DEPARTMENTAL SEMINAR
INTEGRATIVE ZOOLOGY
Summer Term 2014

Programme and Abstracts
Tuesdays, 10-11:30 hrs
SR 3, UZA1, Althanstraße 14, 1090 Wien
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Summer Term 2013

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Programme

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Research in La Réunion: Mouthparts and feeding behaviour of *Glomeremus orchidophilus* (Gryllacrididae)

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Insect mouthparts offer ample opportunity to study form and function in evolutionary context. Various adaptations to floral food sources can be found in the different feeding guilds of flower-visiting insects. The functional morphology of their mouthparts represents the scientific goal of my research group at the University of Vienna (Austria).

The recently discovered, orchid-pollinating raspy cricket, *Glomeremus orchidophilus*, is a unique example among the flower visiting insects since they represent the only reported case of a pollinating cricket, so far. The crickets are able to take up nectar from flowers of the orchid *Angreacum cardetti* although they possess a biting-chewing type of mouthparts. During the nocturnal flower-visits, *Glomeremus orchidophilus* act as pollinators of the orchid *Angreacum cardetti*. This is an amazing example of an omnivorous cricket that feed on nectar. It is not known whether adaptations of the biting-chewing mouthparts to fluid feeding evolved in *Glomeremus*.

The Marelongue Research Station (Saint-Philipp) turned out to be an excellent place to study the nocturnal cricket, *Glomeremus orchidophilus*. With the help of Jacques Fournel and Sylvain Hugel (University of Strasbourg), these insects could be collected during several nights in the forests of the Parc National de La Réunion close to the station. Feeding experiments and video recordings were performed in the station to find out which mouthparts structures are used for fluid uptake on artificial and natural food sources. Ten individuals were preserved in ethanol for subsequent morphological studies of the mouthparts, e.g., cuticle surface, in advanced fluorescence microscopy and SEM.
Environmental Enrichment for zoo-living coatis

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Master’s Thesis  
Advisor: Helmut Kratochvil

Enrichment objects, e.g. boxes or tubes containing food that has to be extracted, are often presented to zoo-living animals. This kind of occupational therapy is used to improve animal welfare and to reduce the occurrence of “abnormal behaviour”, e.g. stereotypic behaviour. Stereotypies are hereby defined as invariant, repetitive behaviour patterns which do not seem to have any purpose.

In my Master’s thesis I am offering three wooden enrichment-boxes with different fastening mechanisms to seven zoo-living coatis (Nasua nasua and Nasua narica) in Tiergarten Schönbrunn, Vienna, Austria and to four coatis (Nasua nasua) in Aachener Tierpark Euregiozoo, Aachen, Germany.

Each of the boxes has a different fastening mechanism. The “sliding lid box” has a cover which has to be pulled or pushed out to open the box. The “triplet box” sub-divided into three compartments which are blocked with different plugs. The “turning lock box” can be opened by turning a wooden bar and then lifting the cap.

To examine, how the coatis handle them and whether these boxes can reduce the occurrence of stereotypic behaviour, the experiments are divided into three parts: 1) observation of original state (no boxes are presented, observation of daily life); 2) observation of exposure to boxes (boxes are presented); 3) observation of post-boxes state (no boxes are presented).

Currently, the first part in Tiergarten Schönbrunn is completed and I am working on the second part, offering the boxes to the coatis and observing the animals’ behaviour while they are handling the enrichment objects.
Pacing, turning (pirouette), rolling on the ground and using a fibre as some kind of dental floss in a repeated manner are common stereotypies in the Vienna coatis. In the second part I mainly concentrate on two individuals which show pacing and “dental floss” behaviour. The abnormal behaviour patterns occur more often in the afternoon than in the morning and appear more frequently when the weather is cold, rainy and stormy and the animals stay inside. The coatis are very interested in the boxes and manage to open them after 30 to 200 seconds.

