The contribution of ancient and modern anthropogenic introductions to the colonization of Europe by the land snail *Helix lucorum* Linnaeus, 1758 (Helicidae)

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Abstract

Helix lucorum is a large synanthropic land snail of substantial economic importance, which has been recently reported from a number of new sites in Western, Central, and Eastern Europe. It is an originally Anatolian and Caucasian species, but its presumed natural distribution also covers the south and east of the Balkans. Populations of unclear origin, known as *Helix lucorum taurica*, live in the south-western part of Crimea. The Balkan and Crimean populations differ in their appearance, were long treated as different species or subspecies, and the Crimean populations are protected by law as a presumably endemic taxon. Here we explore the origins of European populations using phylogenetic analysis of mitochondrial markers. The results point to north-eastern Anatolia and the Lesser Caucasus as the centre of *H. lucorum* diversification. The Crimean conchological form, along with the associated mitochondrial lineage, is not endemic to that peninsula and was likely introduced there. Other European samples belong to a different lineage, which is associated with the nominotypical conchological form of *H. lucorum*. The conchological characteristics of the nominotypical form are unusual within the genus *Helix*, and we propose this reflects a change in habitat use and parallels the evolution of some other lineages of Helicidae. As a result, the typical European *H. lucorum* differs considerably from the Crimean populations, but the two lineages just represent opposite ends of a continuum in conchological characteristics. Their formal descriptions were based on probably introduced populations detached from the main range. Separated from the geographic pattern of the overall variation of *H. lucorum* they appeared distinctive, thus confounding the taxonomy of the species. Currently, the division of *H. lucorum* into subspecies appears unwarranted. *Helix lucorum* may not be a unique example of a large snail successfully expanding from Anatolia, as we argue that even the native origin of Balkan populations is uncertain. However, further sampling in north-western Turkey and analysis of archaeozoological findings from the south-eastern Balkans is needed to evaluate this hypothesis.

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Introduction

Modern means of transport allow not only for human travel, but also provide various other organisms an opportunity to cross distances and barriers they could not overcome on their own. Snails, with “sluggish” active dispersal, may have difficulty naturally colonizing all suitable areas, but some are well suited for accidental passive dispersal by humans and have become pests worldwide (*e.g.* Capinha *et al.*, 2015). Taxa associated with anthropogenic habitats have, particularly good dispersion prospects, the more so if they are able to quickly climb onto parked cars, trucks, and trains (Aubry *et al.*, 2006). In Europe, *Cornu aspersum* (Müller, 1774), *Massylaea vermiculata* (Müller, 1774), *Cepaea nemoralis* (Linnaeus, 1758), and *Monacha cartusiana* (Müller, 1774) are good examples of such species (Langner, 2003; Peltanová *et al.*, 2012; pers. obs. OK and LJ).

Helix lucorum Linnaeus, 1758 is a snail with similar abilities, which, in addition to accidental passive dispersal, is also transported intentionally for

food processing. It is also one of several European land snails that are currently being found at new sites beyond their natural distribution limits, and due to its size and prominent colouration, also one of the most conspicuous snail newcomers to Eastern, Central and Western Europe. Its northward spread has been attributed not only to intensified international trade but also to a warming climate (Peltanová *et al.*, 2012), but as yet most of the new records represent isolated patches in anthropogenic habitats. Many of the findings also come from city centres, which may provide conditions that are warmer than the regional climate. However, the species is probably also spreading at the north-western front of its continuous range, because its present distribution in southeast Serbia is considerably broader than that indicated 110 years ago (Pavlović, 1909).

The present range of *H. lucorum* is disjunctive and extends from France to the north-west of Iran and to the Greater Caucasus (Sysoev and Schileyko, 2009; Neubert, 2014). Sometimes called the “Turkish snail” (*escargot turc* in French), *H. lucorum* has a centre of diversity in Turkey and the Lesser Caucasus. The species is conchologically most variable there (Kobelt, 1902–1906; Neubert, 2014, figs. 30–55; own observations), and the same also applies to the richness of its mitochondrial lineages (Korábek *et al.*, 2015). Anatolia is also the most likely region where *H. lucorum* originated (Fiorentino *et al.*, 2016).

