10–11 May 2022

Simultaneously Hermaphroditic Organisms Workshop

PROGRAMME

School of Biology
Aristotle University of Thessaloniki
Greece

MEETING VENUE
Aristotle University Research Dissemination Center (KEDEA)

ORGANIZER
Alexandra Staikou

RESEARCH COMMITTEE
ARISTOTLE UNIVERSITY OF THESSALONIKI

FINANCIAL SUPPORT
A.U.Th. Research Committee

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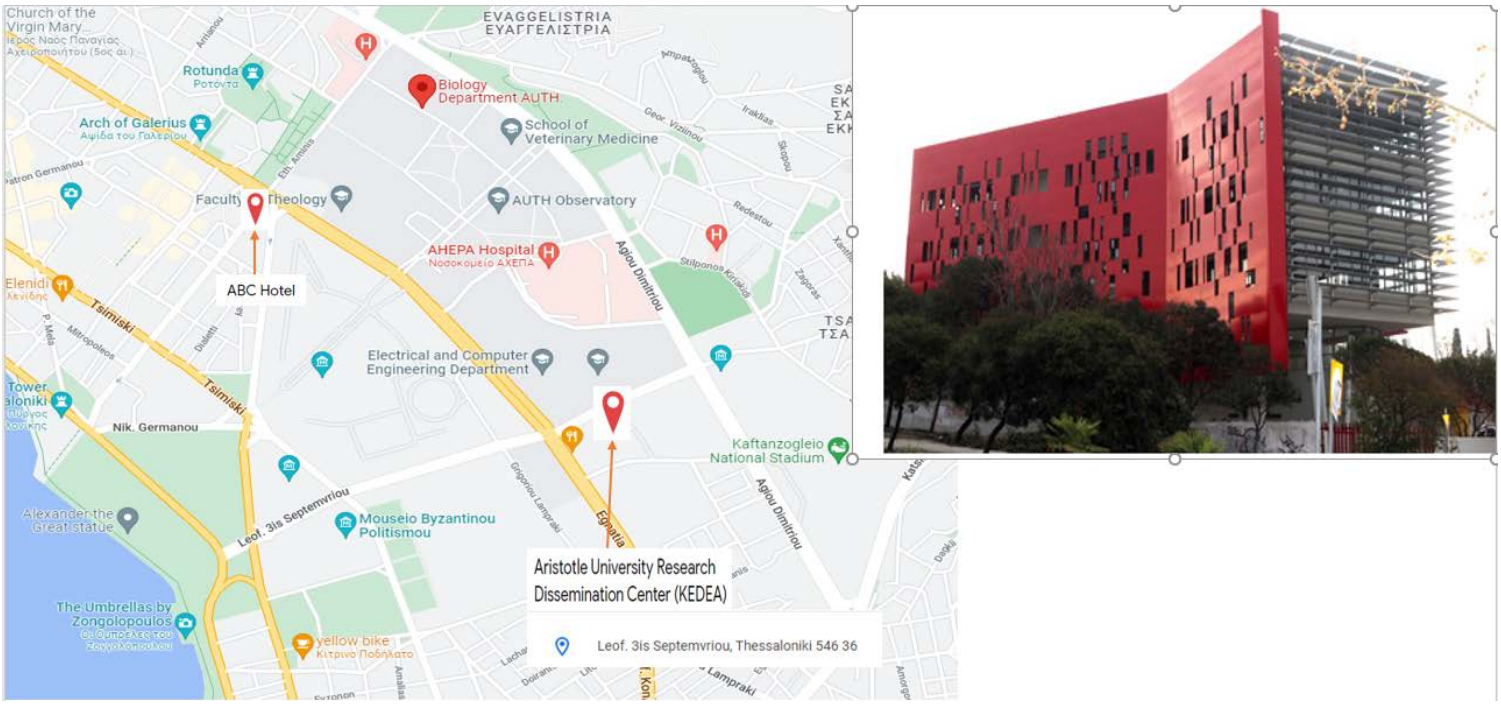
Programme, Participants,



Meeting venue: Aristotle University Research Dissemination Center (KEDEA)