Keywords: coati, *Nasua nasua*, *Nasua narica*, stereotypy, environmental enrichment

**Bone biology and the development of novel biodegradable scaffold material**

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The evolution of many species can be readily seen when examining skeletal remains. While the architecture of bones across species varies greatly, the underlying cellular processes is largely conserved. The maintenance of bone is tightly regulated at the cellular level by bone forming osteoblasts and bone resorbing osteoclasts. Bone remodeling and skeletal maintenance take place in a bone remodeling unit and when bone resorption outweighs bone formation the result is osteoporosis and increased fracture risk. There are many potential therapies that have been designed to deal with bone fractures, however they require extremely invasive techniques, have problems with rejection and maintenance, and time of healing is typically very long. Many therapies include the use of implants or other synthetic material.
Bone biologists in the InnovaBone group in the Department of Pharmacology and Toxicology are working with other institutions across the European Union to develop novel optimally performing bio-inspired synthetic biomaterials mimicking the natural physiological processes underlying bone repair. To that end, in vitro and in vivo models are being used to test the effectiveness of these novel synthetic materials. Ultimately, we will develop smart bioactive biomaterials that fit within bone fractures and lesions, recruiting the body’s cells to reconstruct bone. This will be a radical innovation in state-of-the-art bone biology research that will ultimately improve skeletal regeneration and quality of life.

Neurogenesis of *Nucula tumidula* and *Kurtiella bidentata* (Mollusca: Bivalvia)

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Myogenesis of *Kurtiella bidentata* (Mollusca: Bivalvia)

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Bivalvia is a class of marine and freshwater molluscs including clams, oysters, mussels, and scallops. The majority of bivalves are filter and suspension feeders and in contrast to other molluscs, they have no head and radula. To date only very few studies are concerned with the ontogeny of the musculature and the nervous system in bivalves. In order to shed light on shared and divergent neural and myoanatomical features among bivalves, we study the neuro- and myogenesis of representatives of both major bivalve clades. The present study focuses on two bivalves with different developmental stages, the autobranch
bivalve *Kurtiella bidentata* and the protobranch bivalve *Nucula tumidula*. The existing data on *Nucula tumidula* and *Kurtiella bidentata* include cross morphological analyses of adult individuals, however,

nothing is known about neuro- and myogenesis. In the present study the development of serotonin-, FMRFamide- and α-tubulin- like immunoreactive (lir) components in *Nucula tumidula* and *Kurtiella bidentata* are examined using immunocytochemistry and confocal laserscanning microscopy (CLSM). Myogenesis in *Kurtiella bidentata* is investigated by phalloidin staining combined with CLSM.

The pericalymma larvae of *Nucula tumidula* and the veliger larvae of *Kurtiella bidentata* were reared under laboratory conditions and fixed after different time periods. First results on the neurogenesis of *Nucula tumidula* show serotonin-lir cells in the anterior part of the early pericalymma larva which are part of the apical organ. In contrast FMRFamide-lir components could not be revealed so far. The first studies on neurogenesis of *Kurtiella bidentata* reveal strong FMRFamide-lir signals in the late veliger stage. There are a number of commissures, connectives, different types of paired ganglia anlagen and three or four apical cells clearly recognizable. Preliminary CLSM studies on the myogenesis of *Kurtiella bidentata* indicate different types of striated and non-striated types of muscles such as velum retractors and adductors. Neurogenesis of both species and myogenesis of *Kurtiella bidentata* will be more intensively investigated and compared with existing literature in line with this project. The data generated in both studies will significantly contribute to our understanding concerning the evolution of the bivalve and molluscan nervous and muscle system.
Hoverfly communities in the NP Gesäuse

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Master’s Thesis
Advisor: Harald Krenn

The NP Gesäuse represents an ideal place to study the effects of human influence on forest ecosystems. Hoverflies can serve as indicators for intact forest habitats. In the present study syrphid communities of spruce-fir-beech forests, spruce plantations and avalanche corridors were sampled using a butterfly net and coloured pan traps to compare species composition and diversity of the habitat types and to provide first recent data on this family for the national park.

90 species could be recorded for the NP Gesäuse including 14 stenoecious forest species and 17 xylophilic species as well as the first record of two species for Austria.

Although a lot of species were shared by the habitat types, species communities differed between them and indicator species could be identified for avalanche corridors and spruce forests. Avalanche corridors hosted most species while most individuals were found in spruce forests. Beech forests had lowest species and individual numbers, but a more balanced dominance structure than spruce forests. They also hosted the highest percentage of xylophilic species.

Flower abundance and ambient temperature significantly influenced the number of individuals and species caught during a sampling unit. Differences in these two factors served as explanations for the observed differences in hoverfly communities between the habitat types.

