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Diversity of the land snail genus *Helix* and its relatives (Gastropoda: Pulmonata: Helicidae) from Mediterranean origins to postglacial Central Europe

Diverzita suchozemských plžů rodu *Helix* a jejich příbuzných (Gastropoda: Pulmonata: Helicidae) od počátků ve Středomoří po postglaciální střední Evropu

Doctoral thesis

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Praha, 2017

mé Anně

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Mgr. Ondřej Korábek

CONTENT

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ABSTRACT

The family Helicidae comprises the largest and most widely known land snails of the Western Palaearctic. Yet the knowledge of its diversity until recently relied largely on morphology-based taxonomic work from the early 20th century. Molecular phylogenetic data were needed to resolve several taxonomic issues and to understand the biogeographic history of the group. This thesis focuses on an Eastern Mediterranean group of helicid genera, and in particular on the type genus of the family, *Helix* Linnaeus, 1758. From exploring the diversity and relationships of Eastern Mediterranean and Anatolian lineages, this work follows them on their way from diversification centre up to the postglacial fauna of Central Europe. The results are based on analyses of sequences of mitochondrial genes, conchological examinations, and radiocarbon dating of Holocene subfossils. First, we compared the lineage diversity of *Helix* with the conclusions of a recently published morphology-based taxonomic revision. We assembled a representative dataset covering almost all species of the genus as now recognized, as well as most of potentially related genus-level taxa. We refined the genus limits, revealed several species whose delimitation may require further revision, and pointed out probable differences in how species are being delimited in *Helix* and related genera. Greece, the Aegean, and western Turkey were identified as the core area for the diversity of *Helix* and its relatives; the highest diversity of *Helix* species was found along the Alpide belt from the western Balkans to southern Turkey. We uncovered an exclusively European *Helix* radiation with centre of diversity in the western Balkans. Then we focused on two *Helix* species from this group, which were long considered synonyms of other, more common species. *Helix straminea* Briganti, 1825, described from central Italy, turned out unrelated to *Helix lucorum* Linnaeus, 1758. While the latter occurs in northern Italy, it is a species of Anatolian origin and likely an introduced one in Italy. *Helix straminea* originated in western Balkans, where it lives in Albania and Macedonia, and colonized the Apennine peninsula most likely across the Adriatic Sea. The other resurrected species is *Helix thessalica* Boettger, 1886, a species similar and related to *Helix pomatia* Linnaeus, 1758. Populations of "*H. pomatia*" from southern Serbia, Bulgaria, Macedonia and Greece; but also some from Romania, Ukraine, Moldova and Russia actually belong to *H. thessalica*. Remarkably, we have found the species also in northern Hungary and central Slovakia, as well as in one river valley in southeastern Czechia. Following the taxonomic revision of *H. pomatia*, we aimed to uncover its glacial refugia and sources of postglacial colonization. Large snails as *H. pomatia* are assumed to be particularly poor dispersers. Yet the published fossil data suggested very early arrival of this species to Czechia and Slovakia, possibly from nearby, northerly located refugia. We have assembled a representative set of samples from across the native range of *H. pomatia*, including areas largely neglected by previous phylogeographic work on land snails (Bosnia, the Carpathians). The data revealed a complex pattern of colonization from more than one refugium, but did not suggest any northern refugia. We revised the oldest post-LGM occurrences from Czechia and Slovakia suggested by literature, and directly dated the preserved shell fragments by radiocarbon to establish the true timing of the species' arrival to Czechia and Slovakia. The published earliest records turned out unreliable, strongly arguing for direct dating of the preserved shell fragments to estimate the ages of first postglacial occurrences of individual species. However, the results still suggest that *Helix pomatia* was able to rapidly and effectively colonize the newly emerging postglacial habitats. The findings of the individual studies included in the thesis are discussed in light of some concerns over persisting uncertainties in land snail ecology, evolution and taxonomy. I suggest that what constitutes separate species may differ between regions due to differences in climatic stability. These also affect the apparent mobility of species and lineages over long time scales through alterations of their distribution ranges. It is important to study the effectiveness of passive dispersal along with the nature and strength of interactions between species and populations in order to build a robust taxonomy and better understand spatial patterns of snail diversity. A nearby steep gradient of snail diversity between the Mediterranean and Central Europe offers possibilities to further address these issues.