Financial support: A.U.Th.Research Committee

Organizer: Alexandra Staikou

PROGRAMME

Tuesday, 10 May 2022

12:00 – 14:00 Welcome reception with light meal and registration

14:00 14:45 Benvenuto Chiara and Lorenzi Maria Cristina: "Social control" of reproduction

14:45 – 15:30 Cīrulis Aivars and Abbott Jessica: Effects of sex-limited experimental evolution on a hermaphrodite

15:30 -16:00 Coffee break

16:00 16:45 Fanny Laugier, Timothée Chenin, Patrice David: Genetic conflict and cytoplasmic-nuclear determination of male sterility in a gynodioecious snail

16:45 – 17:30 Nakadera Yumi, van Dijk Shanna, Zizzari Valentina, Koene Joris M.: Evaluating the effects of heat stress on reproduction of a hermaphroditic snail species

17:30 Poster session

Evening formal dinner

Wednesday, 11 May 2022

12:00 – 14:00 Light meal and coffee

14:00 14:45 Lorenzi Maria-Cristina, Robles-Guerrero Franco G., Costantini David: Competing for fertilizing eggs is physiologically costlier than producing eggs in a simultaneous hermaphrodite. Then, why is the male role preferred?

14:45 – 15:30 Radhakrishnan Pooja, Saboul Noé, Gerardo Robles-Guerrero Franco, Lorenzi Maria-Cristina: Sex and the city –how social environment influences body growth and sex change in a sequential hermaphrodite

15:30 -16:00 Coffee break

16:00 - 16:45 Santhosh Santhosh and Schärer Lukas : Sperm morphology and reproductive success in the hermaphroditic flatworm, *Macrostomum lignano*

16:45 – 17:30 Norton Cynthia G and Anderson Olivia: Sperm storage in *Planorbella trivolvis*

17:30 – 18:15 Stoforiadi Anthi and Staikou Alexandra: Effect of mating group size and mate novelty on mating frequency of the land snail *Cornu aspersum*

Discussion and closing of the meeting

ABSTRACTS

"SOCIAL CONTROL" OF REPRODUCTION

Chiara Benvenuto[1] and Maria Cristina Lorenzi[2]

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Males and females usually communicate each other their reproductive status. In some cases, though, the transfer of information can be more complex than just advertising receptivity: some individuals (dominant and/or territorial) also advertise their social rank. Traditionally, dominants have been considered able to control other individuals' reproduction in multi-member groups with high reproductive skew. Social control of reproduction has been described in cooperatively breeding mammals (African mole-rats, banded mongooses), in many fishes (from cichlids to sex changing species), in eusocial crustaceans and, of course, in many social insects. From hymenopteran queens, who impose sterility on workers, to different crustacean male morphotypes who control growth in conspecific males, to sequential hermaphrodites who suppress other individual's change of sex and simultaneous hermaphrodites who affect partners' sex allocation, dominance appears to regulate the physiology of the reproductive state of other individuals. But how can a single individual of one sex control the status of other individuals, hierarchically, inhibiting completely their ability to reproduce or stopping the full optimization of their reproductive output? Alternatively, "subordinates" could self-restrain their reproductive potential in presence of dominant individuals. Using a multi-taxa approach, we propose a resolution of reproductive-skew conflicts based on signaling rather than control, along a continuum of mechanisms of social regulation of reproduction.

