

and correspond ecologically. For instance, the common redstart is a bird species breeding in the lowlands, whereas the black redstart is native to higher altitudes. Some species such as common swift and kestrel, which are originally adapted to enduring in rocky areas, even found a secondary habitat in the house facades and street canyons of towns and big cities. Classic rock dwellers include peregrine, eagle owl, rock-thrush, snowfinch and alpine swift. The presentation focuses on the biology, causes of threat as well as conservation measures taken by the national park concerning the species golden eagle, wallcreeper, crag martin and ptarmigan. Birds breeding in the rocks might not be that high in number, but their survival is all the more fascinating and worth protecting as such!

Abstracts Talks

Alpine and other land snails

Arranged in chronological order of the program

Range-constrained co-occurrence simulation reveals little niche partitioning among rock-dwelling *Montenegrina* land snails (Gastropoda: Clausiliidae)

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Taxon co-occurrence analysis is commonly used in ecology, but it has not been applied to range-wide distributional data on partly allopatric taxa because existing methods cannot distinguish between distribution-related effects and taxon interactions. Our first aim was to develop a taxon co-occurrence analysis method that is also capable of taking into account the effect of different ranges and can handle faunistic records from museum databases or biodiversity inventories. Our second aim was to test the independence of taxon co-occurrences of rock-dwelling gastropods at different taxonomic levels, with special focus on the subfamily Aloiinae of the family Clausiliidae, and in particular the genus *Montenegrina*.

We introduced a taxon-specific metric that characterizes the occurrence probability at a given location. This probability was calculated as a distance-weighted mean of the taxon's presence and absence records at all sites. We applied corrections to eliminate the distorting effects of varying sampling intensity in our data set. Then we used probabilistic null-models to simulate taxon distributions under the null hypothesis of no taxon interactions and calculated pairwise and

cumulated co-occurrences. Independence of taxon distributions was tested by comparing observed co-occurrences to simulated values.

Significantly fewer co-occurrences among species and intra-generic lineages of *Montenegrina* were observed than expected under the assumption of no taxon interaction. This indicates that species divergence preceded niche partitioning and suggests a primary role for non-adaptive processes in the speciation of rock-dwelling gastropods. The method can account for the effects of distributional constraints in range-wide datasets of records, making it suitable for testing ecological, biogeographical or evolutionary hypotheses where interactions of partly allopatric taxa are in question.

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Peculiar points in the phylogeny of the rock-dwelling land snail genus *Montenegrina*

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Montenegrina is a hyper-diverse land snail genus with 29 known species and 106 subspecies, although its distribution range is restricted to the western part of the Balkan Peninsula. The current systematics of *Montenegrina* is mainly based on conchological traits (Fehér & Szekeres, 2016). In the present study we aimed to test the congruency with molecular genetic data based on sections of three mitochondrial genes, *cytochrome c oxidase subunit 1*, *16S rRNA*, *12S rRNA* (*COI*, *16S*,

12S) as well as a short section of two nuclear histone genes (*histone 3 and histone 4*), including the spacer region (*H3H4*). We included nearly 800 individuals assigned to 104 different taxa from 368 localities, covering the whole distribution range. Phylogenetic trees were calculated and compared with the current taxonomic system of *Montenegrina*. Furthermore, the diversity, based on average p-distances, was calculated between and within species as well as between and



Fig. 1. In the course of sampling all taxa of the rock-dwelling genus *Montenegrina* we came across very interesting places, like this hermitage Panayia Eleoussa which dates back to the beginning of the 15th century (right, Foto: H. Sattmann). It is located on the shore of the Prespa lake, where *Montenegrina dofleini prespaensis* (left, Foto: Z. Fehér) occurs.

within populations and clades. The results show a high concordance between traditionally gained taxonomy and the phylogenetic tree. Only in a few cases (around 5%) big discrepancies were found. Possible explanations for these cases and peculiar stories behind the ecology and lifestyle of several interesting taxa are the main focus in this talk. Generally, this study revealed high genetic diversity within this rock-dwelling door snail genus and indicates that the large number of taxa, which mostly have very narrow distribution ranges, are not the result of a taxonomic over-splitting, but reflects mostly actual phylogenetic relationships.

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Stability and variability of anatomical traits in *Montenegrina* species (Gastropoda, Clausiliidae): the case of *M. subcristata* and *M. perstriata*

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The genus *Montenegrina* O. Boettger, 1877 (Clausiliidae) has been recently revised by Fehér & Szekeres (2016) on the basis of a study of shell morphology. Many new taxa have been described due to the discovery of new populations. Moreover, the systematic position and nomenclature of many other taxa have been reconsidered and eventually modified by virtue of synonymization and moving one taxon from a species to another. Often, subspecific taxa have been elevated to species-rank or vice versa. In fact, Fehér and Szekeres (2016) clearly highlighted the complicated nomenclatural history that marks almost all the *Montenegrina* taxa, with remarkable changes in their specific position. These swings were mostly due to the different points of view of the authors, who dealt with the shell morphology, rather than by an univocal and thorough morphological-anatomical approach.

