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**DEPARTMENTAL SEMINAR
INTEGRATIVE ZOOLOGY
Summer Term 2013**

Programme and Abstracts

Tuesdays, 10-11:30 hrs

SR 3, UZA1, Althanstraße 14, 1090 Wien



**Liebe AbteilungsmitgliederInnen, liebe der Integrativen Zoologie
verbundene externe KollegInnen,**

zum zweiten Male darf ich Ihnen nun die Zusammenstellung der Abstracts der Vorträge im Rahmen unseres Abteilungsseminars vorstellen. Ich denke, dass wir hiermit endgültig den Grundstein für eine Kontinuität in der Zusammenstellung wesentlicher an unserem Department laufender Forschungsprojekte gelegt haben. Dieser Band zeigt einmal mehr die Kreativität an unserem Department und die methodische und organismische Vielfalt, mit der sich die Forschung der AbteilungsmitgliederInnen beschäftigt.

Vielen Dank allen Vortragenden für ein wiederum spannendes und lehrreiches Seminar, sowie Sonja Matuš für die professionelle Zusammenstellung und das Layout und Harald Krenn für den Titelbildentwurf.

Mit herzlichen vorweihnachtlichen Grüßen,



Andreas Wanninger, im Dezember 2013

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Comparative developmental studies on Solenogastres (Mollusca)

Maik Scherholz

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PhD Thesis

*FWF Project P24276: Integrative developmental studies on
basal molluscs*

Supervisor: Andreas Wanninger

Although monophyly of Mollusca is widely accepted, the relationships within the phylum remain unresolved. Some recent molecular-based phylogenies support the Aculifera hypothesis, whereby the Solenogastres (=Neomeniomorpha) and Caudofoveata (=Chaetodermomorpha) together with the Polyplacophora (chitons) form a monophyletic assemblage, the Aplacophora. These form the sistergroup to the Conchifera, which comprise Monoplacophora, Bivalvia, Scaphopoda, Gastropoda and Cephalopoda. This is in contrast to some classical morphological phylogenies, which suggest a paraphyletic “Aculifera”, often placing the Solenogastres as first offshoot of molluscan phylogeny, and suggesting the Polyplacophora to cluster with the Conchifera to form the Testaria clade. I use a morphological approach (F-actin staining and CLSM) to analyze solenogaster myogenesis in a comparative framework to elucidate the evolutionary origin of Solenogastres. The new findings support a close relationship of Solenogastres and Polyplacophora and, in the light of the recent phylogenomic studies, support the Aculifera hypothesis.

The phylogenetic position of Mollusca within the Lophotrochozoa is still controversially discussed, but the segmented Annelids are often considered as possible sistergroup. If true, this would increase the likeliness of a segmented

“urmollusk“, whereby serially repeated gills and neuromuscular components in Polyplacophora and Monoplacophora are interpreted as remnants of ancestral segmentation. By using molecular techniques such as in situ hybridization I will test for the expression of so-called “segmentation genes” during development of the solenogaster *Wirenia argentea* in order to assess the function of these genes in potentially basal mollusks.

Evolution and development of body plans in myxozoans

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Myxozoans are probably the most morphologically derived group within the cnidarians. They have established a completely endoparasitic lifestyle with a complex life-cycle, usually involving alternation between a vertebrate and an invertebrate host. Trophic stages, which mostly occur in intercellular spaces or body cavities of the host organisms have lost many fundamental metazoan features like the intestinal tract, nervous system, gametes, gonads, body axes or even epithelial organisation. In this talk I will firstly introduce myxozoans and present the current state of knowledge on their phylogenetic position. I will then focus on developmental features related to the large-scale morphological alterations that have occurred in this group. The last part of the talk compares two closely related myxozoan species that show distinctly different body plans. The worm-like *Buddenbrockia plumatellae* is unique and has retained

a bizarre form of longitudinal musculature that enables vigorous swimming movements. In contrast, *Buddenbrockia allmani* and *Tetracapsuloides bryosalmonae* are spherical, non-motile and lack musculature and any recognisable body polarity. I will present an analysis of morphology and development in *B. plumatellae* and *T. bryosalmonae* using confocal microscopy, electron microscopy histology and developmental gene expression and discuss these results in an evolutionary context.