ABSTRAKT

Čeleď Helicidae (hlemýžďovití) zahrnuje největší a nejznámější suchozemské plže západního Palearktu, nicméně až donedávna se znalost její diverzity opírala převážně o práce z počátku dvacátého století. Řešení řady taxonomických problémů a pochopení biogeografické historie čeledi si přitom žádalo uplatnění molekulárně-fylogenetických analýz. Tato práce se zaměřuje na skupinu východostředomořských rodů hlemýžďovitých, především přímo na typový rod *Helix* Linnaeus, 1758 (hlemýžď). Počínaje zkoumáním diverzity a příbuzenských vztahů linií ve východním Středomoří a Anatolii sleduje jejich cestu od místa jejich diverzifikace až po jejich výskyt v postglaciální fauně střední Evropy. Předkládané výsledky jsou převážně založené na analýzách sekvencí mitochondriálních genů, konchologických pozorováních a radiokarbonovém datování holocenních subfosilních nálezů. Porovnávali jsme diverzitu mitochondriálních linií v rodě *Helix* se závěry nové, na morfologii založené taxonomické revize rodu. Podařilo se nám shromáždit reprezentativní data, pokrývající téměř všechny v současnosti uznávané druhy, stejně jako potenciálně příbuzné rody a podrody. Revidovali jsme vymezení rodu a upozornili na zřejmě rozdílný přístup k vymezování druhů v rodě *Helix* oproti některým jeho příbuzným. Centrem hluboké diverzity hlemýžďů jsou Řecko, Egejská oblast a západ Turecka, zatímco vysoká druhová diverzita se nachází především v Alpinských pohořích od západního Balkánu po jih Turecka. Nalezli jsme jednu čistě evropskou radiaci hlemýžďů s centrem diverzity na západním Balkáně. Znovu jsme popsali dva druhy z tohoto kladu, které byly dlouho pokládány za synonyma běžnějších druhů. *Helix straminea* Briganti, 1825, popsaný ze střední Itálie, se ukázal být zcela nepříbuzným *Helix lucorum* Linnaeus, 1758, za jehož synonymum byl pokládán. Ten, ačkoli se vyskytuje na severu Itálie, pochází ve skutečnosti z Anatolie. *Helix straminea* má naproti tomu původ na západním Balkáně, kde žije v Albánii a Makedonii, a Itálii kolonizoval zřejmě přes Jaderské moře. Druhým znovuobjeveným druhem je *Helix thessalica* Boettger, 1886, druh podobný a blízce příbuzný hlemýždi zahradnímu (*Helix pomatia* Linnaeus, 1758). K tomuto qdruhu náleží populace "*H. pomatia*" z jihu Srbska, Bulharska, Makedonie a Řecka; ale i některé z Rumunska, Ukrajiny, Moldávie a Ruska. Pozoruhodné je, že jsme tento druh nalezli také na severu Maďarska, na středním Slovensku a dokonce v jednom říčním údolí na jižní Moravě. Po této taxonomické revizi *H. pomatia* jsme se pokusili nalézt jeho glaciální refugia a zdroje postglaciálního šíření. O velkých plžích, jako je *H. pomatia*, se předpokládá, že se obzvlášť špatně šíří. Přesto dosud publikovaná data naznačovala, že se na území Česka a Slovenska objevil brzy, což by snad mohlo naznačovat existenci blízkých a nečekaně severně položených refugií. Dokázali jsme nashromáždit reprezentativní soubor vzorků z celého přirozeného areálu druhu, včetně oblastí opomíjených předchozími fylogeografickými studiemi suchozemských plžů (Bosna, Karpaty). Získaná data odhalují komplikovanou historii kolonizace z více jak jednoho refugia, avšak nenaznačují existenci severních refugií. Revidovali jsme nejstarší postglaciální nálezy z Česka a Slovenska, a radiokarbonově jsme datovali dochované fragmenty schránek, abychom zpřesnili dataci příchodu hlemýždě zahradního na území Česka a Slovenska. Publikovaná data se ukázala být nespolehlivá, což demonstruje nutnost přímo datovat dotčené nálezy zlomků ulit, pokud chceme zjistit stáří prvních postglaciálních výskytů jednotlivých druhů. Nicméně naše výsledky přesto ukazují, že hlemýžď zahradní byl schopný poměrně rychle a efektivně kolonizovat nově se utvářející postglaciální prostředí. Výsledky jednotlivých článků jsou diskutovány v kontextu některých přetrvávajících problémů v ekologii, evoluční biologii a taxonomii suchozemských plžů. Domnívám se, že oddělené druhy mohou představovat poněkud odlišné jednotky v závislosti na geografických rozdílech v klimatické stabilitě. Ta, skrze změny v rozsahu areálů ovlivňuje i rozsah mobility jednotlivých linií na dlouhých časových škálách. K dosažení robustní taxonomie a pochopení prostorového rozložení diverzity plžů je důležité poznat efektivitu pasivní disperze plžů a povahu a sílu interakcí mezi jejich druhy a populacemi. Nedaleký strmý gradient diverzity suchozemských plžů mezi Středomořím a střední Evropou nabízí příležitost se těmito problémy dále zabývat.

Helix pelagonesica (Rolle, 1898), a poorly known *Helix* species from Greece and Macedonia
(Greece, Petra Olympou, 2013)

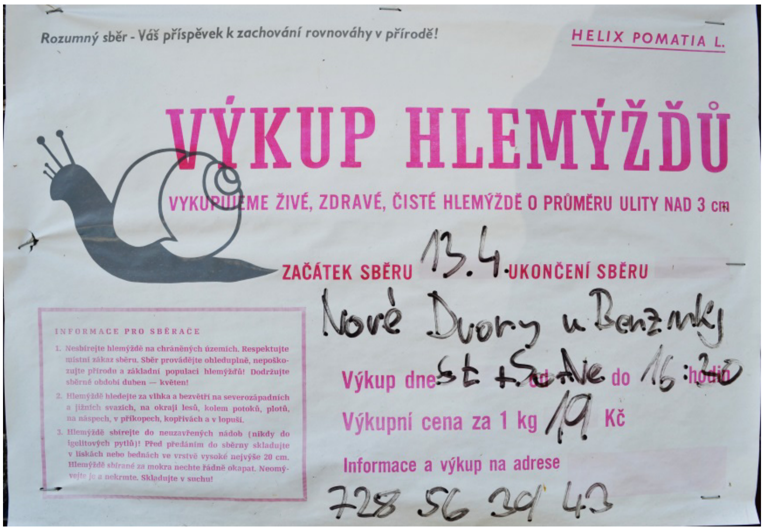
GENERAL INTRODUCTION AND DISCUSSION

The Western Palearctic land snail fauna is, after three hundred years of shell collecting, taxonomic studies and other work, relatively well known, as far as conchological forms and their distribution are concerned. However, the same cannot be said about its evolutionary and biogeographic history. Because only the advent of molecular phylogenetics allowed for robust hypotheses regarding the relationships between species and populations, there is currently a huge body of work ahead to be done in order to lay a solid basis for understanding of the patterns of land snail diversity.

This thesis primarily focuses on systematics, phylogeny and biogeographic history of one land snail genus and its close relatives. As part of the work, two once described, but later synonymised and forgotten species were uncovered. Furthermore, a history of one of the most common snails in Central Europe from the Last Glacial to present has been explored, asking from where and how fast it spread to Central Europe. Although phylogenetic history of any particular taxon is not of general interest, good taxonomy and known phylogenies provide a basis for any further ecological and evolutionary research. Such knowledge, collected from as many species as possible, eventually allows for asking for the mechanisms and factors that determined which species we meet in the landscape around us.