The comparison of the two methods revealed that species composition and relative abundances of the taxa differed between the two methods. Furthermore, much more individuals and species were caught using a net.
A matter of the heart: surprising diversity in insect circulatory organs

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Master’s and Diploma Theses  
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In insects, the pumping of the dorsal heart causes circulation of hemolymph throughout the central body cavity, but not within the interior of long body appendages such as antennae, legs, wings etc. Hemolymph exchange in these dead-end structures is accomplished by special flow-guiding structures or so called accessory pulsatile organs. These auxiliary hearts are autonomous pumps and exhibit a great diversity in their functional morphology. They represent evolutionary innovations of higher insects which makes them of great interest for general aspects of organ evolution.

The circulatory organs of the insect antennae were investigated so far in most of the apterygotan and hemimetabolan orders in considerable detail. The organs of hemipterans and of most holometabolan groups, however, are still to be described in detail. Aim and goal of our master/diploma theses are to fill some of these gaps. The circulatory organs are analysed in selected species at the basis of semithin serial sections, microCT, TEM and SEM. Of a few representatives 3D-reconstruction were made by aid of the software Amira.

The antennal circulatory organs in insects consist of antennal vessels which are connected to basal ampullae and associated pumping muscles. The muscles may have different attachment sites and act either as dilators or compressors of the ampullae.
In Heteroptera (master thesis Christina Heindl), the head anatomy is very unusual due to the development of the sucking mouthparts and the development of novel endoskeletal structures. The investigated antenna-hearts have a different functional anatomy: In Gerromorpha (1 sp.), the antenna-hearts have an ampulla dilator, while in all Pentatomomorpha (3 sp.) it is a compressor muscle.

In Neuroptera (master thesis Judith Kregl) all 6 investigated species have ampulla dilators. The second attachment varies among species. In addition all species have non-muscular tissue attached to the ampulla. At light microscopical level it looks like glandular tissue. Further TEM investigations should help to clarify the nature of these cells.

In Coleoptera (diploma thesis Karoline Loidl), the investigated antennal hearts (5 sp.) have all the same functional morphology which is unique among insects. Therefore it can probably be considered an apomorphy of this insect order.

In conclusion, the antennal hearts of the investigated species show an astounding diversity in their functional morphology. Thereby they represent potential characters for phylogenetic systematics. It must be stated, however, that the antenna-hearts are simply organized making it difficult to discriminate homology from convergence. On the other hand is it this simplicity which makes them useful examples to study general aspects of the evolutionary origin and transformation of organs.
Was erzählen Skelette über die Lebensweise von Tieren? – Eine Bearbeitung der ausgestellten Säugetierskelette im UZA1 inklusive fachdidaktischer Wissensvermittlung zu Lebensraum, Fortbewegung und Ernährung

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Diplomarbeit (Lehramt Biologie und Umweltkunde, Geschichte)
Betreuer: Harald Krenn / Barbara-Amina Gereben-Krenn

Säugetiere besiedeln unterschiedlichste Lebensräume der Erde. Ihr Körperbau weist vielfache Anpassungen an die jeweiligen Umweltbedingungen auf. In der Diplomarbeit werden die Tiere bearbeitet, deren Skelette im Biozentrum UZA 1 Universität Wien am Hauptgang ausgestellt sind. Besonderer Fokus liegt auf Anpassungen im Funktionskreis der Fortbewegung (Extremitäten) und der Ernährung (Gebiss).


Das Ziel der Diplomarbeit ist es, Tafeln zu gestalten, die im UZA 1 zu den Skeletten ausgestellt werden. Neben einer Beschriftung, werden diese die wichtigsten Inhalte zu den Funktionskreisen Fortbewegung und Ernährung enthalten und grafisch sowie fachdidaktisch aufbereitet sein, sodass sie dem Vergleich der unterschiedlich ausgeformten, aber homologen Skelettteile dienen.