Despite relatively shallow divergences with regard to mitochondrial markers (Korábek *et al.*, 2015), the variability in shell shape and colouration of *H. lucorum* is higher than in other *Helix* species (Kobelt, 1902–1906; Neubert, 2014). However, the Balkan and Italian populations are rather uniform in appearance. They are characterized by conical to depressed-conical shells with a relatively small and often dorso-laterally depressed aperture (Figures 1, 2C). The base of the shell is rather flat, as the columella is short and oblique (Figure 2). The shells have a whitish background and a variable number of dark brown spiral bands. These often merge, covering thus most of the shell surface, but a white stripe is always present along the periphery of the shell. The body of the animal itself is dark brown. These south-European populations correspond to the nominotypical form *Helix lucorum lucorum* (Figure 1; neotype from Italy depicted in Korábek *et al.*, 2014). An identical (or nearly so) conchological form is also found in Turkey and up to the Caucasus (*e.g.* Kobelt, 1902–1906; Forcart, 1963). Available molecular data (Korábek *et al.*, 2015) suggest that individuals of the

nominotypical “*lucorum*” form largely group together in the mitochondrial phylogeny, and reveal very shallow divergences within the Balkan distribution of *H. lucorum*.

The presumed native European range of *H. lucorum* comprises northern Greece, Albania, the southern half of Serbia, southern Romania, all of Bulgaria and the European part of Turkey (*e.g.* Damyanov and Likharev, 1975; Grossu, 1983; Neubert, 2014; own observations). Detached from this main range, the species also lives in northern Italy and two areas in southern France (Korábek *et al.*, 2014; Bertrand and Sanègre, 2015; Léonard and Latreche, 2015). While the earliest mentions of introduced populations in France date from the late 19th century (Kobelt, 1902–1906, p. 206; Chevallier, 1994), the Italian occurrences are known since the earliest malacological studies in the region (Gualtieri, 1742, pl. 1 fig. b; Müller, 1774; perhaps depicted already by Aldrovandi, 1606, p. 390 fig. 4). Still, the gap between the Balkans on the one hand and Italy on the other (about 700 km) suggests an anthropogenic origin of both French and Italian populations. Within the Italian range of *H. lucorum*, another likely introduced *Helix* species also occurs (*Helix cincta* Müller, 1774; Neubert, 2014), and both species could have been intentionally imported for food (Kobelt, 1902–1906; Korábek *et al.*, 2014; Neubert, 2014). Note that earlier reports of *H. lucorum* from central Italy actually refer to the unrelated *Helix straminea* Briganti, 1825 (Korábek *et al.*, 2014; cf. *e.g.* Welter-Schultes, 2012).

A peculiar form known as *Helix lucorum taurica* Krynicki, 1833 is found in the mountains between Sevastopol and Simferopol (*e.g.* Kramarenko, 2009) on Crimea, but it is disputed whether this form is indigenous (Kobelt, 1906; Balashov and Gural-Sverlova, 2012; Cameron *et al.*, 2013). It is characterized by yellowish globular shells with large rounded apertures and a reduced spiral, but often very conspicuous dark radial bands on the shell (Figures 1, 3A). However, similarly-looking *H. lucorum* are also known from Anatolia (*e.g.* as “*Helix radiosa* Ziegler” in Kobelt, 1902–1906, plate 354, from Uludağ in north-western Anatolia).

Whenever a report of an introduced individual or population from Europe has been accompanied with figures, these corresponded to the “*lucorum*” form (Devetak, 1978; Kochansky-Devidé, 1981; Allemand and Blanc, 1992; Reinink, 2005; Fischer *et al.*, 2008; Sendra Pérez *et al.*, 2008; Larraz Azcárate, 2010; Mienis and Rittner, 2010; Palmer, 2010; Quiñero

Figure 1. Sampling sites and the mitochondrial phylogeny of *Helix lucorum*. The shape and colour of the symbols showing sampling localities indicate membership to the clade labelled with an identical symbol in a maximum likelihood tree based on concatenated partial sequences of the genes for 16S rRNA and cytochrome c oxidase subunit I. Symbol size in the map corresponds to the number of analysed individuals (one or two). Branches are labelled with asterisks, successively for posterior probability ≥ 0.98 , SH-aLRT ≥ 95 , and bootstrap support $\geq 75\%$. Letters A–C denote the division into three clades as discussed in the text. Geographic origin of the terminal branches is indicated by two-letter ISO country codes, with Crimea considered as being part of Ukraine. A sampling site in Spain (a population of Italian ancestry) lies beyond the western map limit, so only its latitudinal position is indicated. For clade A, a median joining network of 16S rRNA sequences is also shown; haplotypes labelled with a plus sign in the network occur in Turkey. The two European forms are illustrated by figures from Rossmässler's *Iconographie* (Rossmässler, 1835–1837: fig. 291, 1838–1844: fig. 456): “*lucorum*” on the left, and “*taurica*” on the right.