EFFECTS OF SEX-LIMITED EXPERIMENTAL EVOLUTION ON A HERMAPHRODITE

Aivars Cīrulis and Jessica Abbott

Lund University, Department of Biology

The evolution of gonochorism from hermaphroditism can be gradual by increasing investment in one sex role while decreasing in the other, or rapid through the fixation of sex-role sterility mutations, eventually leading to the evolution of sex chromosomes. It is expected that the transition will involve a temporary state of gynodioecy or androdioecy as the mutations are not expected to take place at the same time. If the first mutation is a dominant female-sterility mutation, later accompanied by a recessive male sterility mutation, then an XY sex chromosome system evolves, while the opposite combination of mutations will result in a ZW system. Later on sexually antagonistic (SA) genes can be linked to the newly established sex-determining regions on the sex chromosomes. This is followed by recombination arrest in the region, so that the inheritance pattern is sex-limited for all these sex-specific genes. As our understanding of the very early stages of sex chromosome evolution is mainly based on theory and comparative evidence, we developed a system which we hoped would make it possible to observe in real time what happens after the acquisition of a new sex-determining gene. We used a previously established green fluorescent protein (GFP) line of the simultaneous hermaphrodite *Macrostomum lignano*. We used the GFP locus as a dominant sterility mutation, which is inherited in a Mendelian fashion. By allowing the GFP allele to be inherited only through sperm, we created male-limited selection lines (resembling the early stages in XY chromosome evolution), and by allowing the GFP allele to be inherited only through egg cells, we created female-limited selection lines (resembling the early stages in ZW chromosome evolution). We also created control lines, where the inheritance pattern was equally mixed. After tens of generations, we investigated how these lines have responded on the level of the genome, the transcriptome, and the phenotype. We observed that the female-selected lines seemed to have responded the most at the genomic level. For example, the number of significantly differentially expressed transcripts was largest between the female-selected lines and the control lines. These changes seemed to involve downregulation of testes-biased genes. In addition, we observed the highest number of SVs in the female-selected lines, which could be related to changes in recombination rate. In contrast, the male-selected lines seemed to have responded the most at the phenotypic level, since we observed a decrease in the ovary size and body size in the male-selected lines, as well as behavioural changes that may be related to changes in the ejaculate. Both sex-specific selection regimes showed evidence of alterations in the shape of the stylet. Based on these results, we can conclude that our worms have indeed responded to the sex-limited selection in a way that is generally consistent with our expectations from other young sex chromosome systems. The evidence of a decrease in the testes function in the female-selected lines resembles adaptation towards gynodioecy, and the evidence of a decrease in the ovary size in the male-selected lines resembles adaptation towards androdioecy.

GENETIC CONFLICT AND CYTOPLASMIC-NUCLEAR DETERMINATION OF MALE STERILITY IN A GYNODIOECIOUS SNAIL

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Centre National de la Recherche Scientifique,
Montpellier, France

Physa acuta, a freshwater snail, is the first animal example of cytoplasmic male sterility (CMS) in animals. CMS is usually caused by cytoplasmic (usually mitochondrial) genes, transmitted through female germlines, that suppress male reproduction in a hermaphrodite, to the detriment of biparentally inherited nuclear genes. In *Physa acuta* a mitochondrial haplotype (mitotype D) was found to be associated with a quasi-complete loss of the male function, turning hermaphrodites into functional females. The D mitotype is extremely divergent from the standard (normal N) haplotype as a result of a recent, remarkable acceleration of molecular evolution. We here relate the discovery of a third mitotype in *Physa acuta*, very divergent from both D and N, called mitotype K. The K mitotype also comes with cytoplasmic male sterility, and is more frequent in natural populations than D. In addition, the expression of cytoplasmic male sterility in K snails is dependent on the associated nuclear genome. These results demonstrate the existence of (ii) two mitochondrial lineages involved in CMS, and (ii) polymorphic nuclear genes restoring male fertility in K snails. These characteristics mirror classical observations made in gynodioecious flowering plants, in which multiple male-sterile mitotypes often coexist, each being opposed by specific nuclear restorer alleles. We are curently investigating the variation of female and male fitness of hermaphroditic individuals in the presence of CMS and restorers, as a way to estimate the efficiency and the cost of restoration in the *Physa* system.

COMPETING FOR FERTILIZING EGGS IS PHYSIOLOGICALLY COSTLIER THAN PRODUCING EGGS IN A SIMULTANEOUS HERMAPHRODITE. THEN, WHY IS THE MALE ROLE PREFERRED?

Maria-Cristina Lorenzi[1], Franco G. Robles-Guerrero[1], David Costantini[2]

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[2]Muséum National d'Histoire Naturelle, Sorbonne Universités, CNRS/MNHN, France

A crucial assumption in evolutionary biologyis that eggs are costlier to produce than sperm. As a consequence, at each mating, females are expected to pay larger costs than males; similarly, hermaphrodites playing the female role are expected to pay larger costs than those playing the male role. While measuring the costs of reproduction in separate sex organisms has proven difficult because males and females differ in many traits besides gamete size, we did that in hermaphrodites, where the two sexes are associated in the same body. We set up pairs and groups of the marine worms *Ophryotrocha diadema* in order to get relatively female and male-biased worms and we measured the cost they pay to reproduction in terms of oxidative stress. Unexpectedly, hermaphrodites exhibiting female-biased sex allocation (higher egg production) paid lower costs in terms of oxidative stress than those exhibiting male-biased sex allocation.