In 2013, Robert A. D Cameron outlined in an insightful review paper what he considered to be the currently most important issues in the field of terrestrial malacology (Cameron 2013). Among other, he noted that species as currently recognized are not comparable units between regions and clades. Also, he questioned common prejudices considering the role of seemingly inefficient dispersal and weak competition in diversification of snails and formation of their communities (see also Cameron 2016). Both dispersal over lager distances and interactions between snails are uneasy to capture, hence their mechanisms remain partly obscure and hard to imagine. In my view, Cameron has raised serious concerns regarding the interpretation of the patterns of snail diversity we observe, which relate also to the topics and aims of the papers included in this thesis. More specifically, I think that an important but unresolved question is how much are diversity patterns shaped by dispersal limitation compared to interactions between species, and how their interplay interferes with taxonomic decisions.

Although each one of the papers included in this thesis focuses on a rather specific problem and none aims to tackle the above issues, together they are connected with major questions the malacological research is currently facing. These questions should be considered when interpreting the results, and partly the results could contribute to their solution in the future.



Rozumný sběr - Váš příspěvek k zachování rovnováhy v přírodě!

HELIX POMATIA L.

VÝKUP HLEMÝŽĎŮ

VYKUPUJEME ŽIVÉ, ZDRAVÉ, ČISTÉ HLEMÝŽDĚ O PRŮMĚRU ULITY NAD 3 cm

ZAČÁTEK SBĚRU 13.4. UKONČENÍ SBĚRU

Nové Dvory u Benzinky

Výkup dne St + So od Ne do 16:30 hodin

Výkupní cena za 1 kg 19 Kč

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728 56 39 43

INFORMACE PRO SBĚRAČE

1. Nesbírejte hlemýždě na chráněných územích. Respektujte místní zákaz sběru. Sběr provádějte ohleduplně, nepoškozujte přírodu a základní populaci hlemýžďů! Dodržujte sběrné období duben — květen!
2. Hlemýždě hledejte za vlhka a bezvětří na severozápadních a jižních svazích, na okraji lesů, kolem potoků, plotů, na náspech, v příkopech, kopřivách a v lopuší.
3. Hlemýždě sbírejte do neuzavřených nádob (nikdy do igelitových pytlů)! Před předáním do sběrny skladujte v lískách nebo bednách ve vrstvě vysoké nejvýše 20 cm. Hlemýždě sbírané za mokra nechte řádně okapat. Neomývejte je a nekrmte. Skladujte v suchu!

The Roman snail *Helix pomatia* Linnaeus, 1758 is often the only snail species people in Czechia recall. Here buying up for food processing is being advertised, offering ca. € 0.7 per kg of live weight (Czechia, Čáslav, 2016).

Snail? *Helix*!

In my work, I focused on the taxonomy, phylogeny and phylogeography of selected representatives of the family Helicidae Rafinesque, 1815. It is a Western Palearctic group of large-sized snails, several of which are of some economic value and familiar to the public. The family in its currently accepted sense consists of three subfamilies: Murellinae Hesse, 1918 are endemic to the Apennine Peninsula, Sicily, Sardinia, and Corsica (Razkin et al. 2015; Neiber & Hausdorf 2015b). Ariantinae Mörch, 1864 comprises number of usually rock-dwelling species, diversified particularly in the Alps and the Balkans (Cadahía et al. 2014; Groenenberg et al. 2016). Finally, Helicinae include the most iconic European land snails, such as the grove snail *Cepaea nemoralis* (Linnaeus, 1758), the brown garden snail *Cornu aspersum* (Müller, 1774), and the Roman snail *Helix pomatia* Linnaeus, 1758, and is distributed in most of the Western Palaearctic region except for its northeast. As yet, molecular phylogenies did not unambiguously resolve the relationships within Helicinae, but they suggest existence of three diversification centres (Razkin et al. 2015; Neiber & Hausdorf 2015b). Two are located in the west (northwestern Africa, Iberian Peninsula), while the third one lies in the north-eastern Mediterranean. My research focused on the last one, which corresponds to the tribe Helicini (*sensu* Razkin et al. 2015), and on the genus *Helix* Linnaeus, 1758 in particular.

This thesis is a direct follow-up of a work that started already during my bachelor studies. Back then, the systematics of Helicidae was still largely based on morphological studies from the early 20th century (Kobelt 1902-1906; Hesse 1915-1920), and there had been just a handful of published molecular phylogenetic studies that dealt also with members of Helicidae and *Helix* (Steinke et al. 2004; Koene & Schulenburg 2005; Manganelli et al. 2005; Wade et al. 2007). Due to their scope and methods, these early phylogenetic studies could not contribute much to the systematics of east-Mediterranean Helicidae, but they have already demonstrated polyphyly of the type genus *Helix* as it was widely accepted for decades. There were also relatively recent revisions of the genera *Isaurica* Kobelt, 1901, *Assyriella* Hesse, 1909, *Codringtonia* Kobelt, 1898, and *Caucasotachea* Boettger, 1909 (Subai 1994, 2005; Schütt & Subai 1996; Neubert & Bank 2006), which were a significant step towards a modern species-level classification, although still only based on morphology. And finally, there were taxonomic issues introduced by Hartwig Schütt in his controversial compendium of land snails of Turkey, an area of prime importance for the focal group (Schütt 2010). These related particularly to the genus *Helix*, which was in need of a complete taxonomic revision. Morphology-based revision of most of *Helix* diversity was already under way (Neubert 2014), but given the taxonomic histories of some taxa it seemed clear that without phylogenetic data several issues would remain disputed.

Although the genus *Helix* has been recently thoroughly revised, there remain cases which I find hard to attribute to any of the accepted species. The best example is probably this form originating from the crusaders' castle Krak des Chevaliers in western Syria. In my view, resolving its identity would only be possible with molecular data. Size of the shell is under 3 cm (Naturmuseum Senckenberg, Frankfurt am Main, coll. Schütt ex Kinzelbach).