Figure 2. Shell shapes of *Helix lucorum* “*lucorum*” and the sympatric *Caucasotachea* species illustrating the mutual phenotypic convergences. For comparison, the unusually shaped shell of the closest relative of *H. lucorum*, *H. nicaeensis*, is also included. The line drawing in the background shows the shell shape of the globular-shelled “*taurica*” form of *Helix lucorum* from Crimea (scaled to the same shell width), as a representative of a phenotype typical for the genus *Helix*. The conical or depressed shells differ from globular ones essentially in the lower last whorl and aperture, making the shell base flatter and the shell outline more triangular. *H. lucorum*: A – Turkey, prov. Zonguldak, Zonguldak (by courtesy of E. Neubert); B – Turkey, prov. Trabzon, Mačka env.; C – Serbia, distr. Nišava, Sićevo; *C. atrolabiata*: D – Turkey, prov. Ordu, Ünye; E – Turkey, prov. Trabzon, Mačka env.; *C. vindobonensis*: F – Serbia, distr. Nišava, Sićevo; *H. nicaeensis*: G – Turkey, prov. Bursa. Note that *C. vindobonensis* has been until recently classified as a species of *Cepaea* and *H. nicaeensis* placed in its own genus *Tacheopsis* (Korábek et al., 2015; Neiber and Hausdorf, 2015; Neiber et al., 2016). The size ranges of *H. lucorum* and *C. atrolabiata* overlap broadly.

Salgado et al., 2010; Samperez-Bedos, 2010; Varga et al., 2010; Gargominy and Ripken, 2011; Quiñonero Salgado and Ruiz Jarillo, 2011; Balashov et al., 2013; Henkel, 2013; Serrano Reyné, 2013; Čejka and Čáčány, 2014; Bertrand and Sanègre, 2015; Carcassès, 2015; Egorov, 2017). The only exception was a finding from Belgorod in Russia (Stoiko and Bulavkina, 2010), where the depicted shell closely resembled the Crimean “*taurica*”. Either the “*lucorum*” form is the most often traded and/or transported one, or it is the one most easily establishing new populations.

Helix lucorum is one of just three *Helix* species whose ranges extend from the Anatolian centre of the genus diversity into the Balkans or vice versa (Neubert, 2014; Korábek et al., 2015). The other two are *Helix pomacella* Mousson, 1854 and *Helix figulina* Rossmässler, 1839, with north-western limits

in Bulgaria and Macedonia (FYROM), respectively. For *H. lucorum*, there must have been at least two independent successful dispersal events from Anatolia to Europe – to the Balkans and to Crimea. As it is an edible species, often following anthropogenic habitats and currently expanding, its remarkable success in Europe raises the suspicion that it depended on human activities. After all, the species remains collected and traded to the present day, substantial amounts are being exported from Turkey (Baki, 2010), and sometimes such imports may give rise to new European populations (Brancotte, 2001; Mienis and Rittner, 2010).

In this contribution, we provide mitochondrial sequences from new sampling localities, particularly from Europe (including Crimea, and some recently colonized localities), and combine them with

previously available data (Korábek *et al.*, 2015) to explore the relationships between European and Anatolian *H. lucorum*. We looked for clues revealing the geographic origin of the European populations and evidence suggesting whether the expansion to Europe has been natural or anthropogenic. Altogether, the assembled dataset provides insight into the phylogeography of a species that may become a pest in some parts of Europe, and reveals possible source areas of the introduced populations.

Material and methods

We analysed 54 individuals in addition to the data from Korábek *et al.* (2015), originating from across the present range of *H. lucorum*, but mainly from the Balkan Peninsula. Several samples also originated from recently reported introduced populations from Spain, Czechia, Slovakia, and Russia. The material from Crimea includes samples from a natural habitat near Moroziivka village (Sevastopol, Balaklava Raion), which is near the Baydar Valley and can be considered as part of the area given as the type locality of *Helix taurica* Krynicki, 1833, described as “V Krymu (Baidarskaya dolina, Shulya i proch.)” [In Crimea: Baydar Valley, Ternovka, etc.] (Krynicki, 1833). Observations on the conchological variability of *H. lucorum* are based on our own collections listed in Supplementary Table S1 and examinations of collections of the Senckenberg Naturmuseum, Frankfurt am Main (SMF) and Museum für Naturkunde, Berlin (ZMB), both visited in 2011.

