangulation mechanism (Eggenreich and Kral 1990) was later confirmed, analysing the visually controlled behaviour by means of video recording (Kral et al. 2000). Their highly developed vision, based on the properties of diurnal superposition eyes, makes mantidflies successful hunters (review: Kral 2013).

In 2006 the Faculty of Education was divided, and the Faculty of Natural Sciences and Mathematics was formed, containing the Department of Biology with its Chair of Animal Physiology and Ethology. At the beginning of the 21st century, a new period of animal physiology began at the University of Maribor. New tools and platforms were added to the methods of researching and teaching animal physiology and ethology. Computer-based laboratory technologies were incorporated in the courses. In the period 2001 to 2004, the Chair acquired modern research infrastructure, including histology laboratory equipment, Nikon microscopes and Brüel & Kjær vibration measurement equipment (Figs. 7, 8).

Antlion behaviour has been studied at the Chair from the very beginning. Antlions (Myrmeleontidae) constitute the largest and most cosmopolitan family in the order Neuroptera, with sophisticated prey-capture behaviour at the larval stage (Fig. 9). Thus, a European antlion species – *Euroleon nostras* (Geoffroy in Fourcroy)

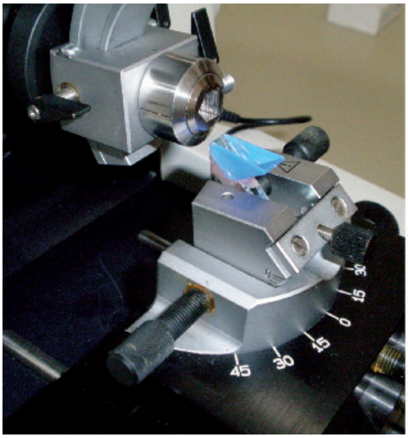

Fig. 7. (*left*). Laboratory of histology: an ultramicrotome is used for cutting ultrathin sections for transmission electron microscopy. Photo DD. **Fig. 8.** (*right*). Microscopy laboratory. Photo J. Podlesnik.

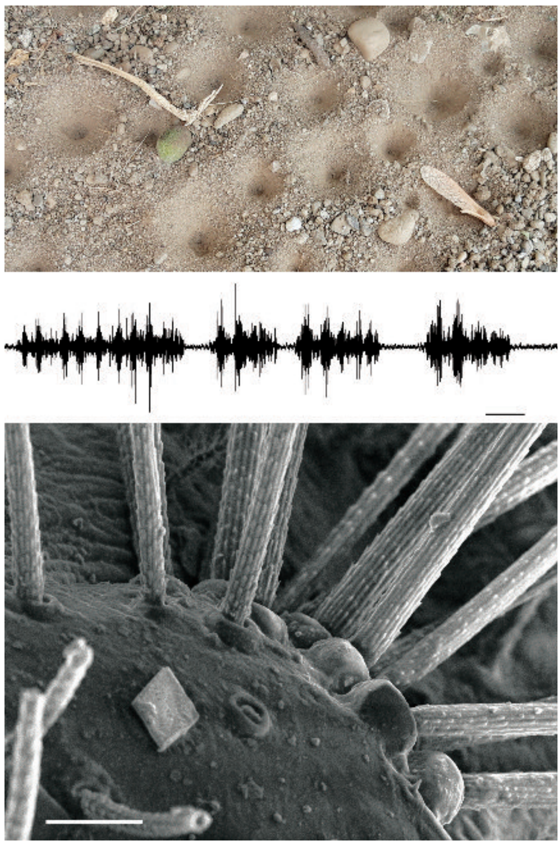

Fig. 9. Antlion *E. nostras* as a model species. (*Above*) Antlions use pitfall traps to capture their prey. Photo DD. (*Middle*) Oscillogram of the vibrations from an antlion larva during sand tossing; scale bar 1 second. Photo DD. (*Below*) Mechanoreceptors on the antlion body surface: hair sensilla and campaniform sensillum. Scale bar 30 µm. Photo M. A. Pabst & DD.

Fig. 10. (*Left*) Vesna Klokočovnik. (*Right*) Jan Podlesnik. Photo DD.

was chosen as a model species for studying ecophysiology and predatory behaviour. An important aspect of these studies was their integrative character, ranging from electron microscopy, biophysics, and ecophysiology to behaviour. Worthy of note is the evaluation of directionality in the predatory behaviour, which means that the reactions of the antlion are directed towards the prey (Mencinger Vračko 2003; Mencinger Vračko and Devetak 2008).

Physiological research on the antlion sensory receptors was complemented by behavioural studies. In her doctoral dissertation, Vesna Klokočovnik (Fig. 10), who compared antlion prey-capture behaviour in different species, recognised and defined two groups of predatory strategists: pit-builders and non-pit-builders (Klokočovnik 2013). The latter group comprises two sub-groups: sit-and-wait and sit-and-pursue predators (Klokočovnik 2013; Klokočovnik and Devetak 2014). The most appropriate method for behavioural analysis was video recording (Fig. 11). In

Fig. 11. Equipment for recording (*left*) and analysing (*right*) the behavioural patterns of predators. Photo V. Klokočovnik.

addition to interactions between antlions and their prey, interactions between intraguild predators have also been investigated; the research group was the first to comprehensively describe the behaviour of pit-builders in interactions – both inter-specific and intraspecific (Klokočovnik et al. 2020).