As a further step in the study of this speciose clausiliid genus, an extensive morphological study of the genitalia has been performed and it is currently ongoing with the aim to identify new characters and features to better define the taxonomy and the systematics of this genus. This comprehensive analysis represents even a new approach for the whole family Clausiliidae. To date, 86 out of the 107 (approximately 81%) taxa of *Montenegrina* (as listed in Fehér & Szekeres, 2016) have been dissected, in total 116 populations and 203 specimens. These numbers will increase as new populations have been recently collected.

The morphological analysis of the genital apparatus revealed an intriguing overall situation. First, it allowed to ascertain the limits of the shell-based taxonomy concerning this clausiliid group. This is here exemplified by the two species *Montenegrina perstriata* (Wagner, 1919) and *Montenegrina subcristata* (Pfeiffer, 1848). Both species show a degree of plasticity and variability of the shell, since all the investigated populations presented slight but somehow significant differences in their morphology. This is reflected both by their high number of subspecific taxa and their systematic-

nomenclatural history. Following a thorough anatomical investigation focused on the inner features of the distal genital apparatus, the two species present a diametrically opposite situation. *Montenegrina subcristata*, despite its large distributional range and the good number of investigated populations, shows a remarkable stability of the genital features that fully meets the recent view of Fehér and Szekeres (2016) (also in accord with unpublished molecular genetic data) to merge all the former subspecific taxa and synonymize them into the nominal taxon. On the contrary, the subspecific taxa of *Montenegrina perstriata* revealed an astonishing genital diversity among all the populations. In the case of *Montenegrina perstriata drimica* Nordsieck, 1972, a subspecies distributed along the Upper valley of the Crni Drin between the Globočica Lake and Debar in Macedonia, seven populations have been subjected to genital morphological analysis. The different populations, ascribed to this subspecies following the shell morphology, presented anyway a slight variability in the shell features but likewise showed substantial anatomical differences seen in Fig. 1. The four populations depicted in Fig. 1 (13-24) present three distinct genital arrangements, in particular concerning the inner ornamentation of the vagina and penis. Combining these totally new anatomical-morphological results with the upcoming molecular genetic data will probably allow to redefine the systematics and the nomenclature of the whole *Montenegrina* genus by means of a new integrative approach.

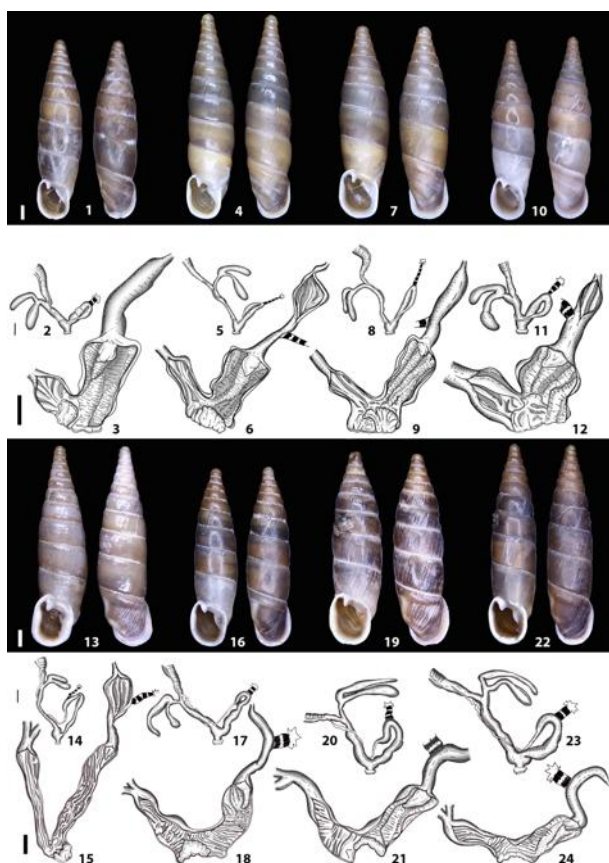


Fig. 1. *Montenegrina* spp. 1-12 *Montenegrina subcristata*: 1-3 Albania, Shkodër district, Shkodër, S side of Rozafa Hill, 1 shells, 2 whole distal genitalia, 3 inner distal genitalia; 4-6 Montenegro, Cetinje, on walls W of the the town, 4 shells, 5 whole distal genitalia, 6 inner distal genitalia; 7-9 Montenegro, Rijeka Crnojevic, rocks along the road, 7 shells, 8 whole distal genitalia, 9 inner distal genitalia; 10-12 Montenegro, Nikšić, ca. 2 km on the road to Podgorica, 10 shells, 11 whole distal genitalia, 12 inner distal genitalia; 13-24: *Montenegrina perstriata drimica* (sensu Fehér & Szekeres, 2016): 13-15 Macedonia, Lukovo, 13 shells, 14 whole distal genitalia, 15 inner distal genitalia; 16-18 Albania, Dibrë district, gorge of Lumi i Drinit te Zi, 16 shells, 17 whole distal genitalia, 18 inner distal genitalia; 19-21 Macedonia, Prov. Debar, Debar, at the dam of Crni Drin River, 19 shells, 20 whole distal genitalia, 21 inner distal genitalia; 22-24 Mecdonia, Prov. Struga, Crni Drin valley, Modrić junction, 22 shells, 23 whole distal genitalia, 24 inner distal genitalia