For the molecular analyses we used similar methods as in our earlier studies on *Helix* (Korábek *et al.*, 2015, 2016). We primarily sequenced a fragment of the mitochondrial 16S rRNA gene, supplemented by a fragment of cytochrome c oxidase subunit I (COI) from selected representatives across the 16S rRNA gene tree. Compared to our earlier data on *H. lucorum* (Korábek *et al.*, 2015), we targeted a longer 16S rRNA fragment (at least ca. 760 bp compared to 400 bp), and we also completed some of our previously published data to the extent of this fragment. That was done, whenever possible, to obtain the full fragment length for unique haplotypes and for the Balkan samples. We used the primer pairs LCO1490: 5'-GGTCAACAAAT-CATAAAGATATTGG-3' and HCO2198: 5'-TAAAC-TTCAGGGTGACCAAAAAATCA-3' (Folmer *et al.*, 2004) for COI, 16Scs1: 5'-AAACATACCTTTTGC-ATAATGG-3' and 16Scs2: 5'-AGAACTGACCT-

GGCTTACG-3' (Chiba, 1999) for the long 16S fragment, and 16Scs1 and 16S_MN3R: 5'-GCTACCTTTGCACAGTCAGWG-3' (Neiber *et al.*, 2017) for completing earlier data (see Korábek *et al.*, 2018 for details). All sequences were deposited in GenBank (see Supplementary Table S1 for accession numbers).

As an outgroup to root the tree we used *Helix nicaeensis* Férussac, 1821 (formerly known as the sole member of the genus *Tacheopsis* Boettger, 1909). This species has a shell very unusual for *Helix* (Figure 2G), somewhat resembling *Cepaea* Held, 1838 (long known as *Tachea* Turton, 1831) and *Caucasotachea* Boettger, 1909 (Boettger, 1909). Molecular phylogenies unambiguously placed it within *Helix*, as a very close relative of *H. lucorum* (Korábek *et al.*, 2015; Neiber and Hausdorf, 2015). The structure of its genital system is in line with this hypothesis (Schütt and Subai, 1989) and we consider the genus *Tacheopsis* a junior synonym of *Helix*. Nevertheless, the divergence in 16S rRNA and COI between *H. lucorum* and *H. nicaeensis* were well within the range of intraspecific divergences, and the monophyly of *H. lucorum* to the exclusion of *H. nicaeensis* was not strongly supported in Korábek *et al.* (2015). Therefore we checked (using the methods described below) that *H. nicaeensis* still falls outside *H. lucorum* within the mitochondrial phylogeny based on our extended dataset. We also ran the analyses with two more distant outgroup taxa added (*Helix pathetica* Mousson, 1854: acc. nos. KP072367 and KP072175; *Helix asemnis* Bourguignat, 1860: KP072208 and KP072159), resulting in even higher support for the mutual monophyly of *H. lucorum* and *H. nicaeensis* than in Korábek *et al.* (2015).

Phylogenetic analyses used similar methods as earlier (Korábek *et al.*, 2015). In brief, the sequences were concatenated and aligned using MAFFT 7 (Katoh and Standley, 2013) as implemented at <http://mafft.cbrc.jp/alignment/server/> (accessed on September 25th, 2017), with default settings and automatic selection of the alignment algorithm. We split the data into four partitions (16S rRNA gene and the three COI codon positions), and selected substitution models and performed maximum likelihood phylogenetic analysis with IQ-TREE 1.5.5 (Nguyen *et al.*, 2015; Chernomor *et al.*, 2016; Kalyaanamoorthy *et al.*, 2017). HKY+G, TrN+I, JC and K81uf+I models were suggested for the respective partitions. 1000 standard bootstrap pseudo-replicates and the SH-aLRT test (Guindon *et al.*, 2010) were run to estimate support values for branches. MrBayes 3.2.6 (Ronquist *et al.*,

Figure 3. *Helix lucorum* “*taurica*” and other globular-shelled *H. lucorum* forms. A – Ukraine, Crimea, Bakhchisaray (“*taurica*” in a strict, original sense); B – Turkey, prov. Bolu, lake Abant; C – Turkey, prov. Tunceli, 20 km from Tunceli to Ovacık; D – Turkey, prov. Konya, Ilgın; E – Turkey, prov. İzmir, ruins of Pergamon; F – Turkey, prov. Manisa, Spil Dağı. Most individuals were not photographed on the original background.

