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How an Ecological Race Is Forming: Morphological and Genetic Disparity among Thermal and Non-Thermal Populations of Aquatic Lymnaeid Snails (Gastropoda: Lymnaeidae)

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Abstract: Hot (geothermal) pools and streams, a specific type of aquatic biotopes having almost worldwide distribution, maintain rich faunas of animals belonging to various taxa. Snails (Gastropoda) represent one of such groups, which form populations in geothermal waterbodies of all continents. Some freshwater snail species produce morphologically distinct hot-water populations, whose rank is often debated (full species or thermal ‘ecotype’, or ‘race’). In this study, we used six species of pond snails (family Lymnaeidae) to investigate the morphological and genetic consequences of infiltration of freshwater snails into geothermal habitats. In particular, we aimed at studying the changes in shell shape and proportions as well as the formation of unique hot-water haplotypes and the occurrence of the latter beyond geothermal waterbodies. All six species studied demonstrate diminutive body size in hot sites accompanied, in four species, by apparent alterations in shell proportions. A phenomenon of phenotypic ‘juvenilization’, when adult and able to reproduce individuals demonstrate shell proportions characteristic for full-grown individuals living under ‘normal’ conditions, is described. Unique ‘thermal’ haplotypes, not found beyond the geothermal sites, were normally restricted to a single locality, and no signs of frequent ‘travels’ of snails from one thermal habitat to another are seen. In the vast majority of cases, these exclusive haplotypes are separated from their ancestors by only a few (1–3) mutational steps, which may indicate their relatively recent origin. We are inclined to relate both size reduction and ‘juvenilization’ to the life-cycle re-adjustment following the penetration of lymnaeids to thermal habitats. The ecological (‘thermal’) intraspecific races of different species, forming in geothermal habitats, exhibit, to a great extent, evolutionary predictability (= convergent evolution; = parallelisms). The dilemma ‘ecological race vs. young species’ in application to the taxonomy of these hot-water populations is briefly discussed.

Keywords: geothermal ecosystems; Lymnaeidae; thermal adaptation; variability; progenesis; geometric morphometry; ecological race; phylogeography

1. Introduction

Linnaeus [1] was the first author who described a species of freshwater molluscs, ecologically restricted to living in thermal aquatic habitats. This species was *Turbo thermalis* Linnaeus, 1767 (= *Belgrandia thermalis* of the current taxonomy) of the family Hydrobiidae Stimpson, 1865, whose type locality is situated in warm springs near Pisa, Italy. The original description of *T. thermalis* is very short and almost lacking in ecological information. The real interest of biologists in molluscs inhabiting geothermal waterbodies arose more than 50 years after Linnaeus.

In 1833, the French naturalist Simon Suzanne Nérée Boubée [2], then the professor of geology in Paris, described three new species of freshwater snails he found in thermal springs of Southern France: *Neritina thermalis*, *Paludina rubiginosa*, and *Limnea thermalis* (later redescribed by Dupuy [3]). According to him, these snails were living in warm mineralized water (water temperature ranged from 18 to 27° C) and could not be found elsewhere. Most probably, it was the first ecological observation on freshwater snails living in geothermal environment ever published. Since 1833, numerous species of freshwater gastropods have been reported from thermal springs and like localities, including some species living exclusively in such habitats (Table 1). This group of ‘hot snails’ represents 19 families and three subclasses of Gastropoda. Such phylogenetic heterogeneity alongside with very broad geographical distribution (thermal populations of snails are known from all continents) presumes numerous independent introductions of freshwater Gastropoda to geothermal habitats. Various aspects of taxonomy, biogeography, and ecology of these molluscs have been debated in malacological literature (see [4–12] for some of the latest publications).

The taxonomic status of many nominal species of gastropods thought to be endemic to freshwater geothermal habitats has been debatable. Some authors dispute their species status and, based on morphological or more often genetic evidence, synonymize them with widespread species, which are believed to form the ‘dwarf’ races, or ecotypes, in hot springs [5,13–20]. On the other hand, certain researchers are inclined to consider such thermal forms as incipient and evolutionary young species, which explains the absence of a pronounced genetic distance between them and their non-thermal counterparts [10,21].

In addition to snails, which constitute one of the most abundant invertebrate groups living in geothermal sites [8,10,11], other animal taxa are known to form stable populations in such habitats, including dragonflies and damselflies [22,23], midges [10], fish [24,25], reptiles [26], amphipods [10], and some groups of microinvertebrates [27].

Geothermal waterbodies, scattered through the whole Earth, from Kamchatka Peninsula to Patagonia, represent a specific environment, with unique temperature regime and, sometimes, chemical composition. The springs, ponds, and swamps of hydrothermal sites are characterized by increased temperature (typically > 20–25 °C) that is maintained the year round, without drastic seasonal fluctuations. From the biological point of view, these habitats represent a very peculiar environment, and animals need to develop special adaptations in order to be able to conquer it [6,28].

Constituting a type of physically similar habitats, not confined to a particular continent, latitude, or bioclimatic zone, geothermal waterbodies represent an ideal place for studies of convergent evolutionary processes in aquatic animals. The model of convergent evolution, according to which non-related organisms living under similar conditions develop similar morphologies, was hotly debated already 120–150 years ago, although the adherents of rivaling evolutionary doctrines had offered different mechanisms for its explanation. The (neo-)Lamarckists insisted that a peculiar environment directly induces similar phenotypic shifts in individuals, and that these shifts can be inherited. The (neo-)Darwinists argued that the phenotypic similarity is targeted by natural selection; one and the same selective force(s) drive(s) organisms of different localities towards similar adaptive responses. Today, when the (neo-)Darwinian paradigm dominates in biology, convergent evolutionary processes are still discussed in theoretical literature [29–33]. This model of evolution has been applied in a host of case studies in order to explain the

observed phenomena (e.g., [34–37]), though there are some data indicating that presumably convergent (or parallel) evolutionary events not always run so parallel as it is assumed [38].

This study primarily aims at testing of a working hypothesis that independent colonization of geothermal habitats by different, not closely related species of freshwater snails will result in some degree of morphological repeatability. In other words, phylogenetically distant species may develop similar morphologies in analogous environments and form ‘ecological’ (or ‘thermal’) intraspecific races, as a consequence of adaptation to life in geothermal habitats. To check this hypothesis, we applied both morphological and molecular genetic analysis. The focus group of our study is the Lymnaeidae, a family of air-breathing (pulmonate) aquatic snails with almost cosmopolitan distribution [13,39]. At least 14 lymnaeid species belonging to four genera are known to form ‘thermal populations’ in the Palearctic (see Table 1); samples of six of these species were included into our analyses based on their availability.

The second goal of this research was to reveal the probable cause(s) of body size diminution, which is frequently observed in populations of the lymnaeids and some other organisms living in geothermal habitats. This so-called ‘thermal dwarfism’ is a special case of miniaturization, a morphological pattern widespread among animals [40,41]. When describing his *Limnea thermalis*, Boubée [2] mentioned that the shell size of this species is considerably less as compared to its congeners. That observation was confirmed, albeit without a statistical support, by other French malacologists of the 19th century [3,42]. A statistical study of thermal dwarfism in populations of ‘*Lymnaea peregra*’ (= *Ampullaceana balthica*) in Iceland was undertaken by Starmühlner [43]. Other examples of miniaturization among freshwater snails, which gained a foothold in geothermal sites, were provided by Hazay [44], Clessin [45], Brues [46], Meier-Brook [14], Khmeleva et al. [47], Aksenova et al. [18,48], Sitnikova & Peretolchina [21], and Chatterjee et al. [49]. However, as Meier-Brook [14, p. 36] stated, ‘the mechanism causing dwarfism in warm springs is not yet understood.’

Table 1. A list of freshwater gastropod species found in geothermal habitats (all species names, except for those not assessed in the recent literature, are given in accordance with current nomenclature).

Subclass: Family	Species Name	Distribution	Reference
Neritimorpha: Neritidae	<i>Theodoxus prevostianus</i> (C. Pfeiffer, 1828)	Eastern Europe (Austria, Hungary)	[50]
	<i>Th. fluviatilis fluviatilis</i> (Linnaeus, 1758); <i>Th. f. thermalis</i> (Dupuy, 1851)	England (Derbyshire); France (Pyrenees)	[51,52]
Caenogastropoda: Thiaridae	<i>Melanooides tuberculata</i> (O.F. Müller, 1774)	Central Europe (Austria, Hungary, Romania *), Indonesia (Sulawesi and Sumatra Islands), USA (Wyoming, Yellowstone National Park, Grand Teton National Park); New Zealand, Jordan *	[53–59]; our data
	<i>Melanooides pamirica</i> Lindholm, 1930	Tajikistan (Pamir Mts); West Himalaya (<i>M. pamiricus</i>)	[60]
	<i>M. shahdaraensis</i> Starobogatov & Izzatullaev, 1980	Turkmenistan; North Afghanistan	
	<i>M. kainarensis</i> Starobogatov & Izzatullaev, 1980	Turkmenistan; North Afghanistan	
Caenogastropoda: Bithyniidae	<i>Bithynia tentaculata</i> (Linnaeus, 1758)	Austria, Hungary, England (Derbyshire)	[44,51,61,62]
	‘ <i>Bythinia</i> ’ <i>rumelica</i> Wohlberedt, 1911	Bulgaria	[63]
	‘ <i>Bithynia thermalis</i> ’	Italy (Lucca)	[64]
	<i>Boreoelona contortrix</i> (Lindholm, 1909)	Russia (Siberia, Baikal area)	[65]
	<i>B. sibirica</i> (Westerlund, 1886)	Russia (Siberia, Baikal area)	[66]
Caenogastropoda: Cochliopidae	<i>Kainarella minima</i> Starobogatov, 1972	Turkmenistan	[67]
	<i>Lobogenes michaelis</i> Pilsbry & Bequaert, 1927	Zaire	[68]