As the resource investment in eggs is extremely high in these worms relatively to that invested in sperm, the increased reproductive cost associated to the male function should be associated to "male" traits other than sperm production, e.g., motility and mate competition. These results suggest that the cost of reproduction should include more traits than mere gamete production and open questions on why in this species empirical evidence suggest that hermaphrodites share a preference for mating as males.

EVALUATING THE EFFECTS OF HEAT STRESS ON REPRODUCTION OF A HERMAPHRODITIC SNAIL SPECIES

Yumi Nakadera, Shanna van Dijk, Valentina Zizzari, Joris M. Koene

Ecology and Evolution, A-LIFE, Vrije Universiteit Amsterdam, the Netherlands

It is widely recognised that exposure to sub-lethal temperatures affects reproductive performances in diverse organisms. Although these effects have been particularly emphasised in males or male functions, it remains to firmly demonstrate that the consequences of heat on fertility are sex-specific. To contribute to this knowledge gap, we examined the impacts of sub-lethal high temperatures on male and female functions in a simultaneously hermaphroditic snail species, *Lymnaea stagnalis*. We exposed the snails to a control treatment (20 °C) and to two heat stress treatments (24 and 28 °C) for two weeks, and measured their growth, gamete production (sperm, eggs) and mating behaviour. This study fully benefits from the advantages of studying simultaneous hermaphrodites, that is, we can examine male and female functions in a same individual. Moreover, this study provides useful information about the potential fertility crisis going on in natural populations due to global warming.

SPERM STORAGE IN *PLANORBELLA TRIVOLVIS*

Cynthia G Norton and Olivia Anderson

Department of Biology, St. Catherine University, St. Paul, MN, USA

The freshwater snail *Planorbellatrivolvis* provides a model system for investigating hermaphrodite reproduction. Self fertilization is rare, and individuals may mate as male, female, or reciprocally; after mating, sperm is stored with recipients laying eggs for 16-18 weeks after a single mating. One of the key unanswered questions in this and other related species involves the fate of sperm. Very little is known about sperm structure, the pathway of sperm post-copulation or the location of sperm storage in the hours just after mating or in the long term. We carried out experiments to describe and determine the location of sperm produced by snails (autosperm) as well as storage of sperm received after copulation (allosperm), using staining and fluorescence microscopy. We familiarized ourselves with the basic anatomy of snails, searched for and described sperm using the DNA stain DAPI to visualize their nuclei under the fluorescence microscope. Autosperm was found primarily in the seminal vesicles but also in the ovotestes and hermaphroditic duct; these cells have a distinctive spear-shaped head with a long spiraling tail. We then performed mating experiments to track sperm location post-copulation. We incubated snails in a treated tap water with the less toxic stain Hoechst 33342 to label sperm in donor snails, mated them to unstained individuals, then tracked the location and longevity of sperm in recipients either several days after mating or weeks later. Just after mating sperm was located in the sperm receptacle sac while long-term storage appears to occur primarily in the seminal vesicles. Further analysis will be necessary to determine how sperm are allocated for fertilization, particularly how autosperm are distinguished from allosperm.

SEX AND THE CITY –HOW SOCIAL ENVIRONMENT INFLUENCES BODY GROWTH AND SEX CHANGEIN A SEQUENTIAL HERMAPHRODITE

Pooja Radhakrishnan, Noé Saboul, Franco Gerardo Robles-Guerrero, Maria-Cristina Lorenzi

Experimental and Comparative Ethology Laboratory (LEEC) UR 4443, Sorbonne University Paris North