Past explains present

Building on the work of Vojen Ložek (Kovanda 2005; Horáčková et al. 2015), the malacological research at the Charles University in the last years focuses on the development of Quaternary land snail communities and their use for palaeoecological reconstructions. A logical step towards the understanding of how communities formed and what influenced their composition would be to identify where the constituent species originated and survived periods of unfavourable climate in the course of Quaternary climatic oscillations. The Holocene communities in Central Europe largely consist of species that spread to the region after the Last Glacial from more southerly located refugia. Ecological factors could have influenced order of arrival of Holocene species to Central Europe, but distance from refugia could also be a crucial factor, because snails are popularly considered poorly suited for dispersal. Priority effects might have also played a role. Furthermore, information on the location of glacial refugia could for example reveal, if there were consistent differences in expansion potential of populations in different refugia, and whether species that now live together also shared their refugia. So far, information on refugia is available only for a few species that have a broad Holocene distribution in Central Europe (Chapter IV). Worse, southeast of Europe, the Carpathians and Balkans, where many of the Central European snail species could have survived considering the existence of related endemic species there, was largely previously neglected by malacological phylogeographic studies. Actually, the only work relevant for search for refugia of terrestrial gastropods in the southeast that employed an adequate sampling was that of Pinceel et al. (2005) on one slug species.

Starting from exploring relationships within the primarily East-Mediterranean Helicini and revising their taxonomy, this work follows this group from Anatolia through the Balkans towards its present northwestern limits established after the Last Glacial. Collecting geographically representative data, spanning from the tribe's diversification centre and long-term refugia to recently colonized areas, is important for obtaining a comprehensive picture of the group's evolutionary dynamics. Regional differences in climatic history, topography, and other factors may be eventually related to differences in diversity patterns and show the relative contribution of the properties of the studied taxa, compared with environmental factors, to the distribution of their diversity.

The time frame of helicid diversification remains more or less speculative due to scarcity of fossils that could be unambiguously associated with a node in the helicid phylogeny. Well preserved *Helix* fossil are known from Miocene deposits at the Black sea coast near Varna, Bulgaria (Wenz 1935; Kojumdgieva 1969). They resemble by shell size, shape, and a very small protoconch the recent *Helix pomacella* Mousson, 1854, which in Bulgaria lives near Burgas. However, shells may be often similar also between unrelated snail species. Scale 2 cm (fossil: Naturhistorisches Museum, Wien; recent: Museum für Naturkunde, Berlin).

Making the acquaintance with *Helix*

In Chapter I (Korábek et al. 2015) we provided the first molecular phylogeny of the genus *Helix* and the eastern Mediterranean Helicinae (i.e. the tribe Helicini), including almost all genus-level lineages and *Helix* species. Such comprehensive sampling could only have been achieved by using tissue remains from dry shell collections and other improperly preserved material in addition to newly collected samples mainly from Turkey and the Balkans. Thus the phylogenies were based on only short and often incomplete fragments of the mitochondrial genes for 16S rRNA and cytochrome c oxidase subunit I (COI or Cox1), and many of the relationships remained unresolved. However, the results allowed us to unambiguously reject placement of some genus-level taxa in *Helix* and reveal the synonymy of *Tacheopsis* Boettger, 1909 with the newly delimited *Helix*. After Fiorentino et al. (2016) demonstrated that *Tyrrhenaria* Hesse, 1918 from Corsica is synonymous with *Helix*, the only remaining issue in delimitation of the genus is now *Helix godetiana* Kobelt, 1878, lately placed to a related genus *Maltzanella* Hesse, 1917 (Neubert 2014). Only a very short fragment of the 16S gene is available from this species at the moment (Psonis et al. 2015), precluding reliable taxonomic placement through phylogenetic analysis. The species had been very rare and declining already in the 1980's (Mylonas 1985), so the chance to resolve this issue may be rapidly vanishing.

Helix nicaeensis Férussac, 1821, formerly *Tacheopsis nicaeensis*, is the conchologically most derived lineage of *Helix*. The species is very small, with shell diameter not exceeding 3 cm (Naturmuseum Senckenberg, Frankfurt am Main, #166508).

Besides the genus *Helix*, our results also indicated that genera *Levantina* and *Isaurica* should be delimited differently, and demonstrated close relationship between *Caucasotachea* and *Cepaea vindobonensis* (Pfeiffer, 1828). The latter has been since confirmed with more data (Neiber & Hausdorf 2015b; Neiber et al. 2016) and *C. vindobonensis* transferred to the genus *Caucasotachea*.

Within *Helix*, we identified four major clades, one which was a radiation in the western Balkans that includes also the type species of the genus, *H. pomatia*. We have confirmed some taxonomic changes proposed by Neubert (2014) – for example the separation of *Helix borealis* Mousson, 1859 from *Helix cincta* Müller, 1774 (Neubert & Korábek 2015), which has significant consequences for interpretation of the present distribution of the latter in Europe. We have nevertheless also revealed several cases of discordance between this up-to-date morphology-based taxonomic revision and relationships inferred by mitochondrial phylogeny, calling for further research on the species limits in some cases. While some species may be synonymised, *H. asemnis* Bourguignat, 1860 from the Taurus Mts. in southern Turkey may comprise two or more closely related species. Even the Roman snail *H. pomatia* has been shown to consist of two different lineages (which we later resolved by recognizing them as separate species in Chapter III; Korábek et al. 2016a). Some of the remaining taxonomic issues within *Helix* can be hardly resolved now due to unstable political situation in Turkey and Syria. However, two major ones remain accessible in Europe, in the western Balkans and the Apennine Peninsula, and may be assessed in near future. Both cases include radiations with closely related species whose relationships cannot be fully resolved with mitochondrial data only. Less known is the diversity in the Apennines, where the division into species proposed by Fiorentino et al. (2016) cannot be used since they did not provide any diagnoses for their species.

Helix dormitoris (Kobelt, 1898) in its natural habitat – an alpine meadow in Šar Planina, Macedonia. The species is part of a European clade of *Helix*, whose phylogeny and taxonomy is yet to be fully resolved, being complicated by hybridization and incomplete lineage sorting. *Helix secernenda* Rossmässler, 1847 from high altitudes at the border between Montenegro and Albania is conchologically almost indistinguishable from *H. dormitoris*, but it has a grey, not yellowish mantle margin (photo by Anna Holubová, 2014).