	<i>Pseudocaspia starostini</i> Starobogatov, 1972	Turkmenistan	[67]
	<i>Semisalsa aponensis</i> (von Martens, 1858)	Italy	[69]
	<i>S. foxianensis</i> (De Stefani, 1883)	Italy	
	<i>Tryonia monitorae</i> Hershler, 1999	USA (Nevada)	[70]
	<i>Tryonia chviscarae</i> Hershler, Liu & Landye, 2011		
	<i>T. julimesensis</i> Hershler, Liu & Landye, 2011	Mexico (Chichuachua)	[71]
	<i>T. minckleyi</i> Hershler, Liu & Landye, 2011		
Caenogastropoda: Tateidae	<i>Austropyrgus nanus</i> Clark, Miller & Ponder 2003		
	<i>Austropyrgus solitarius</i> Clark, Miller & Ponder 2003	Australia (Tasmania)	[72]
	' <i>Hydrobia jenkinsi</i> ' = <i>Potamopyrgus antipodarum</i> (Gray, 1843)	England (Derbshire)	[51]
	<i>Potamopyrgus</i> sp.	New Zealand	[73]
Caenogastropoda: Tomichiidae	<i>Tomichia hendrickxi</i> (Verdcourt, 1950)	Zaire	[68]
Caenogastropoda: Bythinellidae	<i>Bythinella rubiginosa</i> (Bouée, 1833)	France	[74]
	<i>B. schmidtii</i> (Küster, 1852)	Austria	[54]
	<i>B. thermophila</i> Glöer, Varga & Mrkvicka, 2015	Hungary	[75]
Caenogastropoda: Lithoglyphidae	<i>Fluminicola seminalis</i> (Hinds, 1842)	USA (California)	[76]
Caenogastropoda: Hydrobiidae	<i>Belgrandia thermalis</i> (Linnaeus, 1767)	Italy (Pisa)	[1,77]
	<i>Belgrandiella mimula</i> Haase, 1996	Austria	[78]
	<i>Pseudamnicola letourneuxiana</i> (Bourguignat, 1862)	Algeria	[79]
	<i>Pyrgulopsis bruneauensis</i> Hershler, 1990	USA (Idaho)	[80]
	<i>P. bryantwalkeri</i> Hershler, 1994 (= <i>Fluminicola nevadensis</i> Walker, 1916)	USA (Nevada)	[76]
	<i>P. nevadensis</i> (Stearns, 1883)		
	<i>P. thermalis</i> (D.W. Taylor, 1987)	USA (New Mexico)	[81]
	<i>Hadziella thermalis</i> Bole, 1992	Slovenia	[82]
	' <i>Iglica</i> ' <i>veklorhi</i> De Mattia, 2007		[83]
	<i>Radomaniola bulgarica</i> Glöer & Georgiev, 2009	Bulgaria	[84]
Caenogastropoda: Stenothyridae	<i>Stenothyra thermaecola</i> Kuroda, 1962	Japan (Kyushu Island)	[85]
Caenogastropoda: Semisulcospiridae	<i>Juga plicifera</i> (I. Lea, 1838)		
	<i>J. nigrina</i> (I. Lea, 1856)	USA (California)	[76]
Caenogastropoda: Melanopsidae	<i>Melanopsis etrusca</i> (Brot, 1862)	Italy (Tuscany Region)	[86]
	<i>M. daubertii thermalis</i> (Brot, 1868)	Austria, Hungary	
	<i>M. parreyssii</i> (Philippi, 1847)	Bulgaria, Romania	[63,87]
	<i>Melanopsis</i> sp.	Cyprus	own observations
Caenogastropoda: Viviparidae	<i>Angulyagra costata</i> (Quoy & Gaimard, 1834)	Indonesia (Sulawesi)	[53]
	<i>Viviparus contectus</i> (Millet, 1813)	Austria	[54]
Heterobranchia: Acroloxidae	<i>Acroloxus lacustris</i> (Linnaeus, 1758)	Hungary	[62]
Heterobranchia: Chilinidae	<i>Chilina patagonica</i> Sowerby, 1874	Patagonia	[9]
	<i>Ampullaceana balthica</i> (Linnaeus, 1758) **. (Referred to as <i>Lymnaea peregra</i> (Müller) and <i>Radix pereger</i> var. <i>ovata</i> (Draparnaud))	Iceland, French Pyrenees	[2,7,43]
Heterobranchia: Lymnaeidae	<i>A. lagotis</i> (Schrank, 1803) [referred to as <i>Lymnaea zazurnensis</i> ; <i>L. ovata</i> , <i>L. fontinalis</i>]	Northeast European Russia (Nenets Autonomous Region); Siberia (Baikal area); East Kazakhstan	[6,66,88], this study
	<i>Austropeplea tomentosa</i> (L. Pfeiffer, 1855)	New Zealand	[73]
	<i>Galba bowelli</i> (Preston, 1909)	Russia (Siberia, Baikal area)	[66]
	<i>G. sibirica</i> (Westerlund, 1885)	Russia (Siberia, Baikal area)	[66]

	<i>G. truncatula</i> (O.F. Müller, 1774)	Austria, Iceland, Hungary, Tajikistan	[54,62,89]; own observations
	<i>Kamtschaticana kamtschatica</i> (Middendorff, 1850)	Russian Far East and Eastern Siberia	[19,47]
	<i>Ladislavella catascopium</i> (Say, 1817)	USA (Yellowstone Park), Russia (Kamchatka Peninsula), Canada (British Columbia and Yukon Provinces)	[16,46]; this study
	<i>Ladislavella elodes</i> (Say, 1821)	USA (Nevada, Yellowstone National Park)	[76,90]
	<i>Lanx patelloides</i> (I. Lea, 1856)	USA (California)	[76]
	<i>Lymnaea stagnalis</i> (Linnaeus, 1758)	Austria	[54]
	<i>Peregriana peregra</i> (O.F. Müller, 1774)	Croatia, Ireland	[91,92]
	<i>Pseudosuccinea columella</i> (Say, 1817)	Austria *	[54]
	<i>Radix alticola</i> (Izzatullaev, Kruglov & Starobogatov, 1983)	Tajikistan, Nepal	[19,89]
	<i>R. auricularia</i> (Linnaeus, 1758)	Europe (Austria), Russia (Baikal area, Kamchatka), Afghanistan; Tibet	[9,47,48,54,93,94]
	<i>R. 'persica'</i> (Issel, 1865)	Iran	[95]
	<i>R. rubiginosa</i> (Michelin, 1831)	Indonesia (Sulawesi, Flores and Sumatra)	[53]; our data
	<i>R. rufescens</i> (Gray, 1822) [referred to as <i>Lymnaea acuminata</i>]	India (Himalaya)	[49]
	<i>Stagnicola palustris</i> (O.F. Müller, 1774)	Austria, Hungary	[54,62]
	<i>Tibetoradix kozlovi</i> Vinarski, Bolotov & Aksenova, 2018	China (Tibetan Plateau)	[96]
	<i>'Physa fontinalis'</i> (Linnaeus, 1758)	New Zealand	[73]
	<i>'Physa thermalis'</i> Locard, 1899 = <i>Paraplexa cornea</i> (Massot, 1845)	France	[97]
	<i>Physella acuta</i> (Draparnaud, 1805), including <i>Ph. acuta</i> var. <i>thermalis</i> (Boettger, 1913)	USA (Virginia, Utah, Yellowstone National Park, Alaska), Europe (Poland, Slovakia) *; Abkhazia; Russia (North Caucasus) **	[5,46,54,97]; our data
Heterobranchia: Physidae	<i>Ph. cooperi</i> (Tryon, 1865)	USA (California)	
	<i>Ph. johnsoni</i> (Clench, 1926)	Canada (Alberta)	
	<i>Ph. osculans</i> (Haldeman, 1841)	USA (California)	[76,90]
	<i>Ph. propinqua</i> (Tryon, 1865)	USA (Idaho)	
	<i>Ph. smithiana</i> Baker, 1920	USA (Nevada)	
	<i>Ph. spelunca</i> Turner & Clench, 1974	USA (Wyoming)	[5]
	<i>Ph. virginica</i> (Gould, 1847)	USA (New Mexico, Nevada, Utah)	[90]
	<i>Ph. wrighti</i> Te & Clarke, 1985	Canada (British Columbia)	[4]
	<i>Ph. johnsoni</i> (Clench, 1926)	USA	
	<i>Ancylus fluviatilis</i> O.F. Müller, 1774	Austria	[54]
	<i>Anisus spirorbis</i> (Linnaeus, 1758)	Hungary	[62]
	<i>A. vorticulus</i> (Troschel, 1834)		
	<i>Armiger annandalei</i> (Germain, 1918)	East Kazakhstan; Tajikistan (Pamir Mts.)	[98]; our data
Heterobranchia: Planorbidae	<i>Bathymphalus contortus</i> (Linnaeus, 1758)	Austria; Russia (Siberia, Baikal area)	[54]
	<i>Biomphalaria costata</i> (Biese, 1951)	Chile	[99]
	<i>B. thermalis</i> (Biese, 1951)		
	<i>Ferrissia fragilis</i> (Tryon, 1863) **	Austria, Hungary	[54,62]
	<i>Gyraulus acronicus</i> (Férussac, 1807)	Russia (Kamchatka)	[14]
	<i>G. albus</i> (O.F. Müller, 1774)	Austria	[54]

<i>G. baicalicus</i> (Dybowski, 1913)	Russia (Siberia, Baikal area)	[66]
<i>G. borealis</i> Lovén in Westerlund, 1875	Russia (Siberia, Baikal area)	[66]
<i>G. chereshevi</i> (Prozorova & Starobogatov, 1997)	Russia (Chukchi Peninsula)	[100]
<i>G. convexiusculus</i> (Hutton, 1849)	Afghanistan	[94]
<i>G. cf. ignotellus</i> (Dybowski, 1913)	Russia (Siberia, Baikal area)	[66]
<i>G. iwaotakii</i> (Mori, 1938)	Japan (Honshu Island)	[20,101]
<i>G. ladacensis</i> (Nevill, 1878)	Tajikistan (Pamir Mts.)	[98]
<i>G. laevis</i> (Alder, 1838)—described as <i>Planorbis thermalis</i> Westerlund, 1885	Austria, Northeast European Russia (Nenets Autonomous Region)	[14,102]; our data
<i>G. pankongensis</i> (Martens, 1882)	Tajikistan (Pamir Mts.)	[89]
<i>G. parvus</i> (Say, 1817)	Iceland	[14]
<i>G. takhteevi</i> Sitnikova & Peretolchina, 2018	Russia (Siberia, Baikal area)	[10]
<i>G. thermochukchensis</i> (Prozorova & Starobogatov, 1997)	Russia (Chukchi Peninsula)	[100]
<i>Helisoma anceps</i> (Menke, 1830)	USA (Nevada)	[76]
<i>H. trivolvis</i> (Say, 1817)	Austria *	[54]
<i>Planorbarius corneus</i> (Linnaeus, 1758)	Hungary	[62]
<i>Planorbella duryi</i> (Wetherby, 1879)	Hungary	[55]
<i>P. subcrenata</i> (Carpenter, 1857)	USA (Nevada)	[76]
<i>Planorbis planorbis</i> (Linnaeus, 1758)	Austria, Hungary	[44,54]
<i>P. sieversi</i> Mousson, 1873	Afghanistan	[94]
<i>Vorticifex effusus</i> (I. Lea, 1856)	USA (California, Nevada)	[76]
<i>Valvata cristata</i> O.F. Müller, 1774	Hungary	[62]
Heterobranchia: Valvatidae <i>V. pamirensis</i> Starobogatov, 1972	Tajikistan (Pamir Mts.)	[67]
<i>V. sibirica</i> (Middendorff, 1851)	Russia (Siberia, Baikal area)	[65]

* Invasive; ** Though the identity of *Limnaea thermalis* Boubée, 1833 has never been checked genetically, it possibly represents a junior synonym of *Ampullaceana balthica*.