Sequential hermaphrodites adjust their sex allocation by delaying or accelerating sex change, thus varying the resources allocated to either sex. The degree to which the plasticity of sex allocation is socially determined, however, is not well understood. Moreover, existing empirical studies focus almost exclusively on sexually mature adults, which overlooks crucial aspects of how the social environment shapes early life development and how different growth patterns may affect the timing of sex change. *Ophryotrocha puerilis* are protandrous polychaetes. By exposing larvae to varying numbers of adult and young conspecifics or by keeping them in isolation, we examined whether these worms modulate body growth and the extent to which it influences their sex allocation. If larvae adjust their growth rate and sex allocation in response to their social environment, on the one hand, worms should accelerate body growth and change sex earlier when isolated, while conversely, in the presence of conspecifics, they should grow slowly and delay sex change. As predicted, we found that worms grew faster and changed sex sooner when isolated, whereas they grew slower and spent longer as males with an increasing number of conspecifics. Worms also adjusted these traits at varying lengths, depending on the sex and size of the individuals in their environment. Our study provides evidence of plastic early-life development and shows that the timing of sex change and the body size at which it occurs are particularly important for understanding how life history influences an individual's reproductive strategies.

SPERM MORPHOLOGY AND REPRODUCTIVE SUCCESS IN THE HERMAPHRODITIC FLATWORM, *MACROSTOMUM LIGNANO*

Santhosh Santhosh and Lukas Schärer

Zoological Institute, Department of Environmental Sciences, University of Basel.

In reciprocally-mating simultaneous hermaphrodites, where individuals may mate frequently in an attempt to give sperm away, they unavoidably also receive sperm from their partners. As a result, post-copulatory sexual selection—through sperm competition and cryptic female choice—is expected to be very important, yet research attempting to understand mechanisms of post-copulatory sexual selection in such systems is still relatively scarce. Previous research on the reciprocally-mating free-living flatworm *Macrostomum lignano* has shown that most of the variance in male reproductive success is indeed explained by the post-copulatory fitness components, namely the sperm donor's ability to store sperm in a sperm recipient and to convert stored sperm into successful fertilizations. Sperm morphology in *M. lignano* is complex, and includes the anterior feeler, the two stiff lateral bristles and the posterior brush. In this ongoing project, we aim to understand the significance of the variation in these structures in attaining sperm storage, and ultimately fertilization success, in a mating partner. A range of GFP(+) inbred isolines of *M. lignano (LM lines)*, exhibiting between-line genetic variation in sperm morphology, provide a suitable platform to investigate the role of sperm morphology in influencing reproductive success. The GFP(+) LM lines express a green fluorescent protein ubiquitously in all cells, including the sperm cells, thus enabling us to differentiate GFP(+) sperm from GFP(-) sperm within the female sperm storage organ. By competing the LM lines with varying sperm morphologies against a common GFP(-) competitor, we study the relative competitiveness of contrasting sperm morphologies in the post-copulatory fitness components. The results from this study will improve our understanding of post-copulatory sexual selection in the less studied simultaneously hermaphroditic systems.

EFFECT OF MATING GROUP SIZE AND MATE NOVELTY ON COPULATION FREQUENCY INTHE LAND SNAIL *CORNU ASPERSUM*

Anthi Stoforiadi and Alexandra Staikou
Deparrtment of Zoology, School of Biology, Aristotle University, Thessaloniki Greece

Previous studies on intraspecific variation of mating behavior in the simultaneously hermaphroditic land snail *Cornu aspersum* have revealed consistent differences among populations in mating traits such as mating frequency and mating duration. In this species field studies have revealed that populations in dry Mediterranean habitats often are found in high density and large aggregations. Therefore our behavioral observations in the lab were performed on large snail groups and densities that simulated usual density conditions in the field. In this study we tried to evaluate the effect of mating group size on mating rates in adult field caught snails. We performed detailed daily observations and recorded mating activity of 408 snails arranged in groups of two, four, eight and 14 individuals during a two months period. Furthermore we tried to assess the effect of mate novelty on sexual motivation of already mated snails. For this purpose after the initial 3-4 days period of frequent matings which is typical for mating pattern in this species we replaced half of the snails in the rearing boxes with non familiar individuals and recorded their mating behavior. Our observations regarding the effect of MGS revealed an increase of mating frequency at the intermediate mating group size of eight individuals and an increased number of matings with novel partners (Coolodge effect) especially when snails were given the opportunity to select between familiar partners and novel ones.