**Cocktails and pills - a COI primer cocktail for pill millipedes from Austria**

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*Master’s Thesis*

*Advisors: Günther Pass, Daniela Bartel & Nikola Szucsich*

Pill millipedes (Glomerida) represent an intricate order of Diplopoda with a considerable morphological variability which resulted in the description of more than 400 species. There are, however, different opinions about the species status of this variation and most actual taxonomist distinguish only about 280 valid species worldwide. These uncertainties are an ideal starting situation to test DNA-barcoding for its delimitation capability in species recognition. Our study focuses on species from Austria, allowing for a pilot study within the upcoming initiative ABOL (Austrian Barcode of Life). Due to the widely unexplored status of diplopods with respect to barcoding, we tested several methods at the beginning of our study. To avoid possible inhibiting effects on the molecular procedures by the defensive secretions we used only the head of the specimens for DNA-extraction. Furthermore we applied a Non-Destructive-Extraction method (NDE), to preserve
all cuticular structures for subsequent analysis by traditional taxonomy using morphological characters. Only in Trachysphaera, a genus lacking defence glands, with minute species below 5mm body-length, whole specimens were used for NDE. To further optimize the protocol, a cocktail of primers was developed for both the PCR and the sequencing reaction. This used primer-cocktail GlomF1/R1 gave satisfying results for all investigated species. No specific adjustments were necessary for species newly added to the data set. To validate our results we sequenced in addition a fragment of the nuclear 28S rRNA-gene (900bp), spanning both conserved and variable regions. The obtained sequences resulted in clusters fully congruent with the COI based tree.

Up to now we generated from a total of 102 individuals collected in Austria COI barcodes and 28S rRNA sequences. Both markers separated the pill millipedes into 11 well defined clusters. With both markers the trees distances are large among clusters, but small within each cluster. The recovered molecular clusters are congruent with currently accepted species. Only in Haploglomeris multistriata, a species known for a high variability in coloration patterns, a single population is well separated from the remaining specimen, in both markers! A morphological differentiation of the two, seemingly polyphyletic clusters, will be performed in the next future to clarify whether they are independent species.

Establishing our protocol for COI and 28S rRNA, we are eager to include the remaining species collected in Austria into the newly launched ABOL-Initiative. Further collaborations with Michaela Bodner (University of Graz) will deal with taxonomic analyses of the chemical composition of the defense secretions, and the cooperation with Thomas Wesener (Research Museum Alexander Koenig, Bonn) including the German GBOL- COI- dataset.
ABOL - The Austrian DNA barcoding initiative

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DNA barcoding has become a well-established taxonomical tool which complements classical taxonomy, enables taxonomic identification of organisms and can be used in various applied fields. Besides the International Barcode of Life (iBOL), several national projects specifically dedicated to the biological diversity of single countries were launched (e.g., German Barcode of Life, GBOL).

ABOL will bring together Austrian experts from various institutions dealing with biological systematics and taxonomy in the broadest sense to barcode all eukaryote species living in Austria (plants, animals, fungi). For each species several individuals roughly covering the Austrian distribution ranges will be analysed. The principle of ABOL is to obtain the DNA barcode sequence from taxonomically correctly identified specimens that have to be incorporated (or are already part) of a scientific collection. The sequences are stored together with all metadata (e.g., sampling data, habitat information, collection number, etc.).

After a phase of preparation and manifestation, ABOL will start in summer 2014 with a three-year priming project that is aimed to establish the structures, clusters of working groups and project plans necessary to perform our ambitious task. Furthermore, it will include the collection of existing DNA barcoding data of Austrian taxa. After that phase the multi-year main project will start in which the clusters of working teams will perform the comprehensive analyses covering the various taxonomic groups.

ABOL will not only be an up-to-date inventory of biological
diversity in Austria, it will also boost research in many fields of biology and increase public perception and valuation of biodiversity.

**Evolution and control of complexity of lepidopteran proboscis**

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Butterfly proboscis is a flexible fiber serving as a feeding device for almost 160,000 species of butterflies and moths. Proboscis can be considered as a micro and nanofluidic device with extraordinary ability to probe, deliver, and sense different fluids. Proboscis evolution, organization and functionality are poorly understood, though its materials and engineering design is attractive especially for making artificial probes. Proboscis is conventionally modeled as a drinking straw. We show that the inherent structural features of the lepidopteran proboscis contradict the basic assumptions of the drinking-straw model. The calculated pressure differential required for a suction pump to support flow along the entire proboscis is greater than 1 atmosphere when the butterfly feeds from a pool of liquid. We suggest that behavioral strategies developed by Lepidoptera can resolve this paradoxical pressure anomaly. Using X-ray phase contrast imaging, high speed optical imaging and magnetic probes we were able to discover complex mechanisms of food intake. We experimentally discovered and theoretically explained
the essential role of morphological structure in partitioning of feeding devices into wetting/nonwetting regions. Theoretical studies of wettability of complex shaped proboscises allowed one to understand the role of surface morphology in fluid handling by these animals. Along with a complex surface chemistry, butterflies can alter the proboscis taper, the interlegular spacing, and the terminal opening of the food canal, thereby controlling fluid entry and flow by splaying the galeal tips apart, sliding the galeae along one another, and pressing the proboscis against a substrate. Thus, although physical construction of the proboscis limits its mechanical capabilities, its functionality can be modified and enhanced by behavioral strategies. This evolution and adaptive control of proboscis complexity makes Lepidoptera dietary diverse and hence provides new clues to the Lepidoptera diversity in general.