Processing strategies of social bees in complex visual environments

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PhD Thesis

Supervisor: Johannes Spaethe (Universität Würzburg)

A foraging bee constantly selects highly rewarding flowers out of a great variety of co-flowering plants using visual cues such as floral colour, shape and size. Since this high amount of information may exceed the processing capacity of the bee's brain, we asked if social bees use mechanisms of spatial attention. This mechanism allows the animal to concentrate its processing capacity flexibly on a small area of the visual field and to improve processing capacity of the particular area.

First, we present data on the extent to which capacity limitation influences object detection and discrimination in honeybees and bumblebees. In particular, we tested how distractor number affects object detection. Both species had to search for a rewarded target (yellow) among a varying number of non-

rewarding distractors (green) presented on a vertical background. The data showed that bumblebees and honeybees solved the problem of capacity limitation using different strategies. While bumblebees solved all tasks slowly but very accurately, the honeybees' search was very fast and search efficiency depended strongly on distractor number.

Second, we ask if bees do use spatial attention as a strategy to deal with information overflow. In a visual search task, honeybees show a dorso-ventral asymmetry detecting objects presented in their ventral visual field (VVF) more accurately than objects in their dorsal visual field (DVF). Consequently, the experiment addressed the question whether the dorso-ventral asymmetry is caused by a fixed neural pathway or a flexible attentional focus. Honeybees must detect a target among two distractors, whereas the probability of target appearance differed between groups. In the dorsal group, targets appeared only in the DVF – bees improved their search of dorsal targets within three flights. However, in the control group (target either in the DVF or the VVF) the significant performance difference between search flights for targets in the DVF and the VVF persisted during the whole experiment. The results imply that bees can build an expectation of the location of a stimulus and can adapt its visual processing according to its expectations.

Evolution and phylogeny of bees in light of morphological evidence

John Plant

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PhD Thesis

Supervisor: Hannes Paulus

An army of bees — 20,000 species strong – have been the dominant pollinators for the majority of the earth's angiosperms for the past 120 to 130 million years. They maintain the integrity of nearly all terrestrial ecologies. Without bees, human civilization cannot continue and would never have arisen.

How did bees evolve from predatory wasps and become vegetarians? What is the phylogeny of the seven families? The aim of my PhD thesis was to explore these and other questions concerning the higher phylogeny and evolution of bees (=Apiformes, Anthophila).

I used a fresh set of morphological characters in computer-assisted analyses. Despite several broad-based studies utilizing morphological or molecular data, the higher phylogeny of bees has yet to be satisfactorily resolved.

(i) Which family is the most basal group of bees?

Classical hypotheses on the early evolution of bees were rejected in my study that placed the Colletidae at the base of the tree. My results confirm molecular studies that the Colletidae is derived and not an ancestral group. Instead two major clades are at the base of the tree. One contains the short-tongued bee families: Halictidae + (Andrenidae + (Stenotritidae + Colletidae)); the other contains Melittidae plus the long-tongued bees (Apidae + Megachilidae).

(ii) Phylogeny of parasitic bees. 15% of bees are nest parasites on

other bees.

Contrary to the trend of molecular phylogenetic studies which merge the various cleptoparasitic Apinae together and group them with the Nomadinae into a single large assemblage, my results support a multiple origin for the Nomadinae, Isepeolini, Osirini, Melectini, and possibly the Rhathymini and Ericrocidini.

(iii) Phylogeny of social bees of the corbiculate tribes. About 10% of bees are social (parasocial, semisocial, eusocial). The relationships among the corbiculate Apinae bees obtained in the present study: Euglossini + (Bombini + (Apini + Meliponini)) uphold results from other studies based on morphological data; but are contrary to those based on molecular data: (Euglossini + Apini) + (Bombini + Meliponini).

The full richness of the morphology of bees has yet to be tapped (e.g. internal structures have seldom been used and new morphological methods are available). Likewise, only a maximum of seven genes have been used in broad-based phylogenetic publications (in comparison to other insect groups for which up to 1000 genes have been sequenced). Future work should be continued in the areas of molecular phylogeny and classical morphology.

Cryptic bumblebee species of the *Bombus lucorum*-complex in the Austrian Alps

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Master's Thesis

Supervisor: Harald Krenn

Bumblebees are among the most important pollinators in the high mountain regions. Within the *Bombus lucorum*-complex, at least two cryptic species (*Bombus lucorum*, *B. cryptarum*) inhabit the Austrian Alps, a third one (*B. magnus*) cannot be excluded to occur.