The antlion pit (Fig. 9), constructed in fine sand, is a sophisticated and very effective trap for small arthropods. Many questions in connection with the pitfall trap and antlion behaviour have been addressed. The study of the effect of abiotic factors revealed that they have a major impact on the plasticity of behaviour (Klokočovnik et al. 2012, 2016). Furthermore, when comparing two different strategies—pit-building and non-pit-building—surprisingly, it was found that a trap building strategy does not mean greater behavioural diversity (Klokočovnik and Devetak 2014).

Sand particle size is a crucial factor in antlion behaviour. Given a choice, the larvae of most antlion species prefer to build pits in fine sands (Devetak et al. 2005; Devetak and Arnett 2015) and in substrates of low density (Devetak et al. 2012). Similar results regarding sand particle size were obtained in wormlions (Devetak 2008).

Furthermore, sand particle size has an important role in the shape of the pit. For the first time, three-dimensional laser scanning (Fig. 12) was used in antlions to reveal the shape of antlion pits (Devetak et al. 2020). The research was conducted in

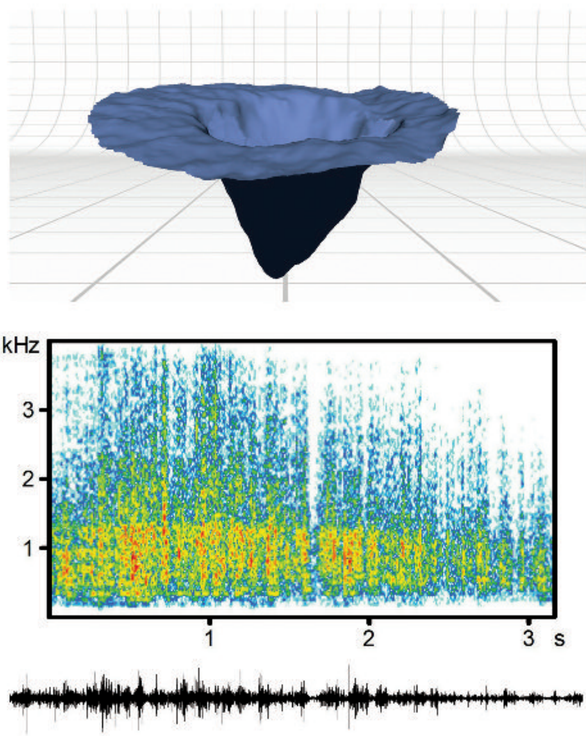

Fig. 12. (*Above*) Scanned pit of *C. lineosa*. Sonogram (*in the middle*) and oscillogram (*below*) of signals from prey moving on the sand surface.

collaboration with Inon Scharf from Tel Aviv University, Israel and Tina Klenovšek from the Laboratory of Morphometry, Chair of Zoology. One species investigated, *Myrmeleon hyalinus* Olivier, constructs pits in shape of a simple inverted cone. The other antlion studied, *Cueta lineosa* (Rambur), constructs a very special pit composed of two inverted cones, in general with steeper walls than the pits of any other antlion studied to date (Fig. 12). The analysis of avalanching using a Hele-Shaw cell revealed that the finest sand is responsible for high values of the maximum angle of stability; consequently, fine sand particles enable stability of the steep pit walls (Devetak et al. 2020). Behavioural analysis revealed that the *C. lineosa* pits were much more effective than the *M. hyalinus* pits when prey capture success was considered; to achieve these results, in 2016, a 3D model of a trap of any predatory insect was used for the first time (Klokočovnik and Devetak 2021).

The antlion detects and recognizes its prey by sensing the vibrations produced by the prey as it moves on the sand surface (Devetak 2014). Bojana Mencinger Vračko (Fig. 2) demonstrated that the antlion can detect prey even when vision is excluded (Mencinger 1998; Mencinger Vračko and Devetak 2008). The research group was among the first to describe the biophysical properties of the transmission of vibrational signals on a sand surface (Devetak et al. 2007) (Fig. 12) and even deep in the sand (Podlesnik et al. 2019). Since 2018, the Chair has been collaborating with Vincent Lorent from the Laser Physics Laboratory at the Université Sorbonne Paris Nord, France, with an emphasis on an experimental approach in the study of substrate vibrations as key signals for prey detection. Jan Podlesnik (Fig. 10) works most intensively with him (Podlesnik and Devetak 2020). As one result of this collaboration, the assumption that antlions are sensitive to subnanometer amplitude vibrations has only recently been confirmed (Martinez et al. 2020).

A research group of the Chair was involved in updating the Biology Curriculum in high schools, especially when Animal Behaviour and selected topics of Animal Physiology were incorporated into the course content (e. g., Devetak 2011b).

Currently, members of the Chair of Animal Physiology and Ethology are Vesna Klokočovnik (head), Jan Podlesnik, Saška Lipovšek (external collaborator), Eva Veler, Bojana Mencinger Vračko and Dušan Devetak (retired).

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