Misleading shells

An important finding of molecular phylogenetic studies in general has been how much morphology can be misleading for systematics. The problem is not that the morphology is useless, but that important traits may be dismissed as unimportant or overlooked, while labile ones were considered informative. Also, the rate of change of a given character varies over time and across lineages. In land snails this holds particularly for conchological characters, where convergence is common and divergence in appearance often does not correlate with genetic divergence (e.g. Haase et al. 2014; Köhler & Criscione 2015; Walther et al. 2016; Chapter I).

The best example of similar shell appearance leading to incorrect grouping among Helicidae is the genus *Cepaea* Held, 1838. Until recently, four similar species were placed into the genus, but with first molecular data it become clear that they are not related (Cadahía et al. 2014; Chapter I). Neiber & Hausdorf (2015b) then demonstrated that there are three *Cepaea*-like lineages, each derived from different major clade of the Helicinae subfamily. A notable result of Chapter I, demonstrating the mismatch between time since divergence and morphological differentiation, was the discovery that the monotypic genus *Tacheopsis* from north-western Anatolia is in fact a young derived lineage of *Helix*. The anatomy suggested relationship with *Helix* long time ago, but divergent shell shape indicated relationships rather with *Caucasotachea* (Forcart 1953). The sister species of *Tacheopsis*, *Helix lucorum* Linnaeus, 1758, exhibits greater variation in shell shape than most of the whole genus *Helix* (Neubert 2014), but is relatively shallowly differentiated in the studied mitochondrial markers (Chapter I). In Chapter I, we also depicted two unrelated *Helix* species, which independently evolved into peculiar lowly conical form with a small aperture and a tooth on columella. In both these cases as well as in *Tacheopsis*, the derived shells probably appeared relatively recently, while the ancestral shell shape remained more or less unchanged during the existence of the genus.

As a result of the mismatch between conchology and molecular data, what turned out to be more than one evolutionary distinct linage has been considered a single species, and vice versa. In Chapters II (Korábek et al. 2014) and III (Korábek et al. 2016a) we re-described two *Helix* species, which were considered synonyms of similar and more widely spread taxa because of similar appearance. While *Helix thessalica* Boettger, 1886 (Chapter III) is closely related to *H. pomatia* Linnaeus, 1758, with which it has been considered conspecific, the Chapter II provides an example of convergent appearance in two unrelated lineages. A species of European origin, *Helix* *straminea* Briganti, 1825 from Italy, has been considered synonym of *Helix lucorum* Linnaeus, 1758, an originally Anatolian species. Although previously overlooked, the separation of these two species from those with which they were synonymised was relatively straightforward. However, other cases where species-level taxonomy may require reconsideration are going to be more complicated.

We distinguished *Helix thessalica* Boettger, 1886 as a species separate from *H. pomatia* after phylogenetic analyses revealed two divergent lineages within the latter. However, already two years earlier Lucie Juřičková noticed an unusually looking "*H. pomatia*" in central Slovakia, which later turned out to be *H. thessalica*. The figured individuals originate from a newly found locality in Czechia (Čučice; lgt. Petr Dolejš, 2016).

Different place, different race

Taxonomic decisions become more complex when the snail taxa are geographically structured into allopatric or parapatric units which to a varying degree differ genetically, phenotypically, or both. The geographic structure often crosses established species limits and extends from genus level to intraspecific variability. Within the tribe Helicini, the best studied example of a geographically structured taxon is the Greek genus *Codringtonia*. The latest taxonomic revision (Subai 2005) recognized seven allo/parapatric species, which has been largely confirmed by mitochondrial phylogeny (Kotsakiozi et al. 2012; own unpublished data). Within these, distribution of mitochondrial lineages exhibits partly also an allopatric pattern. There are also regional differences between populations in shell shape and colouration. Such geographic structure, often on a fine scale, is characteristic especially for rock-dwelling snails, such as *Codringtonia*. Taxonomic problems with the rock dwellers are almost as old as molluscan taxonomy itself, and, besides geographic structure, stem from rapid evolution of shell characters in local populations (e.g. de Bartolomé 1982; Fiorentino et al. 2013). An illustrative case of the problems with geographic structure of rock-dwellers is the Moroccan genus *Rossmaessleria* Hesse, 1907. All of its allopatrically distributed forms arose relatively recently, and they have been now lumped into a single species (Walther et al. 2016). However, its shell shape ranges from globular to flat keeled, exhibiting probably more disparity in shell shape than any other helicid genus. As there were objective differences between the allo/parapatric forms in conchological characters, they were retained for the zoological system as subspecies by the authors.

The geographic structuring is not limited to rock-dwellers, but it can be also observed in *Helix* species around the Mediterranean. One such example is *Helix asemnis* Bourguignat, 1860 from southern Turkey, where there are large differences between populations in their appearance and distribution of mitochondrial lineages follows largely geography. Some local forms are quite remarkable, such as large colourful forms from north of Mersin, and have been previously even regarded separate species, unlike conchologically less conspicuous, but equally divergent populations. Without proper knowledge on interactions between geographically separated but closely related forms (such as *H. vladika* (Kobelt, 1898) and *H. straminea*, Chapter II), or recently differentiated but conchologically markedly distinct forms (such as the taxa closely related to *H. cincta*: *H. anctostoma* Martens, 1974 and *H. antiochiensis* Kobelt, 1895; Chapter I), their synonymization could be an unnecessary loss of information on the actual diversity of life forms.

Easy diversification – uneasy taxonomy

Geographic structure may be an initial phase of speciation, a usually gradual process during which diverging populations become more and more distinct (Mallet 2008). Along the way, they acquire the attributes of separate species. Different of these attributes (e.g. diagnosability, reciprocal monophyly, reproductive isolation, features that would have negative fitness effects in the other lineage) are emphasized by different species concepts, so with time elapsed in separation, as these develop, the diverging populations would be recognized by more and more species delimitation approaches. The both extremes – none and complete differentiation – are clear, while the space in between is free for endless disputes and taxonomic decisions become arbitrary. That is true especially when the structure is unevenly deep across the taxon in question, as it is in *Codringtonia*. Some species are clearly separated, some are not, and within well separated species there is further intraspecific structuring. The structure may be also dynamic in time (e.g. Fiorentino et al. 2013), and the degree of differentiation and geographic separation between populations may vary.