Recent molecular studies indicate that colour-patterns used for identification do not correspond with distinct molecular operational taxonomic units, each of which represents one of the species of the *Bombus lucorum*-complex. Furthermore, no characteristic colour pattern for one of these species was found and some traits show a gradual variation among the species. A reliable identification of females seems to be impossible based on morphological characters.

DNA-barcoding represents an appropriate method for the determination of species and provides a basis for studying altitudinal preferences, ecological and morphological characteristics within the *Bombus lucorum*-complex. The present study focuses on the following research questions: Are there differences in the occurrence of the species in various geographical expositions and elevations in the Austrian Alps? Do the species show different flower preferences? How reliable are morphological characters when re-evaluating DNA-barcoded specimens of the *Bombus lucorum*-complex?

Biomechanics and hydrodynamics of prey capture in the Chinese giant salamander reveal a new, high performance jaw-powered suction feeding mechanism.

Egon Heiss

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Post Doc, Workgroup: Josef Weisgram

During the evolutionary transition from fish to tetrapods, a shift from uni- to bidirectional suction-feeding systems followed a reduction of the gill apparatus. Such a shift can still be observed during metamorphosis of salamanders, although many adult salamanders retain their aquatic lifestyle and feed by high-performance suction. Unfortunately, little is known about the interplay between jaws and hyobranchial motions to generate bidirectional suction flows. Here, we study the cranial morphology, as well as kinematic and hydrodynamic aspects related to prey capture in the Chinese giant salamander (*Andrias davidianus*). Compared to fish and previously studied amphibians, *A. davidianus* uses an alternative suction mechanism that mainly relies on accelerating water by separating the “plates” formed by the long and broad upper and lower jaw surfaces. Computational fluid dynamics simulations, based on three-dimensional morphology and kinematical data from high-speed videos, indicate that the viscerocranial elements mainly serve to accommodate the water that was given a sufficient anterior-to-posterior impulse beforehand by powerful jaw separation. We hypothesize that this modified way of generating suction is primitive for salamanders, and that this behavior could have played an important role in the evolution of terrestrial life in vertebrates by releasing mechanical constraints on the hyobranchial system.

The nervous system of *Paludicella articulata* (Ectoprocta)

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Master's Thesis

Advisor: Andreas Wanninger

Numerous data is available for the development of the nervous system of various invertebrates, while comparatively little is known on the adult ectoproct/bryozoan nervous system. Most of the data on the adult nervous system deals with the basal Phylactolaemata and the most specialized Cheilostomata. The nervous system of the Bryozoa mainly consists of a cerebral ganglion at the lophophoral base, a circum-oral/ circum pharyngeal nerve ring, tentacles nerves and several visceral nerves. Previous studies have shown that in contrast to other bryozoan taxa the cerebral ganglion in the Phylactolaemata contains a lumen which is surrounded by a neuroepithelium. During the ontogeny of all Bryozoa the ganglion originates by an invagination of the aboral pharyngeal epithelium which results in a vesicle-like ganglion in early developmental stages. Preliminary observations have shown that the ctenostome *Paludicella articulata* also possesses a small lumen within its cerebral ganglion. Consequently, this species is subject of the current project in order to contribute to the basic organization of the bryozoan nervous system and whether a neuroepithelium is also present in this species. For that purpose, immunocytochemical stainings as well as sectioning techniques (semithin and TEM) are applied. First results show that a lumen is definitely present in this species which differs in size when looking at retracted and protruded animals. Four tentacle nerves were detected. Three tentacle nerves, namely the abfrontal nerve

and the two laterofrontal nerves have an intertentacular origin, whereas the mediofrontal nerve directly branches off the cerebral ganglion. The four tentacle nerves and their intertentacular origin resemble to the situation found in the ctenostome *Hislopia malayensis*. Further investigation will particularly focus on the presence of a neuroepithelium surrounding the lumen.