2. Material & Methods

2.1. Material Examined

The primary material for this study was obtained in 2009–2019, during fieldworks conducted by our team in some geothermal areas situated in the northern Palearctic (Iceland, Kazakhstan, and Russia) and the northwestern Nearctic (Canada) (Figure 1). We used samples of six lymnaeid species collected from 20 geothermal localities (Table 2; Figure 2), which are kept in collections of the Saint-Petersburg State University (Laboratory of Macroecology and Biogeography of Invertebrates; LMBI), Saint Petersburg, Russia and the Russian Museum of Biodiversity Hotspots (RMBH) of the N. Laverov Federal Center for Integrated Arctic Research of the Ural Branch of the Russian Academy of Sciences, Arkhangelsk, Russia. In addition, we used samples borrowed from the malacological collection of the Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia (ZIN; see Table 2). The selection of species was based on their availability from public museum collections and own samples. We examined only these lymnaeid species that we were able to observe in their natural habitats in the course of our fieldwork.

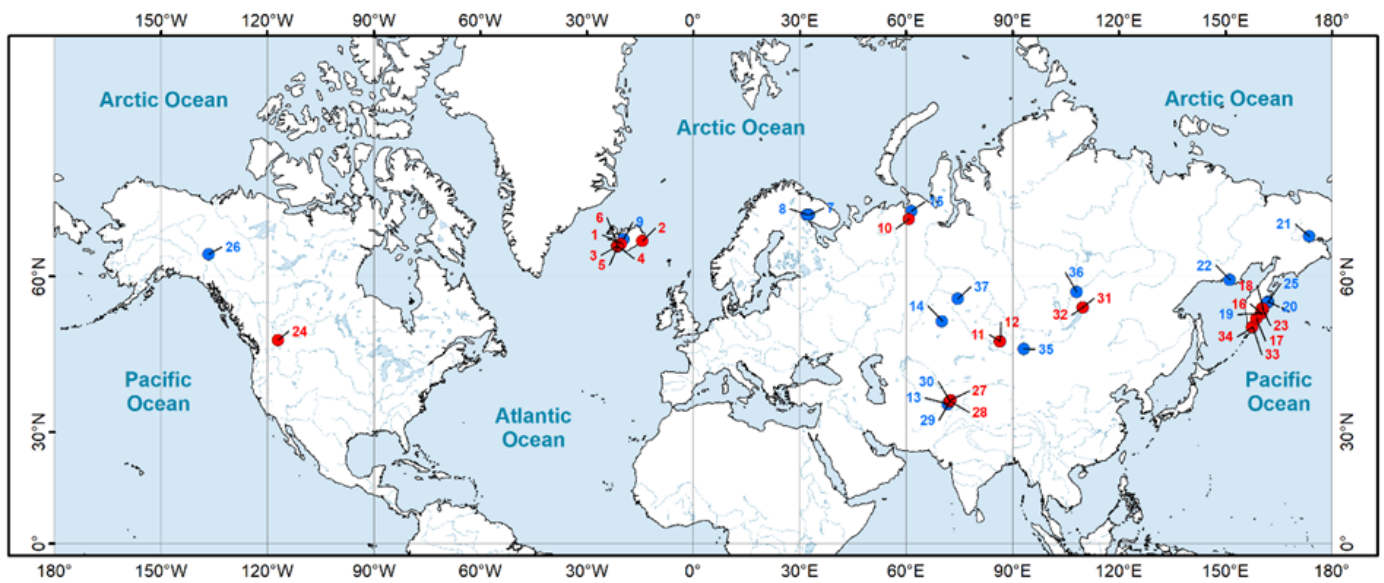


Figure 1. A map showing the geographical position of the studied populations of the lymnaeid snails. The numbers on the map correspond to the numbers in Table 2. Red circles denote geothermal localities, blue circles—non-geothermal.

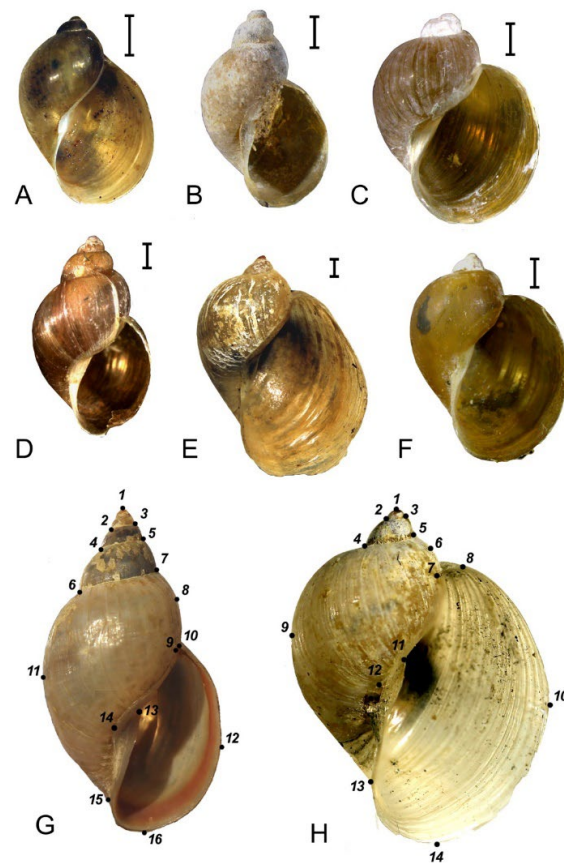


Figure 2. Shells of lymnaeid snails from geothermal populations used in this study (A–F) and configuration of landmarks (black dots) used for the morphometric analyses of *Ladislavella catascopium* (G) and the rest of the species (H). A. *Ampullaceana balthica*, Iceland, Geysir hot springs. B. *A. lagotis*, Russia, Vashutkiny Lakes. C. *Kamtschaticana kamtschatica*, Russia, Kamchatka Peninsula, Nalychevskiye hot springs. D. *Ladislavella catascopium*, Russia, Kamchatka Peninsula, Tumrok hot springs. E. *Radix alticola*, Tajikistan, Pamir Mts., Djaushangoz hot spring. F. *R. auricularia*, Russia, Kamchatka Peninsula, Malkinskiye hot springs. Scale bars 1 mm. Photos by Olga V. Aksenova, Maxim V. Vinarski.

Table 2. Populations of lymnaeid snails from geothermal (GT; red letters) and non-geothermal (NG; blue letters). habitats studied in this research.

No.	Species	Sampling Locality, Sampling Date (Month, Year)	Type of Habitat	Latitude	Longitude	N/n *	Museum Accession Number
1	<i>Ampullaceana balthica</i>	Iceland, Geysir Hot Spring area, a thermal pool, July 2013	GT	64.3144	−20.2991	80/33	RMBH, MLym-195–MLym 198
2	<i>A. balthica</i>	Iceland, hot spring in Djúpivogur, July, 2015	GT	64.6568	−14.2847	26/26	LMBI (not catalogized)
3	<i>A. balthica</i>	Iceland, thermal springs near Hengill volcano, July 2013	GT	64.0538	−21.2894	32/32	RMBH, MLym-190
4	<i>A. balthica</i>	Iceland, a hot brook near Rejkamork settlement, July 2013	GT	64.0058	−21.1811	105/32	RMBH, MLym-184
5	<i>A. balthica</i>	Iceland, hot springs of the Graendalsa River valley, near Rejkakot settlement, July 2013	GT	64.0268	−21.1988	153/30	RMBH, MLym-183
6	<i>A. balthica</i>	Iceland, a hot brook of the Graendalsa River valley, July 2013	GT	64.0241	−21.2036	36/30	RMBH, MLym-189
7	<i>A. balthica</i>	Russia, Kola Peninsula, Chunozero Lake, August 2012	NG	67.6367	32.6330	32/32	LMBI (not catalogized)
8	<i>A. balthica</i>	Russia, Kola Peninsula, Pirenga Lake, August 2012	NG	67.6276	32.1206	32/32	LMBI (not catalogized)
9	<i>A. balthica</i>	Iceland, a brook near Hveravellir, July 2015	NG	64.8675	−19.5456	32/32	LMBI (not catalogized)
10	<i>Ampullaceana lagotis</i>	Russia, Nenets Autonomous Region, Pymvashor hot springs, July – August 2009; December 2009; August – September 2010; December 2011	GT	67.1893	60.8617	336/36	RMBH (not catalogized)
11	<i>A. lagotis</i>	Kazakhstan, East Kazakhstan Region, a thermal pool on the shore of Lake Rakhmanovskoye, July 2018	GT	49.5338	86.5165	33/33	LMBI, 15-3765
12	<i>A. lagotis</i>	Kazakhstan, East Kazakhstan Region, a warm brook on the shore of Lake Rakhmanovskoye, July 2018	GT	49.5309	86.5157	22/22	LMBI, 15-3721
13	<i>A. lagotis</i>	Tajikistan, a wetland in vicinity of Zumagd village, July 2016	NG	36.6853	71.8318	19/19	LMBI, 15-3303
14	<i>A. lagotis</i>	Kazakhstan, Kustanay Region, Lake Maibalyk, July 2016	NG	53.1138	70.1808	22/22	LMBI, 15-895
15	<i>A. lagotis</i>	Russia, Nenets Autonomous Region, Vashutkiny Lakes, July 2009	NG	68.0201	61.5391	26/26	RMBH (not catalogized)
16	<i>Kamtschaticana kamtschatica</i>	Russia, Kamchatka, Teremkovaya hot area, July 2014	GT	54.4341	160.1380	30/30	LMBI, 15-3205
17	<i>K. kamtschatica</i>	Russia, Kamchatka, Nalychevskiye hot springs, July 2014	GT	53.5055	158.7633	24/24	LMBI, 15-2970
18	<i>K. kamtschatica</i>	Russia, Kamchatka, Storozhevskiye hot springs, August 1988	GT	55.1880	160.6580	29/29	LMBI, 15-3222
19	<i>K. kamtschatica</i>	Russia, Kamchatka, Troinoye Lake, July 2014	NG	54.4313	160.1297	19/19	LMBI, 15-3215
20	<i>K. kamtschatica</i>	Russia, Kamchatka, Krasikovskoye Lake, August 2019	NG	56.2575	162.0429	23/23	RMBH, MLym-894
21	<i>K. kamtschatica</i>	Russia, Chukchi Peninsula, Utesinskoye Lake, August 2019	NG	65.2132	173.6357	35/35	RMBH, MLym-876
22	<i>K. kamtschatica</i>	Russia, Magadan Region, a lake near Magadan City, September 2019	NG	59.5726	151.2531	9/9	LMBI, 15-3779
23	<i>Ladislavella catascopium</i>	Russia, Kamchatka, Tumrok hot springs (paratypes of <i>Lymnaea tumrokensis</i> Kruglov et Starobogatov, 1985) **, 1963	GT	55.2049	160.3991	38/38	ZIN, No. 2
24	<i>L. catascopium</i>	Canada, British Columbia, Ainsworth hot springs, July 2017	GT	49.7356	−116.9105	30/30	RMBH, MLym-815
25	<i>L. catascopium</i>	Russia, Kamchatka, Lake Azabachye, August 2019	NG	56.1140	161.8204	30/30	RMBH, MLym-896
26	<i>L. catascopium</i>	Canada, Yukon Territory, unnamed lake, July 2017	NG	63.0196	−136.4683	22/22	RMBH, MLym-660