A structure of allopatric units across different levels of divergence may pose a problem for taxonomy, because it may not allow for applying some of the criteria of species recognition,

Helix asemnis Bourguignat, 1860 has of all presently recognized *Helix* species the highest intraspecific divergences in the studied mitochondrial markers. It is quite variable, with geographic clusters of similar populations. The smaller form on the top originated from NE of Erdemli. The shells had regular low ribs, mantle margins were yellowish and the snails produced bright yellow mucus when disturbed. The large form on the bottom has been described from Gözne N of Mersin as *Helix pericalla* Kobelt & Rolle, 1896. Its mantle margins were pink in adult individuals, the shells were more conspicuously coloured. This form lives also at other places in the area (southern Turkey, 2011).

Another case of geographic differentiation: *Helix buchii* Dubois de Montpéreux, 1839 from north-eastern Turkey. On the top is a medium-sized form from province of Ordu, below a very small one from more easterly site in the province of Giresun. At the bottom is a very large form Rize Province; similar populations are found also farther east in Georgia. *Helix buchii* is the largest *Helix* species, with shell diameter exceeding 6 cm in eastern populations, but in some of its western populations the diameter only slightly exceeds 3 cm. The upper-most individual was basal to the other two in mitochondrial phylogeny (2011).

while exaggerating others (e.g. Hamilton & Johnson 2015; Zachos 2016). If the diverging lineages do not interact, there is effectively a reproductive isolation even if the lineages could interbreed freely if given a chance. There is no selection for intrinsic reproductive isolation and/or niche differentiation, so testing the species limits by ecological differentiation and reproductive isolation may not make sense. Geographic structure may favour monophyly within the geographic units, because of drift within diverging populations and lack of gene flow between them. Applying criteria derived from the phylogenetic species concept could thus favour finer division into species than those of the biological concept.

Important information is always how is the geographic structure maintained and what happens when the geographic forms come into contact. Would they remain distinct? A recent study on a pair of Clausiliidae species (Koch et al. 2017) has demonstrated, that even quite well differentiated taxa, easily distinguishable by conchological characters and distinct in mtDNA (7.9-9.8% p-distance at COI), can effectively merge when they come into contact. I suspect that the same would hold for many closely related snail species in the Mediterranean. The fact that the differentiation appears maintained only by an extrinsic factor of geographic separation does not invalidate obvious differences between two taxa. However, recognition of species separated only by geography becomes hard to justify if these come into contact too often, on large spatial scales, or across their genomes. Again, the decision, what constitutes hybridization and gene flow between two species, and when there is only a single one, is arbitrary. There are further data from clausiliids (Scheel & Hausdorf 2012; Koch et al. 2016) that illustrate the problem.

Slow snail, rapid differentiation

In the beginning, the geographic structure in both the genetic markers and morphology most often depends on lack of dispersal and gene flow between populations. If dispersal is limited, vacant patches of habitat are only colonized by lineages living nearby, leading to distributions consisting of more contiguous and better delimited patches of individual lineages than when they are mobile and the vacant patches may be colonized by lineages living in a greater distance (Chave et al. 2000). Reduced dispersal also leads to low gene flow and monophyly within local populations, and thus to the geographic structure within species (Papadopoulou et al. 2008). Likewise, without dispersal and mixing between lineages the conchological characters are allowed to diverge. The diversity of Helicini is geographically most structured in the mountainous regions around the Mediterranean Sea, where the complex topography may be an obstacle to dispersal and thus gene flow. It may be thus concluded that poor dispersal capabilities of the Mediterranean species is the factor responsible for the pervasive geographic structure.

The variability of rock-dwelling helicids tends to be geographically structured. An example of such taxon is *Codringtonia* Kobelt, 1898 from Greece, represented here by *C. elisabethae* Subai, 2005 from Mycenae (2016).

There seem to be differences in the geographic structuring between helicid taxa. However, differences between regions may be more important. The postglacially colonized areas of Europe are characterized by homogeneity in species composition and their genetic variability over vast expanses, in stark contrast to the Mediterranean mountain ranges. A possible and obvious explanation can be that the postglacially broadly distributed species are more mobile than those more in the south. Perhaps only because of their higher mobility they were able to expand their ranges. Indeed, Dynesius and Jansson (2000) argued that the Quaternary climatic oscillations should have selected for species with good dispersal abilities. Possibly, the difference between the structured diversity in the Mediterranean and homogeneity in Central Europe lies in the dispersal potential of the species. Could that be the case?

Are snails really so sluggish?

When studying dispersal of snails at scales exceeding a few hundred metres, we have to rely on the traces the past mobility left on the present distributions of species and their genetic variability, because the dispersal events are too rare to be observed. Phylogeographic studies may provide some clues on the mobility. On the one hand identical haplotypes shared over large distances provide evidence for recent translocations and thus for dispersal, on the other hand a pattern of allopatric distribution of lineages that diverged millions of years ago suggests very little mobility (i.e. effective and successful dispersal). Knowing whether the lineages in the more southern areas were also subject to rapid range expansions in response to climatic developments, despite having small ranges, would provide some clues on the factors limiting the mobility. Unfortunately, for most species within the focal tribe Helicini only a few sequences are available at the moment, poorly documenting the distribution of their intraspecific variability.

The Quaternary (sub)fossil record offers the possibility to asses snail mobility by quantifying the rates of postglacial range expansion, as has been done before with trees. Our results in Chapter IV provide the first insight into the speed of the postglacial range expansion of *Helix pomatia*. We argue that the species spread quite rapidly, reaching 50°N ca. 2,000 years after the onset of the Holocene. The inferred overall rate of spread was similar to rates attained by some of slowly spreading tree species, such as beech and oak (Giesecke et al. 2017). Clearly, *H. pomatia* can be mobile enough for its lineages to appear anywhere within its range during the Holocene.