Life in freshwater: examples from the Kamptozoa

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Post Doc

Group Leader: Andreas Wanninger

The Kamptozoa or Entoprocta are a small group of invertebrates that predominantly occur in marine habitats. From all of the approximately 180 described recent species only two have been described from freshwater. In general, aquatic animals in marine habitats are hypotonic in regard to their environment whereas the opposite is the case in freshwater inhabitants. In this presentation I show adaptations of the Kamptozoa to freshwater environments. In both described species a complex protonephridial system consisting of numerous terminal organs that are interconnected by thin tubules is present. This is in contrast to the marine representatives of the phylum where only a single pair of slender protonephridia is present. In the latter these probably are of excretory function whereas experimental procedures in the freshwater Kamptozoa have shown that the protonephridial system is purely of osmoregulatory function and excretion is mostly carried out by cells of the stomach roof. Recently, a third kamptozoan freshwater was found in Thailand.

Some specialists regarded this species considered it to be an already described species from that area, considering that it is merely an example of phenotypic plasticity. However, the first morphological results show that this species truly differs in several aspects to any other described species. Moreover, it appears that not only a new species has to be described, but that a separate genus has to be created.

Genetic variability in the Mediterranean mesopsammal mollusc *Philinoglossa praelongata* (Gastropoda, Opisthobranchia)

Daniela Trpisovsky

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Diploma Thesis

Advisor: Gerhard Steiner

The marine mesopsammal is an interstitial pore water-space between sand grains inhabited by a species-rich community of highly specialized animals. Most mesopsammal gastropods belong to the Euopisthobranchia and Acochlidia.

The dispersal potential of the mesopsammal euopisthobranch gastropod *Philinoglossa praelongata* is considered to be low, although it is widely distributed throughout the Mediterranean Sea and beyond. Therefore, genetic variation among separated populations is to be expected. However, a previous study on the interstitial gastropod *Pontohedyle milaschewitschii*, does not confirm high genetic variability of separated populations in the northern Mediterranean.

The aim of this phylogeographic study is to investigate the genetic variability of two widely geographically separated

Mediterranean interstitial *Philinoglossa praelongata* populations and to test, if the genetic differentiation is as low as in *Pontohedyle milaschewitchii* populations. Therefore *Ph. praelongata* has been sampled in the northern Adriatic Sea (Croatia), Tyrrhenian Sea (Southwest-Italy) and Ligurian Sea (Northwest-Italy). Furthermore this investigation can be used to test the conspecificity of these populations.

A dataset of the mitochondrial genes 16S rRNA and CO1 has been obtained for phylogenetic and statistical analysis. Additionally the Coalescent Event of the Italian and Croatian individuals was determined.

All analyses result in two genetically and geographically distinct clades. The maximal interspecific genetic distance ranges from 10.4 to 14.1% and F_{ST} values ranges from 0.911 to 0.962. Furthermore genflow is extremely low at 0.04 migrants per generation. These results indicate high differentiation between “populations” and the presence for two cryptic species.

Additional sequence data on the morphologically similarly *Ph. helgolandica*, and/or additional morphological investigation on the radula of *Ph. praelongata* on both sampling sites (Croatia, West-Italy) will help to confirm the occurrence of cryptic species.

Sexual Signalling in Japanese Macaques

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Master's Thesis

Advisor: Bernard Wallner

Female Japanese macaques (*Macaca fuscata*) express reddest facial skin during their reproductive time in winter. Oestrogen causes a higher oxygenated blood flow, thus increasing the red colour intensity of the skin. The present study examined the importance of colour contrast variances given by female facial skin colouration in guiding visual attention in male Japanese macaques. The results of a conducted pre-study have already revealed that male Japanese macaques exhibit visual preferences towards females with intensive red facial colouration. A more and a less intensively red coloured digital female face were presented to male macaques in a monitor experiment. Significantly more attention was paid towards the intensive red face. Over the course of evolution primate colour vision has been tuned to select relevant environmental stimuli by a joint adaptation of both colour and colour contrast vision. To decipher the impact of colour contrast variances in the present study, the red stimuli used in the pre-study were rotated within the DKL colour space. Thereby the red colour content was excluded while maintaining the natural variation in colour contrast. The colour modified stimuli were presented to the same males again. The results of the current study revealed that colour contrast had no significant effect on the displayed attention regardless of the red colour content. Hence, visual preferences towards the female facial stimuli appear to be less pronounced when lacking the naturally red colouration. It can thus be concluded that in

Japanese macaques the signalling value of the intensive red colour is linked to the physiological information available via the red skin rather than to the colour contrast *per se*.