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Population size, density and dispersion patterns of *Montenegrina subcristata* in the area of Virpazar (Montenegro)

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Introduction

Snails of the genus *Montenegrina*, which includes a large number of taxa (29 species and more than 100 subspecies) are distributed in the southwestern part of the Balkan Peninsula (Fehér and Szekeres 2016). Several studies on this genus have been performed concerning its taxonomy, phylogeny, phylogeography and distribution. However, knowledge about biology and ecology of the species of the genus *Montenegrina* is scarce, like in many terrestrial snails. Only some general assumptions related to similar species are existing (e.g., Schilthuizen 1994; Schilthuizen and Lombaerts 1994, 1995; Welter-Schultes 2000). But such knowledge would facilitate to understand evolutionary processes and mechanisms of speciation. In the present study we focused on population ecology of *Montenegrina subcristata* during one season. In a topotypic population of the subspecies *M. subcristata sublabiata* Wohlbered 1907, at one site in Virpazar, a monitoring pilot study was performed. The aim of this research was to monitor the population, to estimate population size, density and dispersion on a small scale and to record activity patterns. One assumption was that the migration behavior of the snails and also their number would be influenced by microclimatic conditions. We expected that the snails would be quite inactive during warm and sunny days, mostly hidden in crevices while the highest activity will be certainly noticeable after the precipitation, when the conditions for their activity are also most favorable.

Methods



Fig. 1. Study site in the Virpazar area, Montenegro

Three points (A, B and C) were selected in the Virpazar area where the research is being carried out. Based on photos, maps of the study sites have been drawn. At each location, temperature and humidity was monitored at several spots. We started monitoring in April 2017 and it will be performed during one season. The three areas were investigated once a week. First, the snails were searched and registered, counted, and their location in the habitat was documented by photographs as well as via digital maps and translated into a spreadsheet format via a coordinate system. We classified the size and life stage of the snails as juvenile, subadults and adults. Subadults and adults were marked

individually with a letter/number code using non-toxic water proof markers. Juvenile individuals were marked with a dot. During each field visit, marked individuals were documented and their position mapped on a photographic map. New individuals were marked. For recaptured individuals distances from the previous place were measured as a dispersive distance. A protocol was

established to document the counts and mark-recapture procedure.

Estimating the size and density of the population should be done by the "Capture, mark, recapture" method (CMR). Concerning dispersion, every new distance from the previous place is calculated as a dispersive distance. After analysis of mark-recapture data, population size, density and dispersion ability of these animals can be determined. Furthermore, dispersion distance can be calculated, when all distances are accumulated.

Results

First results show that numbers of newly marked individuals (juvenile, subadults and adults) are quite different between these three study areas. Area A is the most dominant one, followed by point B and finally point C, which is recognized as the poorest among them. As we have assumed, the highest activity and the highest number of the registered individuals, both newly marked and already marked, was observed during cloudy and rainy days. During warm and sunny days, the snails were inactive, usually hidden in crevices, between plants and some of them found their shelter in small holes in the soil. As far as their migration is concerned, it is interesting to see that some marked adults from area A were registered on area B and vice versa. From April till July we have noticed a significant change in the number of individuals (all categories included) in all areas. Monitoring is still going on and calculations will be performed at the end of the season. Preliminary results will be presented here.



Fig. 2. *Montenegrina subcristata*

Conclusion

Research of this type has not been done in this snail genus before, and thus represents an innovative approach delivering data that may help to answer various crucial biological questions. The obtained results will help to address important issues of the evolution of this group and mechanisms such as adaptations, selection and speciation. This research can provide

comparative data for some similar research on other species.

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Acknowledgements

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Shell adaptations for heat and water management in a rock-dwelling snail

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Morphological variation often is attributed to differential adaptations to diverse habitats, but adaptations to a similar environment do not necessarily result in similar phenotypes. Adaptations for water and heat budget are crucial for organisms living in arid habitats, and in snails variation in shell morphology has been frequently attributed to selection by stressful environmental factors (Cook 2001). However, their phenotypic divergence often is not accompanied by a relevant niche differentiation and consistent relationships with environmental correlates are lacking (Goodfriend 1986, Gittenberger 1991).

In the species-rich pulmonate genus *Albinaria*, there is great size and shape variation between and within species, and there are two major shell sculpture morphotypes (ribbed and smooth). However, little was certain about its inter- and intra-specific geographical size, shape and ribbing variation. Therefore, we used an inclusive set of *Albinaria* (62 populations of 28 species) to investigate the agents that favor the evolution and maintenance of alternative shell phenotypes, in a context of ecological and evolutionary tradeoffs, considering the effects of phylogeny, and unbiased size and shape estimates, derived from geometric morphometrics. First, we examined whether distinct sculpture morphotypes are associated with size and shape changes and can be unambiguously recognized among and within species. Second, in lab experiments, we investigated whether shell traits are correlated to water and heat budget and, thus, with an ability of these snails to overcome stressful conditions in semi-arid ecosystems. Third, we examined if climatic and geographical gradients are important in shaping the variation of shell traits, and hence, whether these shell characteristics evolve nonrandomly, converging differently in dissimilar climatic regimes.