27	<i>Radix alticola</i>	Tajikistan, hot spring in Djelandy village, July 2016	GT	37.5773	72.5764	60/34	LMBI, 15-3298, 15-3299
28	<i>R. alticola</i>	Tajikistan, hot spring near Djavshangoz village, July 2016	GT	37.3588	72.4168	34/34	LMBI, 15-3300
29	<i>R. alticola</i>	Tajikistan, a warm brook inflowing into Shakh dara River (middle course), July 2016	NG	37.3588	72.4168	44/32	LMBI, 15-3349
30	<i>R. alticola</i>	Tajikistan, a warm brook inflowing into Shakh dara River (mouth), July 2016	NG	37.3588	72.4168	22/22	LMBI, 15-3326, 15-3569
31	<i>Radix auricularia</i>	Russia, Republic of Buryatia, Khakusy hot springs (paratypes of <i>Lymnaea khakusyensis</i> Kruglov et Starobogatov, 1989) ***, September 1976	GT	55.3595	109.8274	8/8	ZIN, Nos 2, 3
32	<i>R. auricularia</i>	Russia, Republic of Buryatia, Khakusy hot springs (paratypes of <i>Lymnaea thermobaicalica</i> Kruglov et Starobogatov, 1989) ***, September 1976	GT	55.3595	109.8274	42/42	ZIN, Nos 2, 4
33	<i>R. auricularia</i>	Russia, Kamchatka, Khodutka hot springs (paratypes of <i>Lymnaea hodutkae</i> Kruglov et Starobogatov, 1989) ***, September 1979	GT	52.1073	157.6573	30/30	ZIN, Nos 2, 3
34	<i>R. auricularia</i>	Russia, Kamchatka, Khodutka hot springs (paratypes of <i>Lymnaea thermokamchatica</i> Kruglov et Starobogatov, 1989) ***, September 1979	GT	52.1073	157.6573	43/43	ZIN, Nos 2, 3
35	<i>R. auricularia</i>	Mongolia, Khar-Nuur Lake, July 2012	NG	48.1333	93.2500	32/32	LMBI, 15-2481
36	<i>R. auricularia</i>	Russia, Irkutsk Region, Kirenga River in Kirensk Town, July 2003	NG	57.7757	108.1108	21/21	LMBI, 15-1335
37	<i>R. auricularia</i>	Russia, Omsk Region, Krivoye Lake, August 2002	NG	56.7720	74.6133	35/35	LMBI, 15-412

* N—the total volume of the sample; n—number of specimens randomly chosen to be included to morphological analyses; ** See Vinarski et al. [16] on the synonymy of this species; *** See Bolotov et al. [15] and Aksenova et al. [17] on the synonymy of this species.

For a comparison, samples of lymnaeid snails collected from the non-thermal (zonal) localities have been examined (see Table 2). In the context of this paper, the term ‘zonal’ is applied to natural waterbodies whose temperature follows annual (seasonal) changes in air temperature. We did not use samples taken from waterbodies with artificially altered temperature regime (such as cooling ponds of thermal power stations and similar habitats). In total, 1646 individuals of lymnaeid snails collected from 37 localities have been included into analyses.

2.2. Morphological Study and Statistical Analysis

Only full-grown, adult specimens were used in morphological analyses. The adult status of individuals was determined either by the absolute size of the body (shell) or, when possible, by dissection.

The absolute shell height (SH), measured with accuracy to the nearest 0.1 mm, was used as a proxy for the snail body size. The measurements have been made by using the ocular-micrometer of a stereoscopic microscope. The Mann–Whitney test was used to assess size differences between thermal and non-thermal populations of the same species. As a measure of the phenotypic distance between a pair of shell samples, the square of the Mahalanobis distance (D^2) was chosen. The values of the first six relative warps (RWs 1–6), yielded during the geometric morphometric procedure (see below), were used as the primary data for calculations of D^2 . The values of D^2 were subsequently subjected to cluster analysis (Euclidean distances; Ward’s method of clustering) in order to visualize the phenotypic differences between samples of the same species (or a group of closely related samples). All these analyses were carried out in STATISTICA 12 for Windows (StatSoft Inc., Tulsa, Oklahoma, USA).

We used both parametric and non-parametric (such as Spearman's rank correlation coefficient and Mann–Whitney test) statistical algorithms in the course of this research. The results were essentially the same irrespective of which approach (parametric or non-parametric) was applied. In the text below, only the results of non-parametric tests are provided. The rationale behind this decision is that we used both freshly collected and, in a few instances, 'historical' museum samples in our study. This could potentially create some heterogeneity in the primary material. That is why we decided to use non-parametric algorithms as being less sensitive to the heterogeneity of the samples.

The geometric morphometric approach allowing one to decompose shell form into shape and size was applied to study shell shape alterations between zonal and thermal habitats. Shell photographs were taken with a Canon EOS 1100D digital camera equipped by Canon MP-E 65 mm macro lens. The photos were made uniformly, in the same position and by the same person.

A configuration of 14 (or 16 in the case of *L. catascopium* shells) landmarks was used to characterize the shell shape (in frontal view). The difference in the numbers of landmarks (14 vs. 16) is explained by the different shell shape of *L. catascopium*, and the larger whorl number in the latter species.

The positions of landmarks (see Figure 2G,H) are described as follows. LM1–shell apex; LM2–5 (2–7 in *L. catascopium*) are placed on the opposite sutural points of the penultimate whorl(s). LM6 (LM8 in *L. catascopium*) is the most external point of the body whorl contour above the aperture. LM7 (LM9 in *L. catascopium*) lies on the border of the parietal and palatal margins of the aperture; LM8 (LM10 in *L. catascopium*) corresponds to the uppermost point of the aperture. LM9 (LM11 in *L. catascopium*) is the most external point of the body whorl contour on its left side. LM10 (LM12 in *L. catascopium*) is the most external position on the external part of the palatal margin of the aperture. LM11 (LM13 in *L. catascopium*) is placed on the border of the parietal and columellar margins of the aperture. LM12 (LM14 in *L. catascopium*) is the most external point of the columellar lip. LM13 (LM15 in *L. catascopium*) is the lowest point of the body whorl at its confluence with the aperture margin. LM14 (LM16 in *L. catascopium*) corresponds to the lowermost point of the aperture at its basal margin.

Landmarks were set on digital shell images using tpsDIG v. 2.26 software [103]. Analysis of the landmark data was performed using PAlaeontological STatistics (PAST) v. 2.0 [104] and tpsRelw v. 1.67 software [105].

2D landmark configurations were superimposed by carrying out generalized Procrustes analysis, and we used the projected Procrustes coordinates as raw data in subsequent statistical analyses. Shape variation was studied using principal components of aligned landmark coordinates (relative warp analysis) implemented in tpsRelw. Thin-plate splines deformation grids were produced to visualize morphological variation along axes of the reconstructed morphospace. We avoided the use of centroid size (CS) as a proxy for body size, since the values of CS appeared to be tightly correlated with SH (Spearman's $r_s = 0.75$; $p < 0.0001$).

The examination of the soft body anatomy of studied lymnaeids was limited to their reproductive system only, since these organs were long recognized as the main source of taxonomic signal, allowing simple and reliable species delineation in the Lymnaeidae [13,106]. All nominal 'thermal' species of this family were described on the basis of both conchology and reproductive anatomy [107,108]. The dissections were made following Kruglov [106]. We were looking for qualitative and quantitative differences in the structure of the reproductive anatomy between conspecific samples collected from thermal and zonal habitats.