2012) was used for Bayesian inference. The analysis was run with two parallel runs of four chains for 1,500,000 generations, sampling every 1000th. The first 500,000 generations were discarded to obtain a posterior of 1000 trees per run.

For the shallowly differentiated clade found in the Balkans (clade A, see below) we constructed a median-joining haplotype network from 16S rRNA data using POPART 1.7 (Leigh and Bryant, 2015). Prior to analyses, a few short sequences were excluded and positions in alignment with gaps and missing data removed, retaining 45 sequences of 751 bp in length.

Results

Phylogenetic relationships

Maximum likelihood and Bayesian analyses resulted in identical topologies except for the youngest nodes.

We recovered three major mitochondrial clades of *H. lucorum* (A–C in Figure 1). The European samples attributed to the forms “*lucorum*” (all except the Crimean ones) and “*taurica*” (Crimean samples) yielded haplotypes of clades A and B, respectively. Clade A was found exclusively among specimens of the “*lucorum*” form, and its range extended along the southern Black Sea coast up to the western Caucasus. We found it in almost all samples of the “*lucorum*” form. An exception to this pattern was a sample from Zonguldak (north-western Anatolia, Figure 2A), which is phenotypically close to the “*lucorum*” morphotype (but even flatter) and yielded a haplotype of clade B.

Balkan samples were not monophyletic with respect to the Anatolian ones, and there was even a shared 16S rRNA haplotype between these two regions. Most of the samples formed a group of closely related haplotypes (Figure 1), but we found a distinctive haplotype group in eastern Greece. Basal to all these European sequences

was a haplotype from a Spanish population founded by individuals imported from Veneto in northern Italy (S. Quiñonero Salgado, pers. comm.).

All four samples from Crimea shared an identical haplotype, most closely related to one obtained from a flattened individual with little transverse banding (Figure 2A) from Zonguldak. However, most of the individuals with clade B haplotypes were of appearance similar to “*taurica*” in shell shape and often also in colour. The clade was found from Azerbaijan (including the region of the same name in Iran) to the Zonguldak province. Clade C seems mainly distributed in the south-west of Anatolia, but we also found it in the province of Artvin in north-eastern Turkey.

High phylogenetic diversity of mitochondrial lineages was found in Anatolia, and especially in the Lesser Caucasus and adjacent areas. The basal-most lineages of all three clades are probably found at the north-eastern limit of their distributions (Figure 1), although the basal position of north-eastern samples did not receive any substantial support in clade C and only from Bayesian analysis in clade B.

Conchological observations

The two conchological forms that are found in Europe, i.e. “*lucorum*” and “*taurica*”, represent just two extremes of a continuum with many forms that cannot be assigned to either. Not only are there intermediates, but some populations are conchologically rather distinctive in their combination of shell shape and colouration (especially south-western Anatolian populations associated with the clade C, Figs. 1, 3D–F). Forms resembling the typical “*taurica*” (Figure 3A: globular, yellowish, and predominantly radially banded) are found from the Marmara Sea up to Iran. Essentially identical shells bearing the locality “Thatieff” were collected in the Lesser Caucasus by C. Haussknecht (SMF 9881, paralectotypes of *Helix ancyrensis haussknehti* Kobelt, 1905). This locality probably corresponds to Tatev in southern Armenia, a UNESCO World Heritage site with an ancient monastery (spelled Tatiff on a German map by Handtke, 1855). Very similarly coloured populations also live in the provinces of Bursa (Kobelt 1902–1906) and Bolu (Figure 3B) in north-western Turkey. The nominotypical “*lucorum*” form is well recognizable in the Balkans, but seems to intergrade to other conchological varieties in north-eastern Anatolia and the Caucasus region. Typical “*lucorum*” can be found along the southern Black Sea coast and locally also

elsewhere in Anatolia (e.g. Antalya Province), but the extent of its natural distribution there is unclear as collections usually originate from the proximity of human settlements. In Azerbaijan, a form with conical and darkly coloured shells is found, but it has a rounded aperture and probably does not correspond to the “*lucorum*” form (e.g. Neubert, 2014, fig. 48 from Şahbulaq near Ağdam). The only available tissue sample from Azerbaijan analysed by us (from Ağdam) yielded a clade B sequence.