We found unambiguous size and shape discrimination between the two morphotypes. Ribbed shells are lighter, taller, and slimmer and have a smaller aperture than the smooth ones.

Moreover, significant correlations between shell traits and heat/moisture budget and climate/geography were revealed. Ribbed and taller shells retain more water on their shell surface and, on the other hand, smooth shells exhibit lower water permeability. Therefore, two strategies are being used to prevent water loss, active retention or resistance to loss.

Consequently, different alternative solutions evolved and were retained as responses to the same stressful factor by the two distinct shell morphotypes. Larger shells occur in southern latitudes, mostly on islands, and at sites where there is a shortage of rainfall. Therefore, the variation of the examined traits is nonrandom with respect to location and to climate, and their evolution can be attributed to selection by environmental factors, with water availability being the key driving agent of body-size variation.

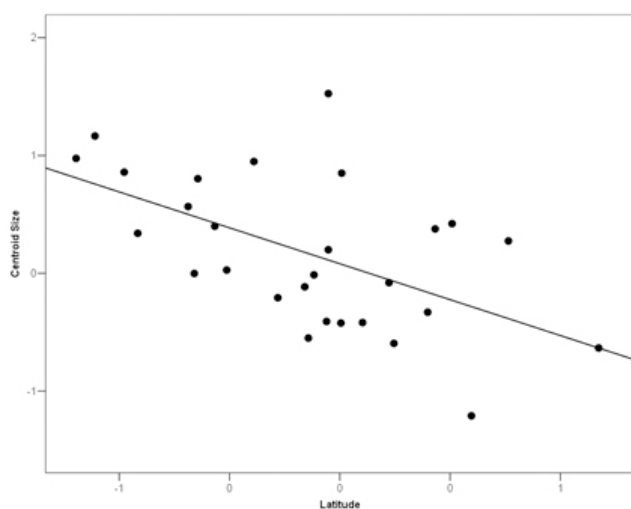


Fig. 1. Regression of centroid size vs. latitude using Phylogenetic Independent Contrasts Analysis.

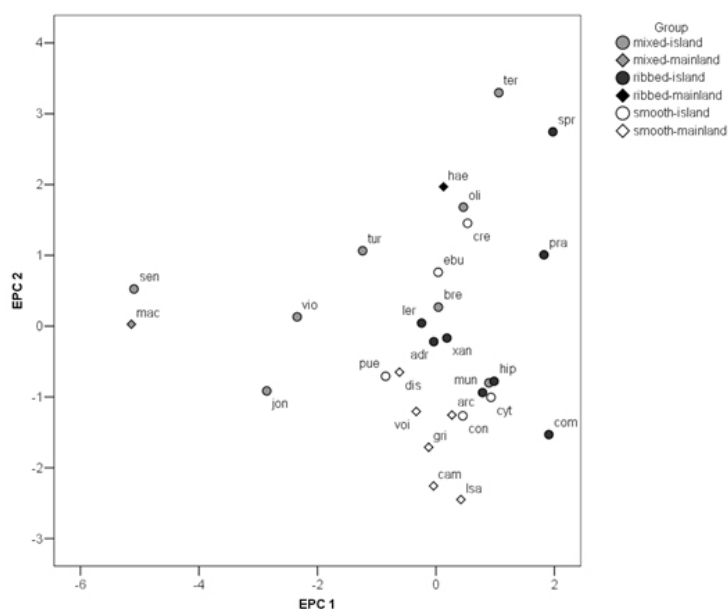


Fig. 2. Ordination of the studied *Albinaria* species with EPCA (Evolutionary Principal Components Analysis) using five predictive variables. The scatterplot of species factor scores shows that most species are grouped near the plot origin. However, on the right upper part of the graph are species having large and slimmer shells, reflect more, retain more water on their surface and are losing more water through their shell. On the left lower part are small and wider species that reflect less, retain less water on their surface and are losing less water through their shell.

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The subterranean snails of genus *Zospeum* (Eupulmonata, Ellobioidea Carychiidae), what do we know about them

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The minute troglolithic snails of the genus *Zospeum* inhabit caves of Northern Spain to the Balkan Dinarides. Most species were described in the latter half of the 19th and 20th centuries based on shell characters such as whorl number, aperture dentition, and shell size as well as shape and number of lamellae circumscribing the columella. *Zospeum* shells typically tend to be very variable in shape from one population to the other and frequently show wide variability within the same population. Twenty-four species and ten subspecies have been described (Jochum et al., 2015). There are questions concerning the validity of many of these species.