It is nevertheless important to note that the observed signs of past movements reflect both past dispersal events and a successful establishment at the destination. Most of the dispersal events fail to leave any traces, because the disperser did not survive or reproduce: it did not find suitable habitat or failed to establish due to biotic interactions. Even if it succeeds, its alleles may rapidly disappear when there is already a conspecific population (Waters et al. 2013; Fraser et al. 2015). The postglacial Central Europe, with soils enriched with carbonate (Andersen 1994) and devoid of competitors, was probably a welcoming place for snail colonizers. Furthermore, geographically structured populations are almost invariably detected in the southern areas of glacial refugia (e.g. Petit et al. 2003; Gómez & Lunt 2007), and the allopatric structure of often monophyletic units is being interpreted as evidence for long-term survival of the taxon in a given area. Thus while during the postglacial range expansion the species may be able to cover a thousand kilometres within few thousand years, the geographic structure in the southern parts of their ranges sometimes persists for at least hundreds of thousand years, if not millions (a great example comes from freshwater amphipods; Copilaş-Ciocianu et al. 2017). The question stands, whether they would still appear more mobile than their southern relatives, if only the stable parts of their ranges would be considered. More than mobility itself, the limiting factor is perhaps dispersal ability combined with interactions with close relatives and conspecifics, due to which the dispersal may often not leave any traces (Waters et al. 2013).

Living together

Newly separated allopatric species may need some time to diverge before they can live in sympatry, depending on the mechanism of speciation (Weber & Strauss 2016). This is because of competition, reproductive interference, or their fusion upon contact. Gittenberger (1991) suggested that the allopatrically diversified closely related species may actually be little differentiated in their ecology, compete with each other, and may mutually restrict the extent of their ranges (see also e.g. Hamilton & Johnson 2015). Within the genus *Helix*, closely related species rarely occur together, while species of the subgenus *Pelasga* live alongside species of the nominotypical subgenus frequently. The only contact zone between close relatives that I had the opportunity to explore in more detail has been the small range of *H. thessalica* in southeastern Czechia, deep within the postglacial range of *H. pomatia* (Chapter III; Korábek et al. 2016b). *Helix pomatia* is dominant species in the region. *Helix thessalica* occurs in patches which are devoid of *H. pomatia*, with which *H. thessalica* comes into contact at their margins. We did not test for hybridization experimentally or using molecular data, but some of the collected shells and occasional mismatch between morphology and mtDNA suggested that hybridization sometimes happens. The two species do not truly live together; rather they seem to be mutually exclusive. Similar experience I have got from Slovakia and Romania.

How long time of separation is needed in different land snail taxa before they can live together is completely unknown, although this may play an important role in the assembly of snail communities. Large regional diversities of Mediterranean snail faunas include numerous cases of presumably young radiations, whose species may simply not be able to live syntopically, contributing to high beta diversity. On the contrary, the postglacially expanding species meet each other in communities that have similar species composition from site to site (Waldén 1981; Cameron et al. 2003). Nordsieck (2007) suggested that while there are fewer Clausiliidae species in postglacially colonized regions, they have more overlapping ranges and are better reproductively isolated than is usual in the Mediterranean. Phylogenetic relationships between species have to be resolved to test whether divergences between the syntopically living species in Central Europe indeed have to be higher than some threshold to allow for their coexistence, or if there is no such filter. Also, we should ask whether interactions between closely related species affect the composition of the land snail communities in postglacially colonized areas, though this is probably not relevant for the studied Helicidae.

Species of the subgenus *Pelasga* Hesse, 1908 often occur alongside species of the subgenus *Helix*. For example, this *H.* (*Pelasga*) *kazouiniana* (Pallary, 1938) has been found at a locality of *H.* (*Helix*) *asemnis* (Turkey, Bebeli near the mouth of the Ceyhan River, 2011).

Origin matters

An important factor for mobility of species and the outcome of their interactions are of course also abiotic conditions. During their postglacial expansion, species and populations from different refugia probably differed in their preadaptation for the postglacial habitats. For example, In the case of *H. pomatia* (Chapter IV), *H. thessalica* (Chapter III), and *C. vindobonensis,* three species of Helicini which reached Central Europe, the populations derived from Balkan refugia did not penetrate further west than Czechia. Is it a more general pattern? The previous phylogeographic work on broadly distributed central European land snails largely neglected the parts of Europe roughly east of Germany, Austria and Italy. Hence, the role of the Balkans and the Carpathians in postglacial colonization compared to more westerly areas could not have been evaluated. In general, it appears that species and lineages of various organisms that survived the Last Glacial in the Carpathians often did not colonize the areas west of them (e.g. Wójcik et al. 2010; Slovák et al. 2012; Weigand et al. 2012; Havrdová et al. 2015; Mandák et al. 2016; but see Wielstra et al. 2015). The distribution patterns of land snails of Central Europe lead to similar conclusions. Snail species with Carpathian affinities are restricted to the east of Czechia (Horsák et al. 2013; Juřičková et al. 2014). Polish forest snail faunas have a higher affinity to the Alps than to the nearby Carpathians (Pokryszko & Cameron 2005; Cameron et al. 2010). Therefore the geographic origin has also to be considered when interpreting patterns of species co-occurrence. However, first it is necessary to collect information on location of glacial refugia for as many species as possible to identify geographic biases in colonization potential.

European latitudinal diversity gradient and future perspectives

The distinction between areas where land snails (including Helicidae) diversified over millions of years and Central Europe where most of the species have arrived only less than 15,000 years ago, can offer important insights into the mechanisms of diversification, dispersal and coexistence of land snails. The land snail diversity is organized differently between the Mediterranean mountain ranges and postglacial Central, Northern, and Eastern Europe (e.g. Cameron et al. 2003, 2015). Linking the differences in diversity patterns with differences in topography, climatic history, and other factors may be a way how to understand the interplay between intrinsic properties of snails and effects of the environment in establishing the present snail diversity patterns.