Discussion

In the malacology of the 19th century, new taxa were often based on unusual individuals or individuals collected at isolated localities. With such practices, introduced populations had a good chance of being picked for formal descriptions. Their ranges were detached from the main distribution and, probably due to founder effects, they may have been morphologically homogeneous and distinctive. Descriptions of both discussed forms of *H. lucorum* were based on populations whose native status is being questioned (e.g. Neubert, 2014; Cameron *et al.*, 2013), and that seems to still affect their interpretation.

Samples of synanthropic origin (or even purchased on markets) are frequent in museum collections, and our dataset also contains numerous samples collected from present or former human settlements. Even in Turkey, the native range of the species is not known with certainty and there are introduced populations (Kebapçı *et al.*, 2012). The original distribution of individual conchological forms thus cannot be described with certainty. In fact, *H. lucorum* presently occurs most frequently in anthropogenic habitats in the Caucasus (Mumladze, 2014; MT. Neiber, pers. comm.) as well as in Anatolia. Sampling directed specifically on the rare populations in natural habitats in Anatolia and the Caucasus has never been conducted.

Colonization of Crimea

Given that the geographically closest sampled Caucasian populations belonged to the “*lucorum*”, not “*taurica*”, form, Holocene colonization of Crimea along the Black Sea appears unlikely. A possible scenario may be colonization of Crimea from the Caucasus before the Last Glacial, but there is no reliable evidence for this and it also remains doubtful if Crimea provided suitable conditions for survival through the Last Glacial

(Cameron *et al.*, 2013). There is a published record of *Helix lucorum taurica* from deposits dated to MIS 5d–b (*i.e.* before the harshest part of the Last Glacial) near its present range (Chabai, 2005; Mikhalescu, 2005), but this study was not conducted by a specialist, used outdated literature (mainly Likharev and Rammel'meyer, 1952) and contains very doubtful species records. For example, two of the recorded species, *Vitrea diaphana* (Studer, 1820) and *Pseudochondrula tetrodon* (Mortillet, 1853) ("*Chondrula tetrodon*"), have never been reported from Crimea by other authors (Balashov and Gural-Sverlova, 2012; Balashov, 2016), including paleontological studies. Their current ranges are distant from Crimea (Central Europe and Transcaucasia, respectively) and their presence in Crimea, now or in the Pleistocene, would be surprising. Additional species listed by Mikhalescu (2005) are also not expected to occur in area of the reported site (Balashov, 2016). The work of Mikhalescu (2005) thus contains numerous misidentifications, and, considering that the material of his study was not preserved and cannot be revised (C. Mikhalescu, pers. comm.), all results of this study should be considered doubtful if not supported by new research.

Overseas dispersal, either natural or human-mediated, remains the most plausible possibility. Natural overseas dispersal seems unlikely given the distance across the Black Sea (at least 260 km). Overseas dispersal has been recently uncovered in another large snail in the Black Sea area, *Caucasotachea atrolabiata* (Krynicky, 1833) (Neiber *et al.*, 2016), but the distance involved was considerably smaller and human aid could not be excluded. Human-mediated introduction thus remains the most likely scenario of the origin of Crimean "*taurica*". The introduction to Crimea could have even been intentional. *Helix lucorum* was used as a lent food (Krynicky, 1833, "together with *H. lucorum* Müll"; Kobelt, 1906), and it is substantially larger than *Helix albescens* Rossmässler, 1839 that is native to Crimea. Established Greek colonies had existed both in southern Crimea and northern Anatolia by the 5–6th century BC (Grammenos and Petropoulos, 2003). In Crimea the Greek minority persisted until Soviet persecution in the 20th century (Agtzidis, 1991), and in Anatolia until the Greek genocide starting in 1914 and the eventual exchange of Greek and Turkish populations in the 1920s (Meichanetsidis, 2015). Southern Crimea and northern Anatolia were parts of the Byzantine Empire, its successor the Empire of Trebizond, and later both areas were controlled by the Ottoman Empire. Worth mentioning is also the late 18th

century immigration of Pontic Greeks to areas newly conquered by the Russian empire: New Russia and the Crimea (Xanthopoulou-Kyriakou, 1991). These cultural connections suggest that there were indeed plentiful opportunities for overseas transport.