Ontogenetic shape change of the seahorse *Hippocampus reidi* with respect to dietary differences

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Master's Thesis

Advisors: Manfred Walzl, Jürgen Herler

Habitat destruction and increasing fishing pressure have become the main threats to seahorses (genus *Hippocampus*). Subsequently, these special marine teleosts were listed in CITES Appendix II in 2005, and increasing efforts for their aquacultural rearing have been undertaken.

The aim of this master's thesis was to study the early developmental stages of *Hippocampus reidi*, bred in captivity on different diets. First feeding regimes consisted of *Artemia sp.* nauplii in experimental group I and a mix of rotifers (*Brachionus sp.*) and copepods (*Tisbe sp.*) in experimental group II. Additionally, a starvation/hunger treatment was employed to evaluate negative allometric growth patterns. Body development during the first 20 days after fry release was assessed through the measurement of key parameters (wet weight, body height) and geometric morphometrics (based on Procrustes shape coordinates of anatomical landmarks).

The experiments showed higher growth rates (wet weight, body height) in experimental group II (fed with mixed plankton) and a

significantly increased survival rate compared to experimental group I (fed with *Artemia*). Principal component analysis of the seahorses' landmark coordinates showed divergent allometric growth patterns in the trunk region and head region of the respective seahorse group. Detailed analysis of the trunk region revealed that PC 1 reflected the main developmental axis, whereas PC 2 reflected the nutritional status of the specimens. Analysis of the head region exhibited similar growth trajectories, but *Artemia* fed seahorses showed significant growth retardation compared to the group fed with mixed plankton. In summary, this study reveals that mixed plankton nutrition enhances growth rates and the healthy development of juvenile seahorses and should be considered as the more appropriate food.

Fitness-related costs of butterflyfish corallivory for *Acropora* corals and the role of mutualistic coral gobies

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PhD Thesis

Advisors: Manfred Walzl, Jürgen Herler

Partial predation can have significant fitness consequences on modular organisms such as plants, sponges or coral colonies. Although some coral-dwelling organisms defend their host colonies against browsing corallivorous fishes, little information is available on the fitness benefits to hosts of such symbionts. By a combination of field observations and *in situ* experiments, this study investigates both the host colony defence capabilities by an

obligate coral-dwelling goby (*Gobiodon fuscoruber*) and the impact of corallivory on colony growth of caged and uninhabited *Acropora selago* colonies. Field observations in the northern Red Sea of the obligate corallivorous butterflyfish *Chaetodon austriacus* showed that the effectiveness of coral defence by *G. fuscoruber* depends on colony size, with a 60% reduced feeding rate on medium-sized host colonies (250-500 cm² horizontal surface area). In an *in situ*-caging experiment using video observation and the buoyant-weighing-method to measure coral growth, high predation by *C. austriacus* on uninhabited *A. selago* colonies triggered size-dependent growth-rate reductions. After 3 weeks, the relation between growth rate and colony size became significantly different between control corals and colonies exposed to predation. The smallest colonies (~0.6 kg) responded with a 40% reduced growth rate whereas larger colonies (>1.6 kg) remained unaffected despite they received more bites. This short-term approach implies that corals can reach threshold sizes at which the colony growth effects of predation by polyp-feeding butterflyfishes becomes negligible. Most notably, bite- and size-related regression functions derived from the experiment show that medium-sized colonies experience a 28-53% relative growth reduction due to the extraordinarily high predation. As mutualistic gobies reduce the bite rate on medium-sized colonies, it is concluded that they increase coral fitness through a higher growth rate compared to uninhabited colonies and hence reduce the timespan host colonies need to reach threshold sizes.