2.3. DNA Analysis, Sequence Alignment and Phylogeography

DNA extraction, PCR, sequencing, and sequence alignment were performed as described in our previous works [7,19]. In particular, total genomic DNA was extracted from ethanol-preserved samples using the NucleoSpin® Tissue Kit (Macherey-Nagel GmbH &

Co. KG, Düren, Germany), following the manufacturer protocol. A barcode fragment of the cytochrome c oxidase subunit I (COI) gene was amplified using the standard Folmer's primers pair LCO1490 and HCO2198. The PCR products were bidirectionally sequenced on ABI PRISM 3730 (Applied Biosystems, Thermo Fisher Scientific Inc., Waltham, Massachusetts, USA). The sequences were aligned through the MUSCLE algorithm of MEGA7 [109]. We generated new DNA sequences from 37 pond snail individuals (Supplementary Table S1). The phylogeographic analyses were performed on the basis of a median-joining network approach using Network v. 5.0.0.1 software with default settings [110]. Additionally, 927 reference COI sequences from specimens of different localities of Europe, Siberia, Tibetan Plateau, Central and South Asia, Russian Far East and North America were used (Supplementary Table S1). The sequence lengths leaving the datasets were 603 bp (*Ampullaceana balthica*), 657 bp (*A. lagotis*), 657 bp (*Kamtschaticana kamtschatica*), 633 bp (*Ladislavella catascopium*), 627 bp (*Radix alticola*), 572 bp (*R. auricularia*) long due to the removal of missing sites and cuts of different lengths of available sequences.

3. Results

3.1. Variation in Shell Size and Proportions

The shell measurements of all six lymnaeid species we studied followed the uniform trend—shell height of individuals taken from thermal populations is significantly lower than those of their conspecifics from zonal habitats. Typically, these 'hot snails' are 1.25–2.00 times smaller as compared to their counterparts from the non-thermal waterbodies (Figures 3 and 4; Table 3). This trend is expressed most drastically in *R. auricularia*, where the mean size in zonal populations appeared to be 2.37 times higher than that in thermal samples (see Table 3; Figure 3F). It should be acknowledged, however, that the tendency described above in some cases is not very pronounced; some exceptions from this general trend as well as their probable causes are discussed below.

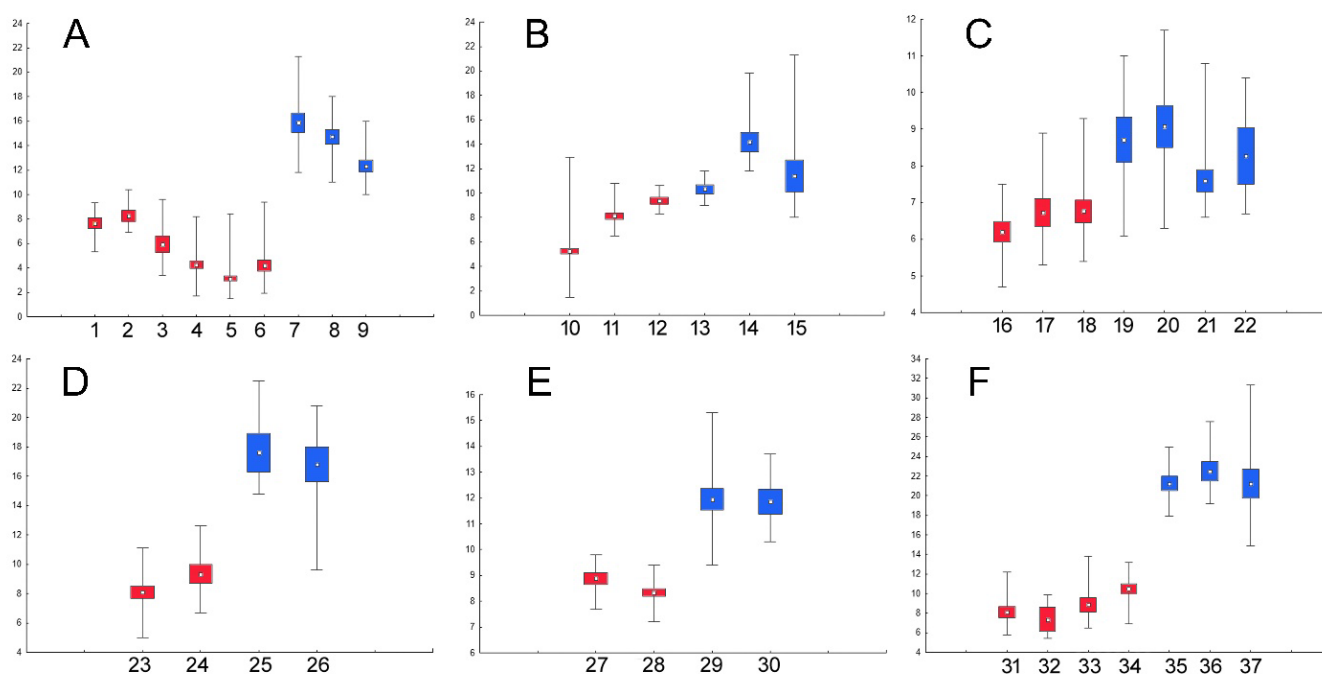


Figure 3. Shell size (in mm) in thermal (red colour) and non-thermal (blue color) populations of six lymnaeid species. (A). *Ampullaceana balthica*. (B). *A. lagotis*. (C). *Kamtschaticana kamtschatica*. (D). *Ladislavella catascopium*. (E). *Radix alticola*. (F). *R. auricularia*. Numbers correspond to numbers of populations in Table 2. Box and whisker graphs show the minimum and maximum values (whisker extremes), the confidence interval (boxes), and the mean value (small squares within boxes).

Table 3. Size differences between conspecific lymnaeid snails from thermal (pooled) and non-thermal (pooled) populations. All differences (based on the Mann–Whitney test) are statistically significant.

Species	Mean SH, mm ($\pm \sigma$)		Statistical Significance of the Difference (Z Adjusted; <i>p</i> -Value)
	Thermal Populations	Non-Thermal Populations	
<i>Ampullaceana balthica</i> , all samples	4.0 \pm 1.6	14.3 \pm 2.3	11.80; 0.00
<i>A. balthica</i> , Iceland populations only	4.0 \pm 1.6	8.9 \pm 3.2	11.28; 0.00
<i>A. lagotis</i>	7.7 \pm 1.6	11.0 \pm 2.6	−7.84; 0.00
<i>Kamtschaticana kamtschatica</i>	6.6 \pm 0.9	8.3 \pm 1.2	−9.54; 0.00
<i>Ladislavella catascopium</i>	9.7 \pm 1.8	17.1 \pm 2.5	8.29; 0.00
<i>Radix alticola</i>	8.5 \pm 0.6	11.9 \pm 1.3	−10.51; 0.00
<i>R. auricularia</i>	9.1 \pm 2.0	21.6 \pm 3.2	−12.5; 0.00

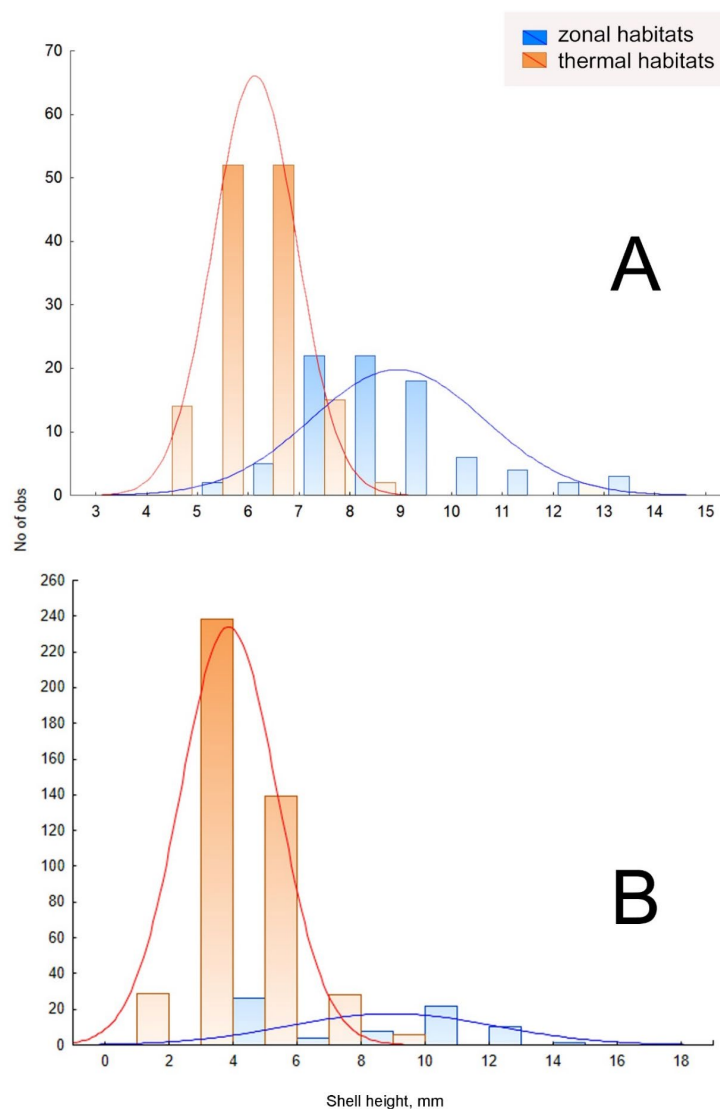


Figure 4. Distribution of shell heights in thermal and zonal populations of *Kamtschaticana kamtschatica* (A) and *Ampullaceana balthica* (B).

A morphometric study of *A. balthica* shells collected in Iceland in a temperature gradient +15 ... +40 °C has shown that there may be a negative correlation between water temperature and shell height, when the highest mean SH was found in the coldest

sampling site (See Figure S1 in Supplementary Materials). However, this relationship is not statistically significant (Spearman's correlation coefficient $r_s = -0.27$; $p > 0.05$).

The geometric morphometric analysis has demonstrated that the six lymnaeid species studied can be divided into two groups. The first one includes *Ampullaceana balthica* and *A. lagotis*, and the second—the rest of the species. In the former group, shell proportions in zonal and thermal habitats do not differ significantly, and the PCA is unable to differentiate between hot- and cold-water snails on the basis of their shell habitus. All studied individuals fall within a single 'cloud' of points, or a continuum, in the first two RW axes, which makes it impossible to delineate a certain 'thermal' ecotype differing from the zonal conspecifics by its shell shape (Figure 5). The diminutive size remains the only conchological trait distinguishing between thermal and non-thermal populations in *A. balthica* and *A. lagotis*.