Status of Helix lucorum taurica

The taxonomic status of Crimean *Helix taurica* has been debated since early shell imports from the Caucasus. It was soon recognized that the "*taurica*" form also occurs outside Crimea (von Martens, 1874), but substantial confusion in nomenclature (reviewed in Kobelt, 1906) concealed the match of Anatolian forms with Crimean "*taurica*". During the second half of the 20th century, the subspecific division of *H. lucorum* has been largely abandoned and *H. taurica* has thus disappeared from literature as one of its numerous synonyms (*e.g.* Zilch, 1952; Schileyko, 1978; Neubert, 2014). In our view, the Crimean "*taurica*" cannot be delimited as a diagnosable group, and we currently see no basis for subspecies recognition in *H. lucorum*. Therefore we consider *H. taurica* Krynicky, 1833 a synonym of *H. lucorum* Linnaeus, 1758.

However, in the influential work of Likharev and Rammel'meyer (1952), *H. lucorum taurica*, with an indicated range extending to the Caucasus, was listed as a distinct subspecies. It was also included in a monograph on Armenian mollusc fauna (Akramovski, 1976). At present, *H. lucorum taurica* continues to be cited as a valid subspecies by Russian-speaking authors, in faunistics or as a model in neurophysiology (*e.g.* Leonov, 2009; Balaban *et al.*, 2016). Despite the long-recognized affinities to some Caucasian and Anatolian *H. lucorum* populations, it is protected on the national level as a presumed Crimean endemic subspecies under Ukrainian law (Akimov, 2009) as well as on the regional level in Crimea under the control of the Russian Federation (Ivanov and Fateryga, 2015). Considering that "*taurica*" is clearly not a Crimean endemic, but more likely a taxon introduced from Anatolia (Figs. 1, 3; see also Kobelt, 1906), its conservation status should be revised. Invasive species are not eligible for a conservation status under IUCN guidelines (IUCN, 2012). However, as "*taurica*" was long the only *H. lucorum* in Ukraine, the species is protected as a whole. In southern Ukraine, including Crimea, introduced *H. lucorum* of the typical form have been reported (Leonov, 2006; Balashov *et al.*, 2013), which certainly does not need to be protected.

Conchological peculiarities of typical Helix lucorum

The shell shape of the nominotypical form of *H. lucorum* is derived within *Helix* (Korábek *et al.*, 2015) and, in contrast to the usual globular *Helix* shells, exhibits a tendency towards a shape similar to the genera *Caucasotachea* (eastern Pontic Mountains, Caucasus, Alborz, Balkans) and *Cepaea* (primarily Western Europe) (Figure 2). Both these genera are also often rather conspicuously coloured, with a high contrast between dark banding and the light background; *C. atrolabiata* sometimes even develops dark radial stripes (Neubert and Bank, 2006, figs. 12–21). Due to their similarity, Boettger (1914) even considered a giant form of *Cepaea* from the last interglacial found in the vicinity of Nice, France (originally described as *Helix paretiana* Issel, 1867; Rambur, 1869; Dubar, 1984) to be a close relative of *H. lucorum*.

Possibly, the conchological similarities reflect convergent adaptations to commonalities of the life style of the three lineages. Broadly conical shells, with a smaller, lower aperture compared to other *H. lucorum* forms, may be an adaptation to climbing onto vegetation, while globular shells with large apertures have been regarded an adaptation to resting on the ground and burrowing (Heller, 1987; Slatyer *et al.*, 2007; Köhler and Criscione, 2015). Both *Caucasotachea* and *Cepaea* often crawl onto herbs and bushes and rest on the vegetation. From our field experience, the nominotypical *H. lucorum* form is a relatively agile climber within the genus *Helix*, and we very often found it resting high on vegetation or various structures. The variegated and variable colouration of these three lineages may provide some protection against predators, especially when looking from below against a matrix of penetrating light and leaf shadows. Observations on the habitat and behaviour of *H. nicaeensis* (Figure 2G) and rigorous quantification of the climbing frequency between nominotypical *H. lucorum* and the globular-shelled forms should be performed to evaluate the hypothesis of a relationship between the shell shape and climbing on vegetation.