Six anatomical studies provide the current knowledge upon which morphological findings of this investigation are based. Bole (1974)

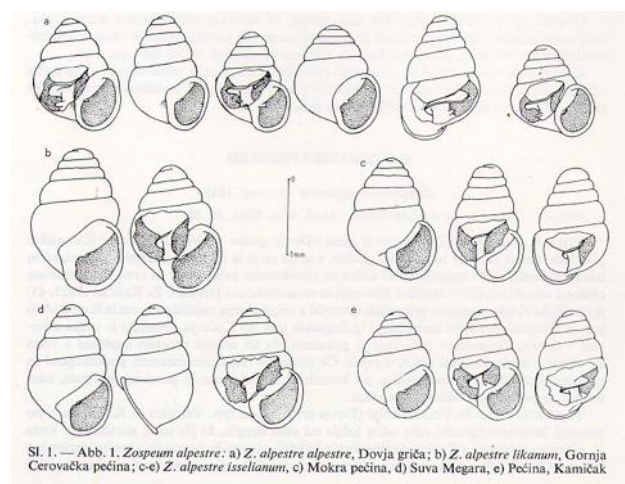


Fig. 1. *Zospeum alpestre* from different caves (drawing J. Bole)

anatomically examined four different species and subspecies of *Zospeum*, emphasizing that his findings provided nothing taxonomically remarkable. Giusti (1975) conducted the first anatomical investigations on *Zospeum spelaeum* (Rossmässler, 1839) and *Zospeum tellinii* Pollonera, 1889. De Mattia (2003) specifically compared the genital anatomy of *Zospeum spelaeum* from six populations from different caves and one population of *Z. isselianum* from the widely cavernous region of Trieste. Weigand et al. (2011) conducted the first molecular analysis of seven Dinaric *Zospeum morphospecies*. Jochum et al. (2015) find high intraspecific variation for *Zospeum* collected in different caves while a high incidence of cryptic allopatric speciation for several taxa was uncovered.

Knowledge about the ecology of the *Zospeum* species is very scarce. It is known that they live in caves and fissures and that they probably feed on the detritus that is found in loam and in cave sediments. In caves, they occur on walls, on the ground beside puddles, or on organic matter (rotten wood) (Slapnik, 2001).

We also know something about activity and movements in undisturbed snails of *Zospeum isselianum* in the “alpine karst” caves. The snails passed over distances from 1 to 15 cm per week. Snails were more or less creeping around the place where they were first found, or they moved to the upper part of the sampling surface (Slapnik, 2001).



Fig. 2. *Z. spelaeum schmidtii* (Foto: R. Slapnik)



Fig. 3. Distribution map of genus *Zospeum*

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Phylogeny of the land snail genus *Schileykula* (Gastropoda: Pulmonata: Orculidae) based on mitochondrial and nuclear DNA sequences - Evidence for repeated hybridization

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The land snail genus *Schileykula* Gittenberger, 1983 is distributed in arid limestone areas, from western Turkey to north-western Iran. The cylindrical shells are small (4.7–11.8 mm in height) and the last shell whorls bear several inner lamellae and plicae, which probably serve as barriers against predators and body-water loss. These structures of the aperture play an important role in species recognition. In his revision on Asian Orculidae, Hausdorf (1996) classified eight species and eight subspecies within *Schileykula*, two species were described only recently.

In the present study, we performed a molecular genetic study on nine out of ten species including all four subspecies of *Schileykula trapezensis* and three of six subspecies of *Schileykula scyphus*. A section of the mitochondrial *cytochrome oxidase subunit 1* gene was analyzed in 56 specimens of *Schileykula* and 31 specimens of the outgroup *Sphyradium doliolum*. For 35 *Schileykula* and nine *Sphyradium* specimens we additionally obtained partial sequences of the mitochondrial genes for the *12S rRNA* and the *16S rRNA*, and a section of the nuclear *H4/H3* gene cluster.

The results of the phylogenetic studies based on the mitochondrial and nuclear makers disagree with the present morphology-based classification. As a consequence, some taxonomical conclusions are drawn (some subspecies are elevated to species level, and one species is classified as a subspecies of another species). The patterns in the mitochondrial and nuclear trees differ in regard to the grouping of some species or specimens, providing evidence for at least two independent hybridization events. The present results exemplify the importance of integrating morphological and genetic data and imply that (at least sporadic) hybridization across distantly related lineages might occur more frequently than previously assumed.

Progress in understanding the European species of *Bythiospeum* with an outlook on Austrian taxa

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Species of the genus *Bythiospeum* Bourguignat, 1882 are confined to groundwater systems in Europe. First molecular analyses and additional morphological studies of Central European *Bythiospeum* revealed that the currently accepted concept with a comparatively high number of mostly endemic species with narrow ranges is not reflected in the genetic diversity (RICHLING et al. 2016). Data suggest that the number of well differentiated species in Germany drops from 25 to three with one locally endemic and two more widely distributed species. The recent distribution pattern and low diversification within the clades/species is best explained by postglacial

recolonisation of Southern Germany. However, the localisation of possible refugia still remains obscure because the samples did not yet cover the – newly understood – full range of the species. Therefore, we extended the sampling towards the Southwest and East, i. e. Southeastern France and Austria. Equally to Germany with its previously assumed high diversity of *Bythiospeum*, current inventories of the Austrian mollusc fauna list twelve endemic species and additional taxa in the genus *Iglica*. The latter is not clearly understood in its phylogenetic relationship to and differentiation from *Bythiospeum*. The current presentation will show and discuss preliminary results.