In Chapter I we noted that there may be differences in taxonomic practice between *Helix* and the rock-dwelling genera, but perhaps this is not something that needs to be fixed. In my view, it is questionable whether it is reasonable to apply strictly consistent approaches, criteria, and thresholds to species delimitation across taxa differing in ecology and across regions differing in topography and climatic history. In regions, where the variation is strongly geographically structured, populations appear separated from each other and there are objective differences between them. There, division into species at a finer temporal and spatial scale, than where there is less pronounced structuring, may be appropriate to capture the diversity patterns. In other parts of the continent, species may be broader units, or may be better intrinsically separated. It has to be investigated if there is any systematic variation between regions differing by climatic history in interactions between snail species. We may also ask for differences between taxa that differ in their mobility. The Linnean binomial system, categorical in nature, forces taxonomists to decide whether the studied entity is a separate species or not, assuming that species is a standard unit of biodiversity (e.g. Zachos 2016). If the term species has indeed somewhat different meaning in different parts of the world and different taxa depending on past climatic stability and properties of the organisms, the incomparability between them is not our fault but a characteristic of biodiversity. Probably it would be more appropriate to state in which respects the discussed units are separated, how long and to what degree, than attempting to reach a definitive classification.

The geographic structuring should be quantified across taxonomic levels to compare it between regions and taxa, and so get a solid basis for the above considerations. For most species in the south we lack detailed sampling of their ranges, so we do not know how sharply the geographic units are separated and how old is the geographic structuring. We also do not know the true extent of gene flow between populations that seem isolated, and the character of their other interactions. It is unknown how long it typically takes a species of *Helix* or other snail genus to reach reproductive isolation and become truly separated. Interactions between snail species have to be studied and mechanisms of dispersal should be uncovered in order to evaluate their relative contribution to the observed geographic patterns.

It is surely true that the poor active dispersal abilities, resulting in leptokurtic dispersal where rare long-distance transports are important, contribute to spatial structuring of (not only) snail diversity (e.g. Sauer et al. 2013). However, the applicability of popular assumptions regarding the mobility of snails (which is considered sluggish) in different contexts should be rigorously tested. Unexpected cases of probable oversea dispersal were uncovered (Chapter II, Neiber et al. 2016b), and high mountain massifs may not always be as good geographic barrier as we may think (e.g. Neiber & Hausdorf 2015a). The data from *H. pomatia* (Chapter IV) suggest that postglacial range expansion of snail species was not particularly slow, and that the Alps were probably not an obstacle to colonization of Central Europe. The vectors and frequency of passive long distance dispersal should be investigated. We should also ask how are the patterns of spatial differentiation are influenced by interactions between related lineages and the pattern of "founder takes all" at the level of both species and alleles (Waters et al. 2013). Against homogeneity stands not only dispersal limitation, but probably also lack of extinction. Strong structure across levels is a sign of long-term stability, which may be expected in topographically complex regions (e.g. Tzedakis et al. 2002), and perhaps also for rock-dwelling species (Couper & Hoskin 2008). Stability does not create the vacated habitats needed for successful mobility and homogenization.

Insights into the role of dispersal and both inter- and intraspecific interactions can be gained from studying the process of postglacial recolonization of those parts of Europe where most of the present snail fauna has been swept out by the Last Glacial. However, the full potential of such studies is still beyond reach. The number and precise location of glacial refugia is not known for most of the postglacially widely spread snail species. Therefore at moment we cannot identify the filters that determined which species and populations expanded and which did not. Quaternary malacology remains largely a national affair, with different focus and methods in different countries and lack of well-documented data in many. The past research did not focus on individual species, so the presently available data cannot be used to precisely track species distributions and estimate the rates at which the snails are able to move across the continent. That would also require identification the glacial refugia.

The papers presented in this thesis are a small piece of the knowledge needed to address the above problems. I believe that some parts of the work are presently unique advancements in the understanding of diversity of European land snail faunas. We have sampled in some seriously understudied regions (e.g. Bosnia), and sought to utilize fossil data in a way novel for malacology. We have revealed that one of the most iconic and common land snails in Europe, *H. pomatia*, consisted of two species. In a broader perspective, the presented data and considerations should help to explain why the Mediterranean is so amazing place for us, European mid-latitude malacologists, who are used to very differently organized diversity.

It is important to study the whole range of a focal taxon also for the trivial purpose of understanding its habitat tolerance. *Caucasotachea vindobonensis* Pfeiffer, 1828 is in Central Europe known as species characteristic for dry, warm open habitats. Here we have found it abundant on *Petasites* growing on an inundated valley bottom (northern Greece, Skrá Waterfalls, 2013).

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CHAPTER I:

MOLECULAR PHYLOGENY OF THE GENUS *HELIX* (PULMONATA: HELICIDAE)

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CHAPTER II:

RESURRECTING *HELIX STRAMINEA*, A FORGOTTEN ESCARGOT WITH TRANS-ADRIATIC DISTRIBUTION: FIRST INSIGHTS INTO THE GENETIC VARIATION WITHIN THE GENUS *HELIX* (GASTROPODA: PULMONATA)

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CHAPTER III:

SPLITTING THE ROMAN SNAIL *HELIX POMATIA* LINNAEUS, 1758 (STYLOMMATOPHORA: HELICIDAE) INTO TWO: REDESCRIPTION OF THE FORGOTTEN *HELIX THESSALICA* BOETTGER, 1886

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CHAPTER IV:

GLACIAL REFUGIA AND POSTGLACIAL SPREAD OF AN ICONIC LARGE EUROPEAN LAND SNAIL *HELIX POMATIA* (PULMONATA: HELICIDAE)

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APPENDIX:
COMMENT ON PSONIS ET AL. (2015): ‘EVALUATION OF THE TAXONOMY OF *HELIX CINCTA* (MULLER, 1774) AND *HELIX NUCULA* (MOUSSON, 1854); INSIGHTS USING MITOCHONDRIAL DNA SEQUENCE DATA’

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