POSTERS

HOW DO HERMAPHRODITIC POLYCHAETES SIGNAL THEIR SEX? FIRST EVIDENCE

Elise Jeanne, Franco Robles-Guerrero, Maria-Cristina Lorenzi

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Although sexual signals are well documented on separate sex-species, little is known about how hermaphrodites signal their sex, even though they are extremely sensitive to the presence of conspecifics and adjust their sex allocation accordingly. When few partners/rivals are there, they invest most of their reproductive resources in the female function, whereas in larger groups they exhibit relatively more male-biased traits. However, it is uncertain what cues they use to estimate their social environment. We addressed this question in the outcrossing simultaneously hermaphroditic marine polychaete *Ophryotrocha diadema*, where individuals perceive conspecific presence via species-specific, water-borne chemical cues. We exposed pairs of worms to either clean or conditioned water in which twenty mature conspecifics were kept either in isolation (so that they biased their sex allocation towards the female function) or in groups (male-biased sex allocation). We measured their response in terms of investment in both the male (i.e. motility) and the female (i.e. egg and cocoons) functions. We expected that, if they only assessed the quantity of potential mates/rivals, the worms would exhibit male-biased sex allocation irrespective of whether conditioned water came from male or female-biased worms. In contrast to our expectation, the results suggested that worms detected the presence of potential partners/rivals and adjusted their sex allocation differently depending on whether they were exposed to water from male or female-biased worms, suggesting that sexual signals/cues in these hermaphrodites might convey information about sex allocation.

MATING MOTIVATION: THE EFFECT OF ELIMINATING THE MALE FUNCTION ON SEXUALBEHAVIOUR IN A SIMULTANEOUS HERMAPHRODITE

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That unequal investment in gametes, called anisogamy, leads to sexual conflict is well-accepted for separate sexed species. Simultaneous hermaphrodites also produce two types of gametes, but the conflict gains in complexity because each sperm donor is also a sperm receiver. For the great pond snail *Lymnaea stagnalis* previous studies indicated that being inseminated can be costly for the sperm recipient's reproductive success because accessory gland proteins transferred in the mating partner's ejaculate can temporarily lower female and male reproductive success. As a result, potential sperm recipients have been found to exhibit behaviours that suggest that they are trying to avoid being inseminated. To find out whether such behaviours are indeed motivated via the sperm receiving, female role, we here experimentally eliminated the male role using a simple surgical procedure. We subsequently observed mating behaviour and quantified hatching success of the eggs laid as a proxy of female reproductive success. Although we did not find an effect of feminization on hatching success, we did find a decrease in biting of the mating partner, one of the previously identified female behaviours, in feminized individuals compared to sham operated and control snails. The other prominent female behaviour, crawl-out, did not differ between the treatments, which suggests that this is not eliminated by the surgical treatment and is motivated via the female role. These findings suggests that feminized snails invest less in biting behaviour because the male role is eliminated and they no longer have to defend their paternity success. The used experimental approach and species enabled us to disentangle sexual motivations of a simultaneous hermaphrodite and show that not all components have the same motivational basis.

JUICY GENOME INFORMATION: COMPARATIVE GENOMICS OF ACCESSORY GLAND PROTEINS IN GASTROPOD MOLLUSCS

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As modulators of reproductive biology, accessory gland proteins (ACPs) are essential ingredients of an ejaculate, the complex cocktail of spermatozoa and other substances. In molluscs, study of ACPs has focused mainly on two gastropod species, *Lymnaea stagnalis* and *Cornu aspersum* (formerly *Helix aspersa*).ACPs trigger behavioral and physiological changes in recipient snails, thought to benefit reproductive success after mating. To address the underlying fundamental questions about ACP function and -evolution in these hermaphrodite snails, it is crucial to identify ACP homologs in additional gastropods. With genomic Next-Gen Sequencing (NGS) data at our disposal, we applied previously obtained peptide sequences to characterize full gene sequences for *L. stagnalis* ACPs and *C. aspersum* love dart allohormone. Subsequent computational sequence similarity searches against NGS data to take inventory of ACP-encoding sequences among select hygrophilid and stylommatophoran gastropods indicated that some ACPs are present in many species, while others are species-specific. These initial intra- and interspecific comparisons, i.e. exploration of micro- and macro-evolutionary patterns, provide ample direction for follow-up studies at the genomic/transcriptomic level, but also at the functional level. We will present plans to proceed and propose some key species and comparisons that we anticipate will help to broaden knowledge of snail ACPs.

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