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Where is the border to neighbors garden? – Assessing population size in *Cylindrus obtusus*

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Sampling strategies are always among the first and most important decisions to make in a zoological project. In the course of our numerous excursions to collect Alpine land snails we have been wondering how large a snail population might be and how to define snail populations. How distant should individuals be collected from each other to avoid getting only members of the same snail family? As population genetic analyses were part of our study on *Cylindrus obtusus* (Helicidae), we chose this species to have a closer look on population size. *C. obtusus* is a hermaphroditic land snail, endemic in the Austrian Alps, which is restricted to high elevations (1600 to 2500 m asl) and limestone. As a specialist of high alpine rocky habitats, *C. obtusus* has a quite patchy distribution area (Klemm 1974). Previous investigations revealed geographic differences in the genital apparatus: All specimens from the more western populations had one stylophore and two equally developed mucus glands more than twice the length of the stylophore. In contrast, in individuals from the eastern margin of the species these structures were highly variable (Schileyko, 1996, 1997; Schileyko et al. 2016; Zopp et al., 2017). Microsatellite data showed that all eastern populations (from Veitsch to Schneeberg) have a high excess of homozygous individuals. Nearly all individuals are homozygous in all microsatellite loci (although different alleles were found within populations). Kruckenhauser et al. (2017) concluded that in the eastern populations selfing as predominant reproducing strategy is the cause of this excess of homozygotes.

However, it also might be that population structures in the two geographic regions are different and the observed phenomenon is due to extremely high population sub-structuring in the eastern populations. Earlier investigations on individual numbers and dispersal rates by Bisenberger et al. (1999) in the Gesäuse were a first attempt to estimate population size in *C. obtusus*. In the present study we take a new approach: Nine researchers located 3 m to 28 m apart from each

other collected 20 individuals in a one-meter radius. This procedure was followed in one of the selfing populations on the Schneeberg, and in an outcrossing population on the Hohe Nock mountain. The 348 samples were analysed with the same microsatellite loci as in Kruckenhauser et al. (2017). Data analysis with Bayesian cluster analysis and principal component analysis will show, whether the populations at these two sampling grids are sub-structured and will give a better assessment of the population size of *C. obtusus*.



Fig. 1. *Cylindrus obtusus*



Fig. 2. Sampling grid on the Hohe Nock. Six of the nine samplings sites are indicated by persons, one by a rucksack.

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Reduction as one of the important ways of Pulmonata (Gastropoda) evolution

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In the stated subject the main question to be discussed is: reduction of what? Let us consider separately the main components of an organism.

1. Shell. Numerous cases of shell reduction at all stages are known in the row: snail – semislug – slug.
2. Cephalopodium and its elements. Cases of the cephalopodium reduction are unknown, but in some small mollusks (Vertiginoidea) the lower tentacles are absent. This phenomenon is secondary and, perhaps, connected with miniaturization.
3. Nervous system. Evident cases of reduction are not established.
4. Digestive system. Cases of reduction are unknown, but in the streptaxid genus *Careoradula* (Seychelles) both odontophore and radula are totally absent (Gerlach, Bruggen, 1998). Shortened (reduced) intestine in carnivorous mollusks is not a real reduction and is connected with their specific nutrition. The same phenomenon is observed in all carnivorous animals.
5. Excretory system. Cases of reduction are unknown.
6. Respiratory system. Cases of reduction are unknown, but in slugs the lung is comparatively smaller than in related snails. Seemingly, this is connected with a reduction of volume of the visceral sac and an increasing importance of skin breathing.
7. Circulatory system. Cases of reduction are not established but in the majority of small snails vascularization of the lung roof is very weak (*Vertigo*, *Truncatellina*, *Punctum*).
8. Muscular system. Cases of reduction are unknown.
9. Reproductive tract. Cases of reduction of this apparatus as a whole are not known, but there are numberless cases of reduction of various additional organs and their elements (flagellum, stylophores and their derivatives, sarcobelum, penial or epiphallic caecum, mucus glands, etc.). Thus, the regular and permanent reduction down to full disappearance concerns two structures only: shell and additional organs of the reproductive tract. That is why pulmonate taxonomy is mainly based on just these structures. In essence, the current systematics of Pulmonata is the systematics of reproductive tract and, to a lesser degree, their shell.