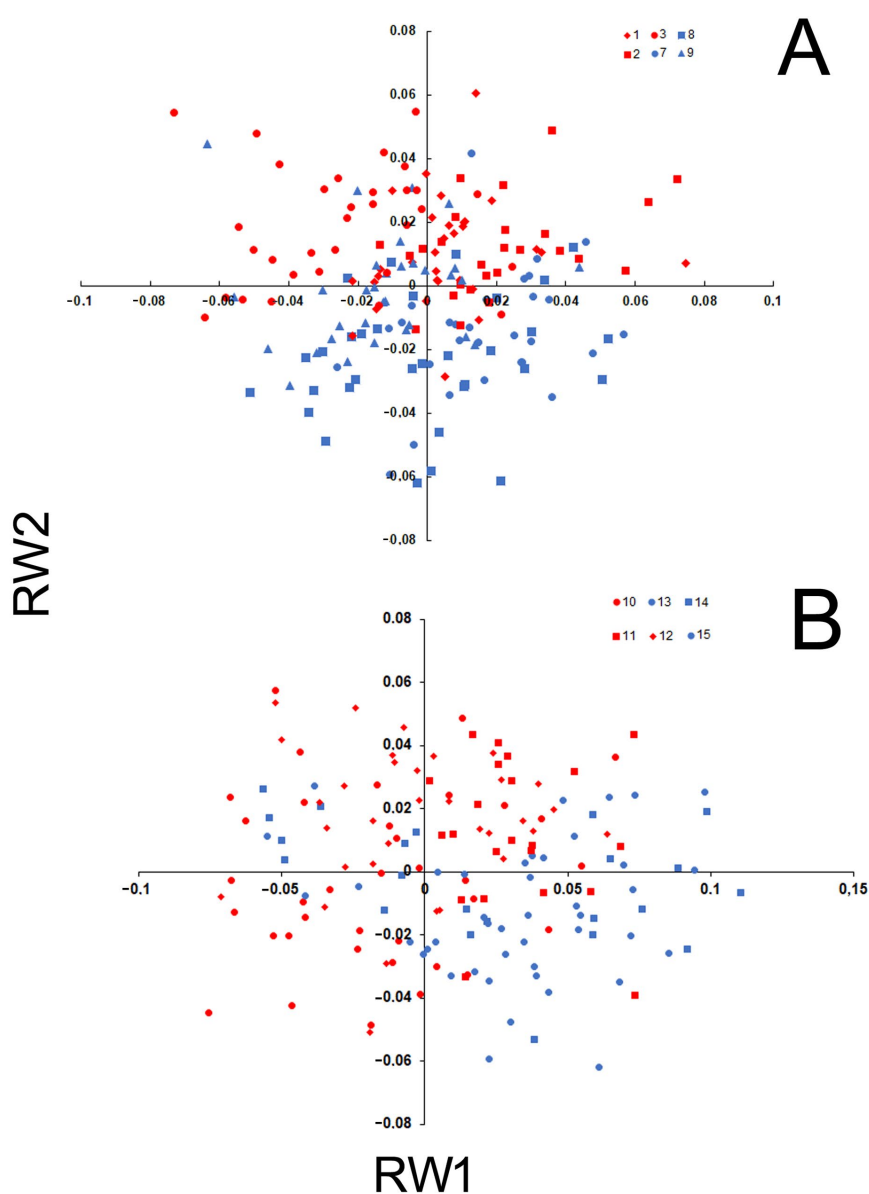


Figure 5. Position of individuals of *Ampullaceana balthica* (A) and *A. lagotis* (B) from thermal (red symbols) and zonal (blue symbols) populations along the two first relative warps axes. Numbers correspond to number of populations in Table 2.

In the four rest species, the individuals also form continuous ‘clouds’ of points; however, some differentiation between thermal and non-thermal populations can be observed (Figure 6). In *Kamtschaticana kamtschatica* and *Ladislavella catascopium*, the hot-water snails tend to occupy the right half of the graph, while in two *Radix* species, thermal individuals are grouped in the left half. The only exception to this tendency was found in a sample of *K. kamtschatica* from Troinoye Lake (locality No. 19 of Table 2). It is a cold lake, but the snails inhabiting it exhibit the ‘thermal’ shell morphology (their size is, however, typical for zonal habitats; see Figure 2C). This discrepancy can be explained by the very young age of this waterbody. The lake was formed in 2007, as a result of a strong mudflow that flooded a river valley, where hot springs were located (Kamchatka, the Valley of Geysers). The population of *K. kamtschatica* from this mudslide lake has, evidently, originated from hot spring populations, and, probably, the snails still retain their original ‘thermal’ morphology (but not miniature size!)

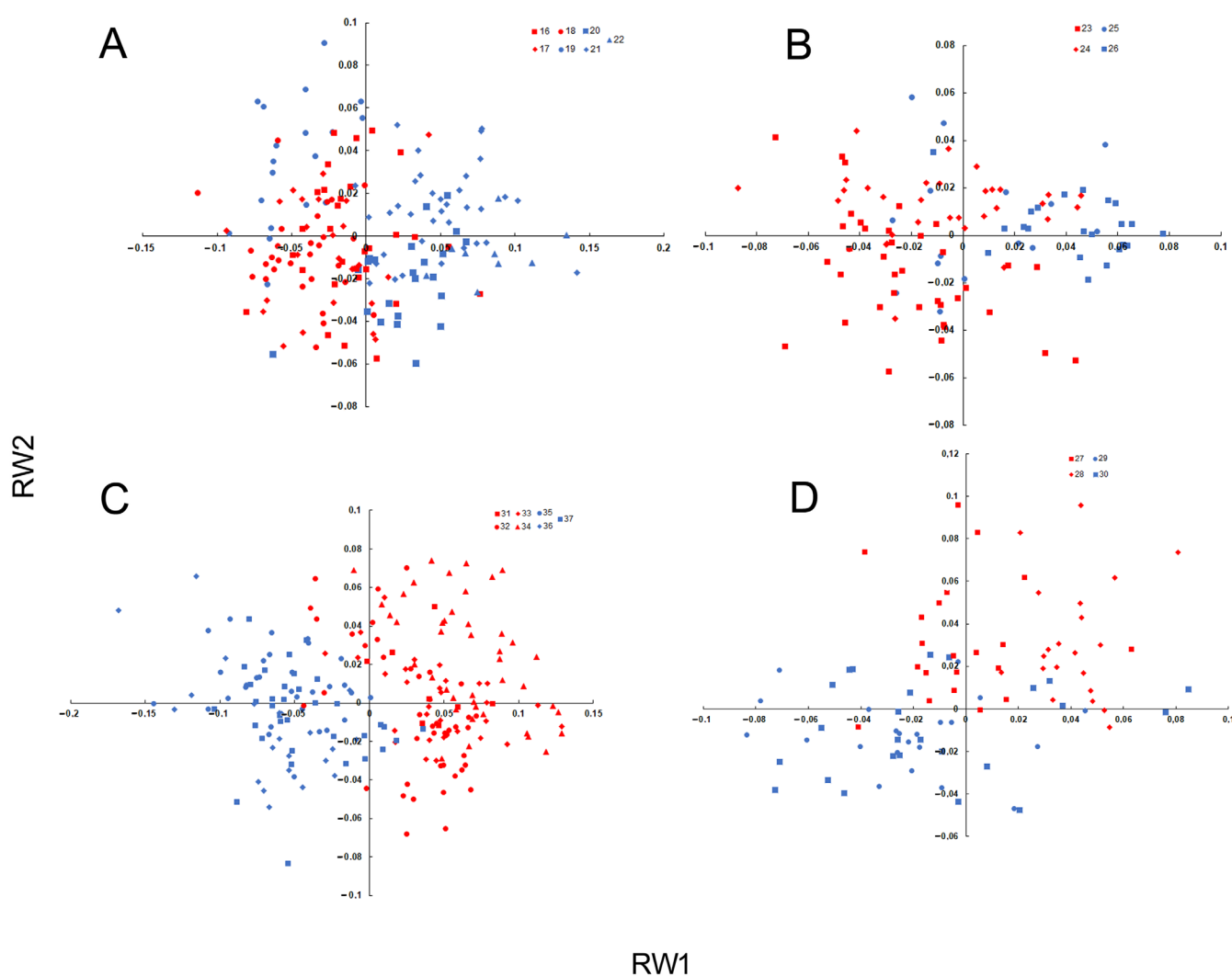


Figure 6. Positions of individuals of *Kamtschaticana kamtschatica* (A), *Ladislavella catascopium* (B), *Radix auricularia* (C), and *R. alticola* (D) from thermal (red symbols) and zonal (blue symbols) populations along the two first relative warps axes. Numbers correspond to number of populations in Table 2.

In the two species of *Radix* studied, the snails living under thermal conditions have more slender and high-spired shells as compared with shells of their conspecifics from zonal habitats (Figure 7). The shell aperture in thermal populations becomes narrower; its

shape changes from auriculate to ovoid. Remarkably, *L. catascopium* demonstrates an opposite pattern—in this species, snails from zonal habitats have more slender and high-spired shells (Figure 8). A similar shift in morphology has been found in *K. kamtschatica* (not illustrated here).