Bio: Professor Kostya Kornev leads the Micro and Nanofluidics Systems Research Group in the Department of Materials Science & Engineering at Clemson University, SC, USA. His group is actively working on fiber-based nanofluidics. Dr. Kornev graduated with a PhD degree in Physics & Mathematics from Kazan State University (KSU) in Russia in 1988. From 1988 until 1990, he worked at the Institute of Mechanics and Mathematics at KSU. In 1990 he has been invited to join the Institute for Problems in Mechanics of the Russian Academy of Science in Moscow, the leading institution of the Russian Academy of Sciences in the field of mechanics. While at RAS, he was an Associate Professor of Physics at the University of Aircraft Technology. In 2000, he joined the Textile Research Institute in Princeton, NJ. He moved to Clemson University in 2006. Dr. Kornev's research interests include arthropod inspired materials, biomechanics of insect feeding, and wetting and capillary phenomena.
The cryptic Bombus lucorum-species complex in Austria

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Master’s Thesis
Advisor: Harald Krenn

During the last decades, there was great disagreement about the taxonomy of Bombus lucorum and the closely related B. cryptarum and B. magnus. Nowadays, the species status of three distinct species in the so-called Bombus lucorum-complex is widely accepted, primarily due to investigations of nucleotide sequences and marking pheromones. In contrast, there is heavy doubt about the species identification based on morphology and several authors claim the species to be indistinguishable. In addition, information about diagnostic characters from the literature is often confusing or even contradictory. As a consequence of the difficult species recognition, the current knowledge about their autecology is like an unsolvable puzzle: one the hand the literature provides a flood of unreliable data from hundreds of authors from the last centuries. On the other hand, there are very few studies concerning their ecology that provide adequate species identification with biochemical methods. This also applies for Austria, where B. lucorum and B. cryptarum are widely distributed and co-occur in several areas. There are indications, that B. cryptarum occurs predominantly in the Austrian Alps, whereas B. lucorum is more widespread in the lowland.

The phylogenetic analyzes using nucleotide sequences of the mitochondrial cytochrome oxidase I gene (COI) for species recognition is the method of choice: it has been used for various insect groups and was successfully applied for species identification in the Bombus lucorum-complex.
My study consists of three major emphases: At first, a critical review about the taxonomy and the distinguishability of the taxa of the *Bombus lucorum*-complex provides an urgently required reappraisal to pave the way for future issues. Second, phylogenies of Austrian specimens of the species complex are reconstructed based on phylogenetic analyzes using nucleotide sequences of the COI. Therefore we conducted an extensive sampling of 387 specimens from 18 collection sites all over Austria. Further it will be examined how the Austrian specimens will suit into the European context. Are there different haplotypes in the UK, Scandinavia or Germany?
Thirdly, this study is a contribution to sharpen the ecological profile of the species in Austria, based on identification with a reliable method. Therefore I will examine distributional patterns concerning altitudinal differences, habitat types and climatic conditions.
Cryptic diversity in Mediterranean gastropods

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Species are fundamental units in Biology, yet their delimitation has been somehow neglected methodologically. Species limits are typically defined based on the presence of fixed (intraspecifically invariant or non–overlapping) diagnostic morphological characters which distinguish them from other species, and we are still gathering these morphological information and describing species as we have done for the last 250 years. Taxonomic impediment is now hampering accelerating the process of inventoring Biodiversity, given the paucity of resources supporting taxonomy. Integrative Taxonomy has been developed to address this challenge, as a sort of partial automatization of the process of inventorying biodiversity, given also that it has been estimated that on average 15 years are necessary from sampling to describing a new species. The DNA age has brougth remarkable innovation in the type of data, with billions new nucleotides available every day in the GenBank. How to use these genetic (DNA) data?