Myogenesis in the wood boring bivalve *Lyrodus pedicellatus*

Andrea Wurzinger-Mayer

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Diploma Thesis

Advisor: Andreas Wanninger

The shipworm *Lyrodus pedicellatus* is a wood-boring and feeding mussel that has an unusual wormlike body. Although their larvae are brooded, the general appearance of a mussel larva is maintained. Here, the myogenesis of *L. pedicellatus* is described by labelling the filamentous actin (F-actin) in muscles and compared with other bivalve taxa in order to detect homologous structures that might contribute to the ground pattern of bivalve musculature. Five muscle systems were identified, the velum, foot, larval retractor, mantle and adductor system. For a short time, an accessory larval and velum retractor appears. Early in development, an oral velum musculature arises in the postoral region, while in late stages the lateral and dorsal mantle musculature, paired finger-shaped muscular structures and an accessory adductor are formed. As in other bivalves, *L. pedicellatus* exhibits three velum retractor muscles, but in contrast, one disappears early in larval development. Contrary to former assumptions, it is likely that they might contribute to adult musculature in bivalves, because in metamorphic competent larvae the velum retractors seem to be remodelled and incorporated into the elaborated mantle musculature. Furthermore, the origin of the foot retractor at the larval velum retractor also indicates a contribution of larval muscles to the adult musculature.

Further research will reveal, whether or not these components will pass metamorphosis to be incorporated into the adult body.

Neurogenesis in *Lyrodus pedicellatus* (Bivalvia) as inferred by immunocytochemistry and confocal microscopy

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Diploma Thesis

Advisor: Andreas Wanninger

Although some data concerning neurogenesis of molluscs are already available, bivalve neurogenesis is only little investigated. The shipworm *Lyrodus pedicellatus* is a wood-boring bivalve mollusk with a worm-shaped body that develops via dramatic metamorphosis from a common, veliger-type larva. In this work the larval development of serotonin-like (serotonin-lir), FMRFamide-like (FMRFa-lir) and acetylated α -tubulin-like immunoreactive components were examined using immunocytochemistry and confocal microscopy. Neurogenesis starts in the late trochophore stage at the apical pole, where three serotonin-lir flask-shaped cells. Two FMRFa-lir flask-shaped and two non-sensory, round cells appear in the apical organ. In the late veliger / early veliger the flask-shaped cells disappear and posterior the cerebral ganglia, consisting of serotonin-lir cells and FMRFa-lir neurites, appear. The pedal ganglia appear in the mid-veliger stage and express both serotonin-lir and FMRFa-lir cells. In the visceral region, already in the trochophore stage, serotonergic and FMRFamidergic signal appears. The pleural ganglia present only FMRFa-lir cells and it appears in the trochophore stage. In the late veliger / early pediveliger stage the cerebral and pleural ganglia fuse to one ganglion.

This work offers a profound and detailed description regarding the development of the nervous system of bivalves. Comparing it to other bivalves shows similarities - they all have an apical

organ and later on the cerebral ganglion develops. However no other study about bivalve neurogenesis results in a nervous system so well developed as in *Lyrodus pedicellatus*. The nervous system of *Lyrodus pedicellatus* has much more in common with the larval nervous system of gastropods. The apical organ has the same number of cells, the cerebral and pleural ganglia fuse to one ganglion and they all have pedal and visceral ganglia.

Genetic variability of geographically widely separated Mediterranean populations of two syllid species (Polychaeta)

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Diploma Theses

Advisor: Gerhard Steiner

The term “mesopsammon”, introduced by Remane in 1940, defines animales living between sandgrains. This habitat is characterized by a high diversity of highly adapted species. Among them are the Syllidae, one of the most specious polychaete families, comprising more than 70 genera and over 700 species. They show some of the most spectacular specializations in reproduction, like epigamy, where the whole animal transforms into a pelagic sexual state, or schizogamy, by stolonisation. This phylogeographic study compares genotypic variability of geographically distant populations of two syllid polychaete species, *Plakosyllis brevipes* Hartmann-Schröder, 1956 and *Sphaerosyllis* sp. Claparède, 1863 from Croatia

(Northern Adriatic Sea) and Italy (Tyrrhenian Sea). Due to their small body size, brood care and the lack of pelagic larvae, their dispersal potential is limited and, therefore, a high differentiation between the two sample sites is predicted. We use three molecular markers to assess the genetic population structures: the mitochondrial genes 16S rRNA and Cytochrome oxidase subunit 1, and the nuclear ITS rRNA gene. The phylogenetic and population genetic tools we apply comprise Bayesian Inference, Statistically Parsimony, Maximum Parsimony, and various phylogeographic analyses. The preliminary results confirm expectations of genetically well differentiated populations in both species. The presence of shared haplotype lineages, however, indicates conspecific populations in both species. Genetic variability within populations is low. Future coalescence analyses to estimate divergence dates will be compared with that of opisthobranch gastropods from the same areas.

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