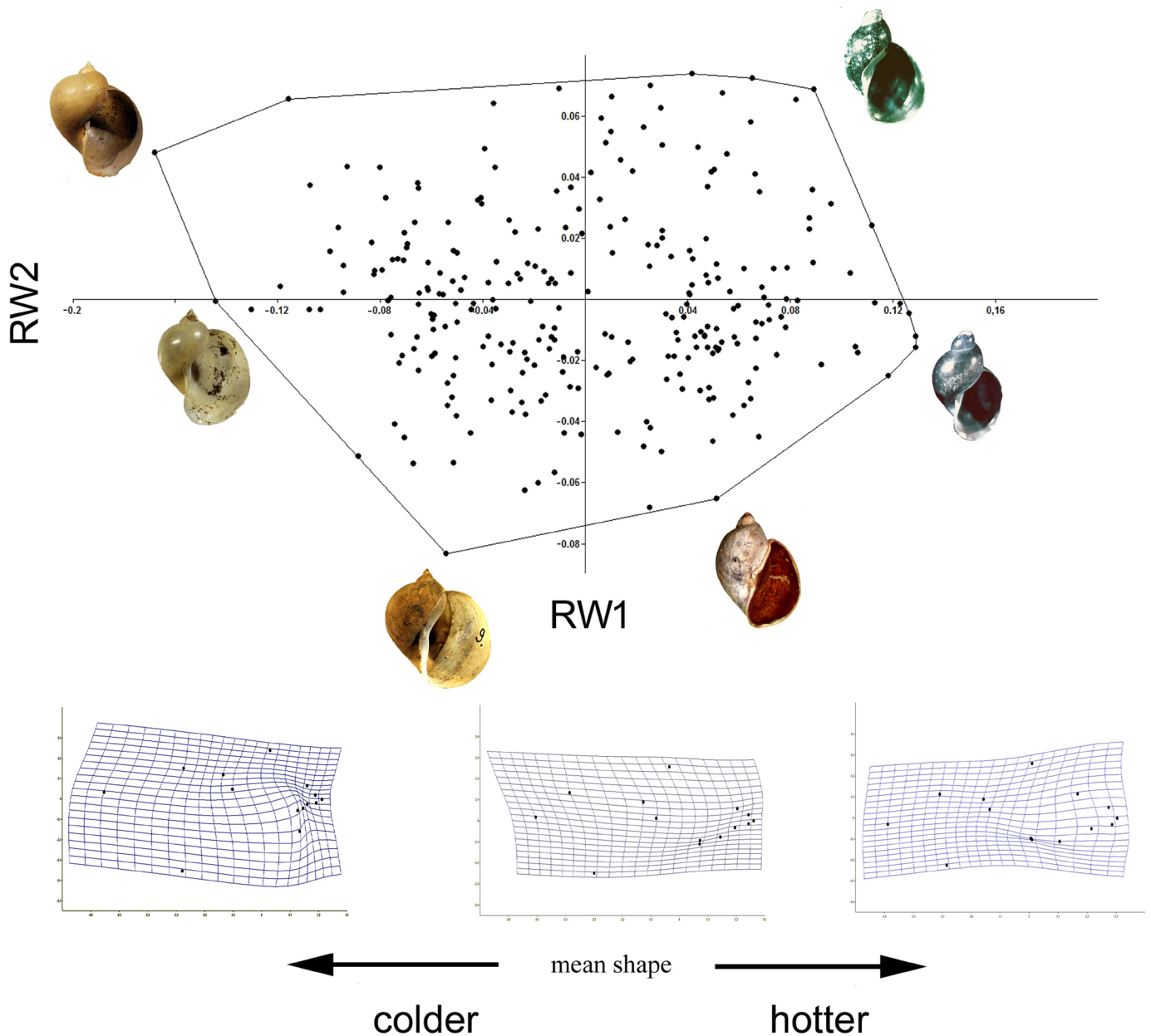


Figure 7. Relative warp analysis of shape of *Radix* shells, axes 1 and 2, and the thin-plate spline deformation grids illustrating morphological variation along axes of the reconstructed morphospace. Shell images (sizes not in scale) illustrate specimens located at the extreme points of the convex polygon. Specimens from the left part of the graph taken from zonal habitats; shells situated right of the *oy*-axis collected from geothermal habitats.

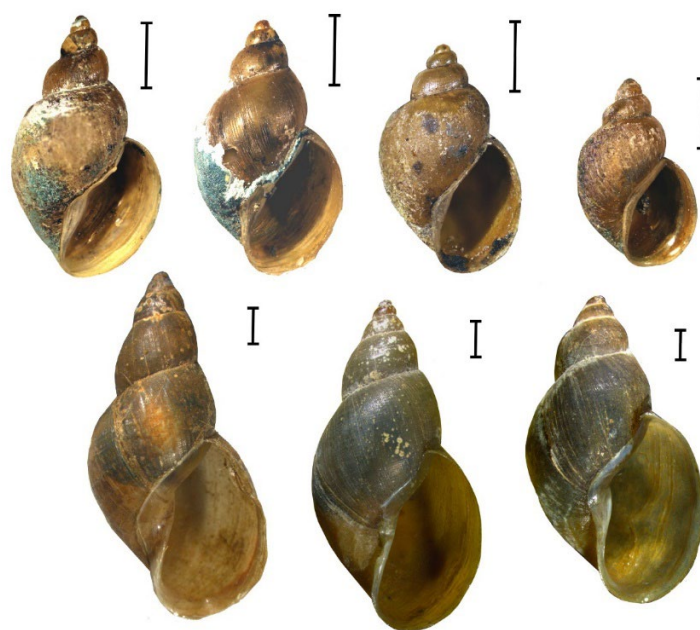


Figure 8. *Ladislavella catascopium* from Kamchatka. Upper row—Tumrok hot springs. Lower row—Lake Azabachye (zonal habitat). Scale bars 1 mm. Photos: Olga V. Aksenova, Maxim V. Vinarski.

In all cases, the values of Mahalanobis distance, separating two samples of the same lymnaeid species, were smaller between populations taken from localities with the same thermal regime (i.e., thermal vs. thermal and non-thermal vs. non-thermal), while the samples from habitats with different thermal regime were separated by significantly greater phenotypic distances (see Tables S2–S4 in Supplementary Materials). Within the genus *Radix*, thermal populations of *R. auricularia* were phenotypically more similar to thermal populations of *R. alticola* than to zonal populations of the same species (see Table S5 in Supplementary Materials). The cluster analyses based on D^2 values in virtually all cases demonstrated that the thermal and non-thermal populations form two separate clusters on a dendrogram (see Figures S2–S5 in Supplementary Materials). The first exception was *K. kamtschaticana* samples from lakes Utesinskoye and Troinoye (see above). Specimens taken from these cold lakes fell into the ‘thermal’ cluster on the dendrogram (see Figure S4 in Supplementary Materials). In *A. balthica*, the division of the studied samples reflect their geographic origin: all populations of this species from Iceland formed a single cluster irrespective of the thermal regime of waterbodies inhabited by them (see Figure S2 in Supplementary Materials). Unfortunately, we had only a limited number of *A. balthica* samples from other regions to check if the ‘geography’ is a more influential factor than the ‘thermal regime’ in determining shape differences between spatially separated populations of this snail. The lack of *A. balthica* samples may seem surprising in the case of such a widespread species. However, most of the museum samples identified as ‘*A. balthica*’ (or, much more often, as *Lymnaea ovata*—a long-used name of this species based on its junior synonym) could not be included into our analyses. The point is that the shell of *A. balthica*, as well as of *A. lagotis*, its congeneric, is extremely variable, and the shell alone is utterly misleading as a tool for identification. Therefore, we cannot be sure that numerous museum samples identified as ‘*A. balthica*’ really belong to this species.

3.2. Anatomical Variation

After dissection and anatomical examination of several tens of specimens of *K. kamtschaticana* and *R. auricularia* from habitats of different type, we are unable to report here any substantial differences between conspecific lymnaeid snails from thermal and non-thermal habitats. The ‘thermal’ snails exhibit a completely developed reproductive

system, albeit of smaller size as compared with their counterparts from zonal waterbodies (see Figure S6 in Supplementary Materials). All differences are, thus, of an exclusively quantitative nature.

3.3. Intraspecific Genetic Diversity and Phylogeography

In all six lymnaeid species studied genetically, specimens collected from thermal habitats formed single network with those living under zonal temperature conditions (Figures 9–11). In all species, except *A. lagotis*, some haplotypes were found to occur in both habitat types, i.e., in zonal and thermal waterbodies (see, for example, haplotypes 2 and 3 of *A. balthica* in Iceland; Figure 9). In most cases, such ‘eurythermic’ haplotypes were restricted to a single geographic region, though one can find exceptions to this rule. For example, haplotype 1 of *A. balthica* (see Figure 9) was present in populations located in the northern part of European Russia, Spain, Germany, and France as well as in thermal springs of Iceland. The absence of the ‘eurythermic’ haplotypes in *A. lagotis* may be due to lower number of sequences and to insufficient geographical coverage.

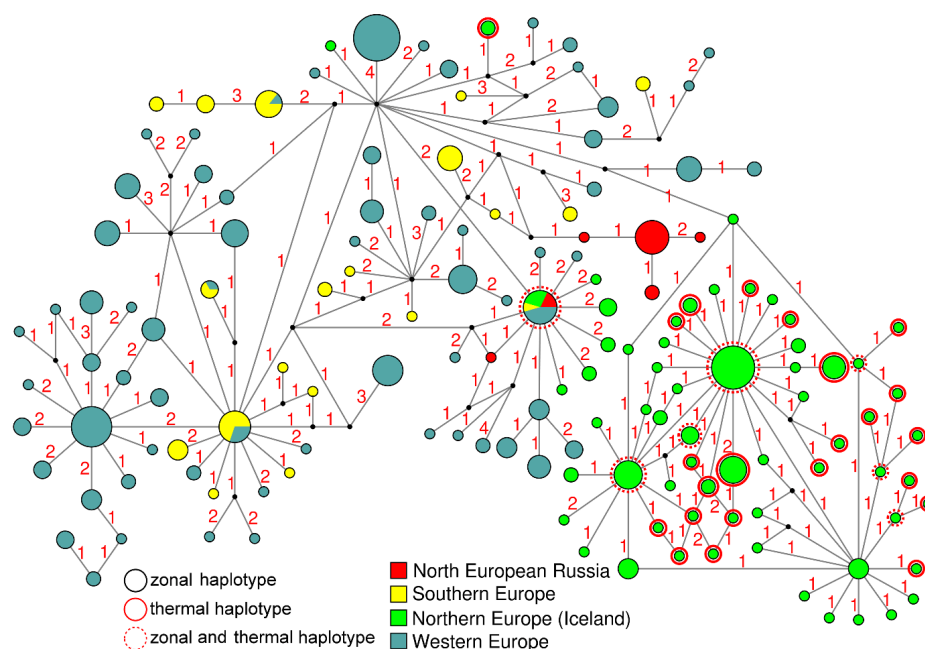


Figure 9. Median joining network of the COI sequences of *Ampullaceana balthica*. Circle symbols represent different haplotypes, with the size reflecting their frequency (smallest = 1). Numbers near branches are numbers of nucleotide substitutions per site. The dataset contains 383 COI sequences (length = 603 bp).