I will give a brief overview of the recently developed methods for analysing DNA data to delimitate species. I will focus on the following methods: ABGD (Automatic Barcode Gap Discovery) based on genetic distances; GMYC (Generalized Mixed Yule Coalescent) based on a preexisting phylogenetic hypothesis and on the evaluation of the ramification types; PTP (Poisson process) which assumes that the probability that a substitution gives rise to a speciation event follows a Poisson distribution; BSD (Bayesian Species delimitation) based on the estimate of θ (popolazione size) and of τ0 (age of tree root).
Some of these methods have been recently used to uncover cryptic diversity in Mediterranean gastropods. Case studies from the genera *Gibbula* (Trochidae), *Cerithiopsis* (Cerithiopsidae), *Ocinebrina* (Muricidae), and the nudibranch *Calma* (Calmidae) are presented.
Neurogenesis of *Nucula tumidula* and *Kurtiella bidentata* (Mollusca: Bivalvia)

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**Master’s Thesis**
**Advisor: Andreas Wanninger**

Bivalves are the second most speciose molluscan clade and exhibit diverse body plans. Surprisingly few studies are, however, concerned with the ontogeny of the nervous system in bivalves. In order to shed light on shared and divergent neural features among bivalves, this study describes the neurogenesis of representatives of both major bivalve clades. The present work focuses on two bivalves with different developmental stages, the autobranch bivalve *Kurtiella bidentata* and the protobranch bivalve *Nucula tumidula*. The existing data on *Nucula tumidula* and *Kurtiella bidentata* include cross morphological analyses of adult individuals, however, nothing is known about their neurogenesis. In the present study the larval development of serotonin-, FMRFamide- and α-tubulin-like immunoreactive (lir) components in *Nucula tumidula* and *Kurtiella bidentata* are examined using immunocytochemistry and confocal las erscanning microscopy (CLSM). The pericalymma larvae of *Nucula tumidula* and the veliger larvae of *Kurtiella bidentata* were reared and fixed after different time periods. In *Nucula tumidula*, two serotonin-lir flask-shaped cells are part of the apical organ in the anterior region of the early pericalymma larva. In the late pericalymma three serotonin-lir cells are visible in this region which degenerate subsequently during metamorphosis together with the test cells of the larva. The shape and the ontogenetic fate of these apical cells and other morphological features are similar to those of the scaphopod trochophore larva; characteristics which support the Diasoma
concept. In contrast FMRFamide-lir components could not be revealed in all stages. In *Kurtiella bidentata* FMRFamide-lir and serotonin-lir elements are first present in the late veliger stage. There are three ventral cells with eight neurites projecting into the velum and two paired visceral strands with two roundish cells at the end clearly recognizable. This study highlights the different modes of neurogenesis present in bivalves. The data generated will significantly contribute to our understanding concerning the evolution of the bivalve and molluscan nervous system.

**Myogenesis of *Kurtiella bidentata* (Mollusca: Bivalvia)**

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*Master’s Thesis*
*Advisor: Andreas Wanninger*

Bivalvia is a class of marine and freshwater molluscs including clams, oysters, mussels, and scallops. The majority of bivalves are filter and suspension feeders and in contrast to other molluscs they have no head and radula. Since only very few studies are concerned with the ontogeny of the musculature in bivalves comparative data are needed to assess the condition in the last common ancestor of bivalves. This master project focusses on the myogenesis of *Kurtiella bidentata* which is investigated by phalloidin staining combined with confocal laserscanning microscopy (CLSM). Data are further analysed with 3D-reconstruction programs. So far five distinct muscles have been identified: the anterior adductor, the velum retractors, the velum muscles, the foot retractor and the stomach muscles. In all stages are four pairs of velum retractors present which project fibres into the velum. Also an anterior
adductor, extends from valve to valve and a foot retractor is recognizable. The latter consists entirely of striated muscles. In later development stages (21 and 24 days post fertilization) the stomach and velum muscles appear. Similar to other bivalves, *K. bidentata* exhibits striated muscles. In common with *Pecten maximus*, four pairs of velum retractors could be found. These and further findings of the study will significantly contribute to the understanding regarding the evolution of the bivalve and molluscan muscle systems.
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