The origin of Balkan and introduced populations of typical H. lucorum

There is currently no unambiguous evidence for the presence of *H. lucorum* in Europe before the Holocene. The European fossil taxa attributed in the past to *H. lucorum* (*Helix lucorum pliocenica* Coppi, 1881 and *Helix lucorum supralevantina* Wenz, 1942; Coppi, 1869, 1881; Wenz, 1942) are of dubious systematic

position, because there are no traits truly demonstrating they represent *H. lucorum*, and assignments to other taxa are equally likely. Therefore, these fossils cannot be interpreted as evidence of an earlier presence of the species within its European range. There are claims of Pleistocene *H. lucorum* from the vicinity of Skopje in Macedonia (Pavlović, 1909; Petrboč, 1943) and Varna in Bulgaria (Petrboč, 1948), but without details on the sampling site and sampling procedures to demonstrate that the shells were not in fact recent. The reports of the Czech malacologist J. Petrboč are not very trustworthy, because throughout his career he documented his research sloppily and selectively presented findings in countless chaotic papers. Moreover, the depicted alleged Pleistocene shell (Petrboč, 1943, fig. 3) was not crushed, but was glossy and fully coloured, and thus appears rather unlikely to be a subfossil. However, the general lack of records may well be a result of the scarcity and poor knowledge of Quaternary fossil record in the Balkans, which also applies for the likewise missing Holocene data. In the future, archaeological research may provide hints on the earliest occurrences in particular areas (*e.g.*, the Copper Age record from a site in Thrace by Georgiev *et al.*, 2009), but accessible data are missing at present.

Although Anatolia and the Balkans were last connected during the Last Glacial (*e.g.* Aksu *et al.*, 2002) and presently are separated only by the narrow straits of Bosphorus and Dardanelles, the Balkan populations of *H. lucorum* are markedly homogeneous in shell appearance and mitochondrial variation when compared with those from north-western Anatolia. The four Anatolian samples of clade A we obtained were dispersed across the clade phylogeny, and identical or nearly identical haplotypes in the Balkans and Anatolia provide evidence for a relatively recent genetic exchange between the two (Figure 1). Given the general patterns of diversity within *H. lucorum*, the exchange was more likely from Anatolia to the Balkans than in the opposite direction. In any case, the exchange was probably not limited to a single dispersal event, but rather involved multiple crossings of the Bosphorus.

The shared haplotype between Anatolia and the Balkans may well be the result of a recent colonization of the Balkans, which could have been intentional for this edible species. After all, it would not be exceptional among Helicidae, as several other edible species have been spread by humans in the Mediterranean Basin (*e.g.* Däumer *et al.*, 2012;

Ketmaier and Glaubrecht, 2015; Korábek et al., 2015; Sherpa et al., 2018). If true, we suggest that the south-eastern coast of the Black Sea region could be a source for the introductions. The divergent haplotype from a Spanish sample of Venetian ancestry, not sampled in the Balkans, hints that the historical trade ties between Trabzon in the Pontus region of Turkey and the north-Italian Venezia after the fall of Constantinople in 1204 could have played a role in the colonization of Italy by *H. lucorum*. There are even reports of *H. lucorum* findings from archaeological excavations near Bologna dated to the 13–14th century (Farello, 1990, 1999, 2001), but these may as well refer to the nearby-living *H. straminea* (Korábek et al., 2014). The native status of the “*lucorum*” form in Georgia has been also questioned (Mumladze, 2014), while the haplotype found there also occurs in the Turkish province of Trabzon, which could be the ultimate source of the most invasive form of the species. Unfortunately, detailed sampling in northern Anatolia, currently unfeasible, is necessary to test the hypothesis of human-aided dispersal.

Maritime trade across the Mediterranean and the Black Sea led to the exchange of species between coastal areas (Schütt, 2010; Welter-Schultes, 2012), blurring zoogeographic boundaries. It has been demonstrated that snails were unknowingly transported in the Mediterranean for more than three millennia (Welter-Schultes, 2008). Probably at least since Roman times, edible snails were transported intentionally (e.g. Ant, 1971; Davies, 1971; Chevallier and Dufournet, 1974; Pollard, 1975). That a part of species range may be the result of ancient introduction is often not immediately apparent, and sometimes not even detectable. Still, these cases need to be identified so that they do not mislead biogeographic analyses, taxonomy, and conservation decisions.

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Online supplementary information

SI. Details of the samples used for molecular analyses and our own new shell collections.