The phenomenon of shell reduction I have already considered here, in our previous seminar (Schileyko, 2014). In short, I consider the shell as a “break” of biological progress, since the shell, being an effective protection, significantly inhibits the progressive evolution of mollusks, since for any external influences the snail responds with a stereotyped reaction – by withdrawing into the shell. A slug, devoid of such protection, must assess the situation more critically – to crawl away, to stay in the place, to hide in a shelter or something else. In other words, slugs are “cleverer” and more flexible in their behaviour than snails. This is confirmed by the fact that the density of synapses in the procerebrum of a slug (*Limax maximus*) is much higher than in the brain of a snail (*Helix pomatia*) (Zs.-Nagy and Sakharov, 1970). That is why it is no surprise that we observe a universal tendency to the loss of shell among many taxa (there are more than 20 cases of independent shell reduction in Stylommatophora) in the extant species.

Let us consider the cases of reduction of elements of the reproductive tract. In this context, I would like to recall a well-known fact: the reproductive tract is the only system that does not play a vital role in maintaining the life of the individual and the only system that ensures the continuation of the life of the species. From this fact, in particular, it follows that the morphological

transformations of the reproductive tract can be carried out beyond any connection with the evolution of other organs and systems of an organism.

For further discussion one has to answer the question: what is the original state for the pulmonate reproductive tract – simplicity (additional organs are absent) or complexity (genitalia have accessory organs)?

Simplicity can be of a twofold nature: either it is the initial condition, or it is a consequence of the reduction (disappearance) of some additional elements. So, there is an important problem: what is the plesiomorph condition for Pulmonata and, in particular, for Stylommatophora – simplicity of the reproductive tract or complexity. I presume that the plesiomorph condition for Pulmonata is simplicity. It follows from the fact that the genitalia of all Basommatophora, as a rule, do not possess any accessory organs, and that Stylommatophora originated from basommatophoran ancestors.

There are a number of groups whose reproductive tract is always and, seemingly, originally simple: Partuloidea, Endodontoidea, Streptaxidae, Polygyridae, Acavidae, Achatinidae, Clavatoridae, Bulimulidae, Urocoptidae, Clausiliidae, Zonitidae, and Succineidae. So, these groups are out of the current discussion. At the same time, for many groups the initially complex genitalia are very characteristic: Pupilloidea, Enidae, Bradybaenidae, Xanthonychidae, Epiphragmophoridae, Cochlicellidae, Helicarionidae, Helicodontidae, Hygromiidae, and Helicidae. The cases of reduction of accessory organs of the reproductive tract in listed taxa are numerous and various.

Thus, for orthurethral groups which, as a whole, are characterized by the presence of a peculiar penial appendix consisting of five sections, in Odontocycladinae (Orculidae) there is the genus *Walklea* with normally developed appendix, and the related genus *Odontocyclas*, which has no appendix. In Orculinae we see the series *Orculella-Schileykula-Orcula*: species of *Orculella* have a modified but quite developed appendix, in the genus *Schileykula* the appendix is rudimentary, and in *Orcula* the appendix is absent. In the species of African genera (*Anisoloma*, *Fauxulus*) the appendix is also absent, but I think, the reduction of the appendix in European and African Orculidae took place independently.

In the family Pupillidae the appendix is normally developed, but in the related family Vertiginidae the appendix is absent.

Among Enidae the majority of the genera have the traditional appendix, but a number of taxa have no appendix (*Mordania* s. str., *Chondrula*, *Meijeriella* and some others). Among three closely related genera of Multidentulinae *Multidentula* has both diverticle of the spermarhecal duct and appendix, *Improvisa* has no diverticle but an appendix is present, *Senaridenta* has a diverticle but appendix is absent. In two representatives of Enidae – *Brephulopsis bidens* and *Geminula isseliana callilabris* – partial reduction of the penial appendix was observed in some populations.

In Bradybaenidae the members of the Aegistinae subfamily have a flagellum while in Bradybaeninae the flagellum is absent.

Among Hygromiidae: members of Trochulinae have 4 stylophores (upper pair is rudimentary, without darts) while in Hygromiinae there are 2 stylophores which occupy an unilateral position on the vagina (upper one is rudimentary).

In the Helicidae family there is a genus *Helix*. Nearly all representatives of this genus have a stylophore and branched mucus glands; however, in the monotypic subgenus *Naegelea* both stylophore and mucus glands are totally absent.

In Helicarionoidea (Helicarionidae, Ariophantidae, Euconulidae) the genitalia have a very complex structure and the full set of additional organs includes sarcobelum, spiral caecum, and lime sac. However, in reality we see a lot of taxa with deprived organs in different combinations.

Reduction can occur in two ways: gradually, over several generations, or instantaneously, through a single mutation. Evidently, the reduction of the shell can occur only gradually, and the sudden mutagenic origin of shell loss can be excluded. Reduction of accessory organs of the reproductive tract may be brought about, as it was noted, in both ways.

1. Gradual reduction is the more orthodox route, the main stages of which one can trace in the chain of recent forms. Such an evolutionary path has been established, for example, for such correlatively related organs as the flagellum and diverticle of the spermathecal duct, the length of which can vary within one population (sometimes down to total disappearance). The gradual reduction is characteristic for the upper pair of stylophores of Hygromiidae where it is possible to trace all stages of reduction. Mucus glands of *Cylindrus obtusus* also demonstrate all stages of reduction.

2. "Instant" and full reduction of organs by mutation. A vivid example of a mutagenic disappearance of organs is a pair of Central Asian species – *Nanaja cumulata* and *Archaica heptapotamica* (Hygromiidae). These two species live together in proportion of about 50/50 and differ by only one feature: the first has two pairs of stylophores, while in the second there is one pair occupying an unilateral position on the vagina.

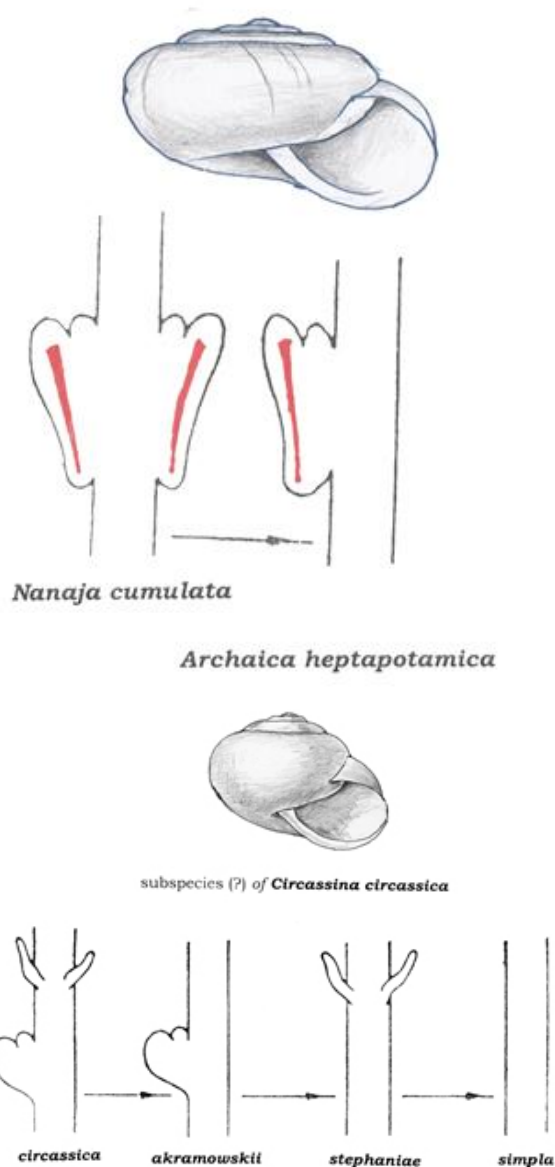
Another good example of mutagenic (instantaneous) reduction, also of Hygromiidae, is *Circassina circassica*. In this species there are four groups of populations (subspecies?) with all possible combinations: a pair of stylophores and mucus glands is present (*Circassina circassica*); stylophores are present but mucus glands are absent (*Circassina akramowskii*); stylophores are absent but mucus glands are present (*Circassina stephaniae*); both stylophores and mucus glands are absent (*Circassina simpla*).

It should be emphasized that no one has ever seen these organs in a rudimentary state - they are either normally developed or there are none at all. The mentioned example with *Helix* – *Naegelea* shows one more case of instant disappearance of all accessory organs.

A particular case of mutagenic reduction is the partial disappearance of additional elements of the reproductive tract. As has been mentioned, this is a rare and rather exotic method of reduction, which is known for two species of Enidae only – Crimean *Brephulopsis bidens* and Asian *Geminula isseliana callilabris*. In these two species, among specimens with a normal penial appendix, specimens have been found in which the basal section of the appendix (A-1) is absent, and A-2 falls directly into the penis. These examples demonstrate that the reduction of accessory organs is a common and widely spread pathway in the evolution of pulmonates.

Naturally, the question arises what could be the causes of organ reduction. I would suggest that there are at least two correlated reasons.

1. Necessity of economy of energy. Indeed, the mentioned additional organs (mucus glands,



stylophores etc.) consist predominately of glandular and muscular tissues which consume much energy.

2. As the reduction concerns mainly the reproductive tract, it is logical to assume that the appearance and complication of various appendages are somehow connected with copulation in the broad sense of the word, in particular, with the formation and complication of isolating mechanisms which could minimize the risk of introgression. Probably the most archaic way to create such mechanisms is morphological complication. However, the appearance of additional morphological structures inevitably entails an additional expenditure of energy.

Theoretical basis for our consideration is the principle of oligomerization of homological organs proposed by V.A. Doghel (1954). The essence of this principle is that the newly formed organs often have multiple anlage, and in the course of further evolution oligomerization takes place, i.e. the number of elements is reduced. As an example, one can specify the American genus *Humboldtiana*, whose members have 4 stylophores, and each of them contains two darts, i.e. the number of stylophores in the hypothetical ancestor was 8. However, there is a monotypic subgenus *Oreades* which has neither stylophores nor mucus glands.

Thus, I have tried to demonstrate that the reduction is a really common method of evolution of pulmonate molluscs.

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