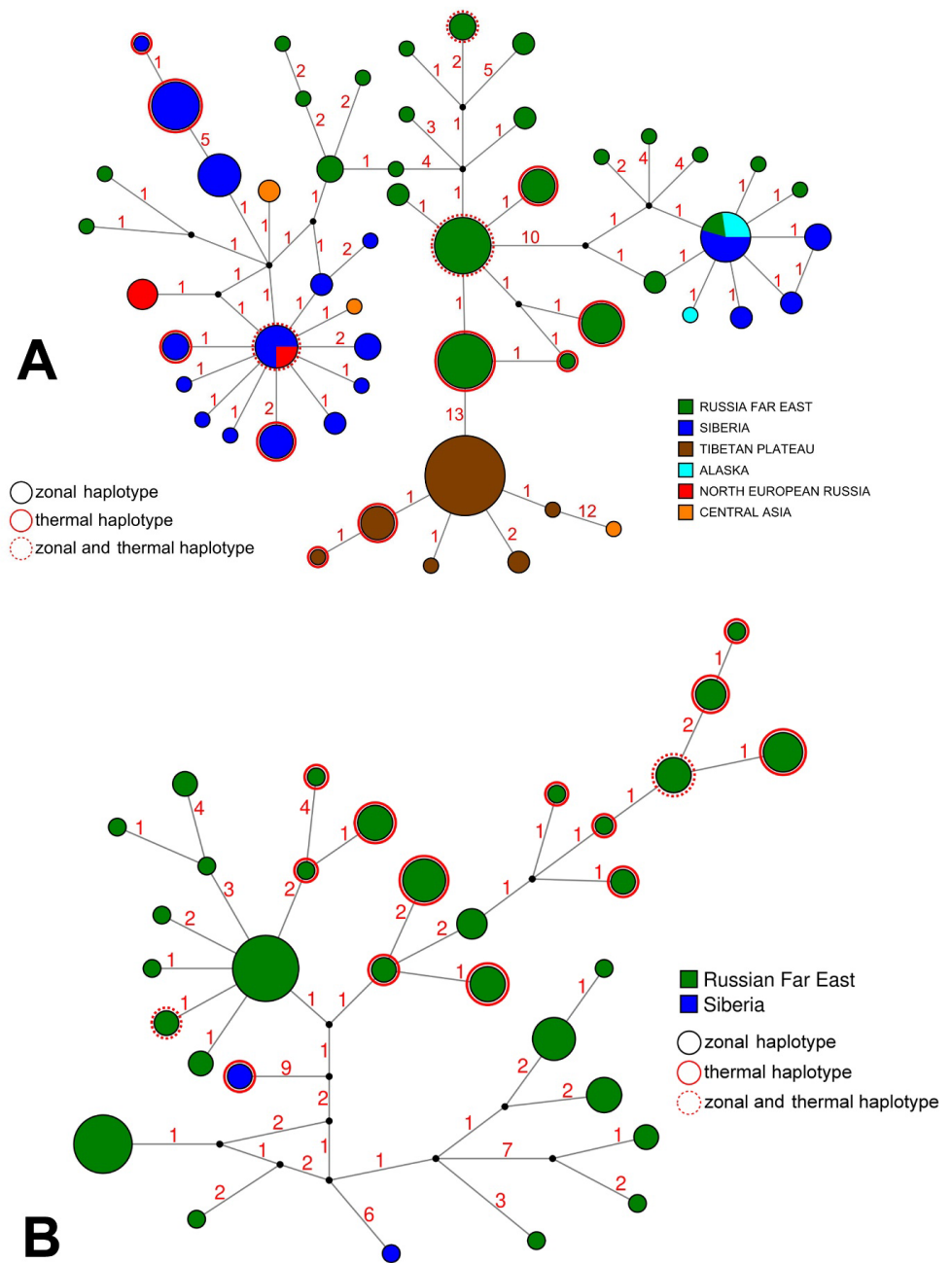


Figure 10. Median joining network of the COI sequences of *Radix auricularia* (A) and *Kamtschatica kamtschatica* (B). Circle symbols represent different haplotypes, with the size reflecting their frequency (smallest = 1). Numbers near branches are numbers of nucleotide substitutions per site. The datasets contained 179 COI sequences of *R. auricularia* (length = 572 bp) and 93 COI sequences of *K. kamtschatica* (length = 657 bp).

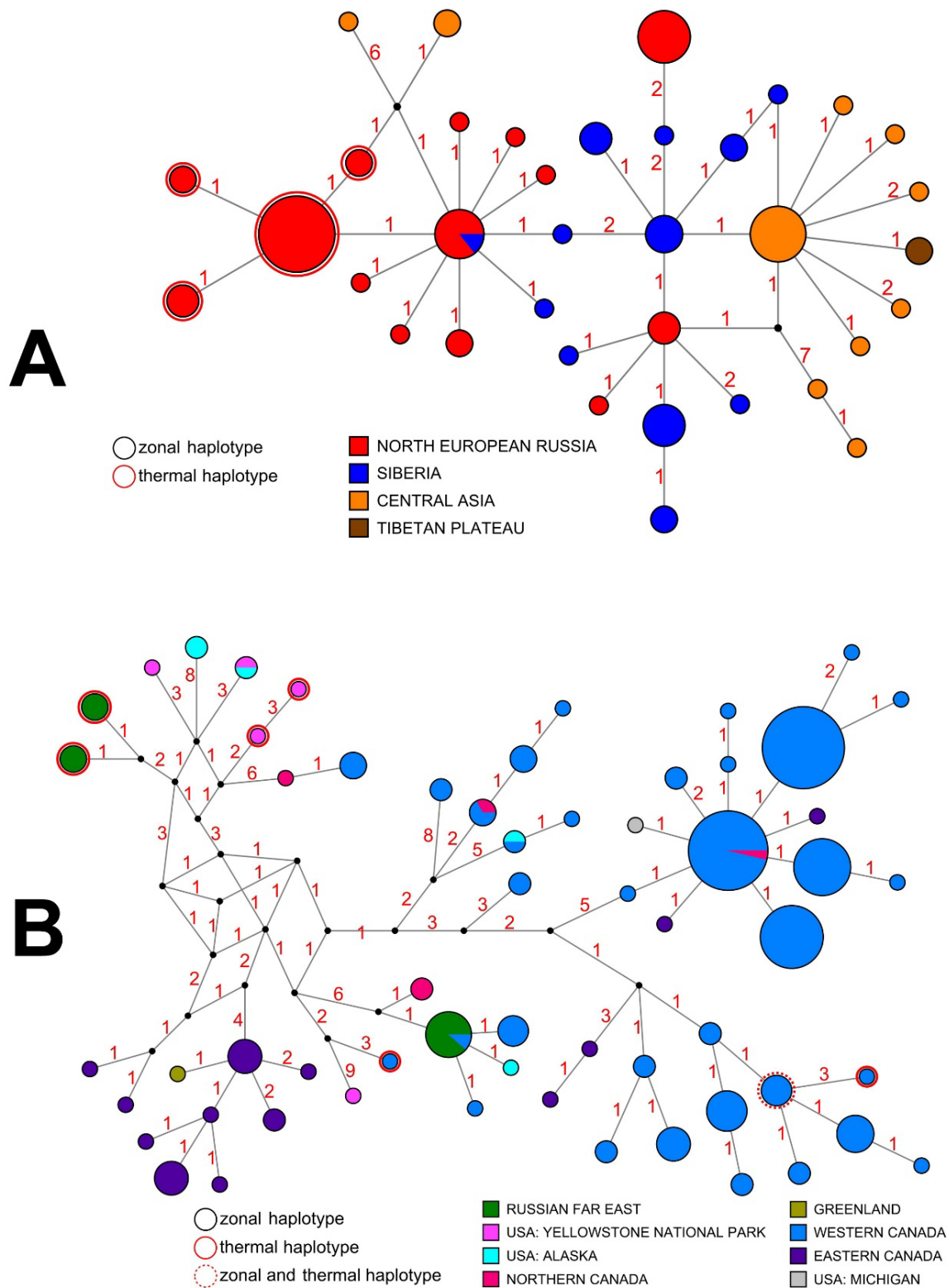


Figure 11. Median joining network of the COI sequences of *Ampullaceana lagotis* (A) and *Ladislavella catascopium* (B). Circle symbols represent different haplotypes, with the size reflecting their frequency (smallest = 1). Numbers near branches are numbers of nucleotide substitutions per site. The datasets contained 93 COI sequences of *A. lagotis* (length = 657 bp) and 203 COI sequences of *L. catascopium* (length = 633 bp).

Exclusively ‘thermal’ haplotypes (like No. 4 in Figure 9), not known beyond the geothermal sites, are usually found only in a single locality, and no signs of frequent ‘travels’ of snails from one thermal habitat to another have been revealed. In the vast majority of cases, these unique haplotypes were separated from their ancestors by only a few (1–3) mutational steps. Remarkably, none of these ‘thermal’ haplotypes was found to form the center of a star-like network, which would correspond to expansion of a geographically widespread haplotype. Typically, the ‘hot’ haplotypes are situated at the terminal positions in the networks.

4. Discussion

4.1. Origin and Evolution of Thermal Lymnaeid Populations

Most species of freshwater Mollusca of the temperate zone of the Northern Hemisphere are adapted to live in zonal waterbodies, whose thermal regime follows annual changes in air temperature. In such habitats, a summer temperature peak is usually observed, which is invariably followed by a significant winter cooling. The mean annual temperature in such environments is rather low; that, however, does not prevent mollusks from occurring even in localities situated far to the north of the Polar circle [11,111–114]. Another manifestation of temperature tolerance in freshwater snails are species capable of withstanding a consistently high (from warm to hot) temperature regime existing in the geothermal springs and other similar waterbodies with naturally heated water. Water temperature may reach 40 °C in such habitats (see Figure S1 in Supplementary Materials).

Thermal extremes induce numerous damages in organisms, both at the molecular and biochemical levels [115], that makes thermal springs and similar habitats rather unsuitable for most species of freshwater animals. The damaging effects of extreme temperatures on physiology and biochemistry of animals are summarized in Hochachka & Somero [116] and Williams et al. [115]. However, it seems that, among freshwater Gastropoda, the ability to withstand the thermal stress and to form sustainable populations in the geothermal waterbodies is phylogenetically widespread and is not unique to one or a few clades (see Table 1). A successful thermal acclimation, albeit very costly at its first stages, allows snails to form a monospecific community in a thermal habitat and, thereby, avoid interspecific competition and gain unlimited access to abundant consumable resources (such as algal and bacterial mats). The press of predators and parasites should, probably, also be greatly relaxed in such waterbodies, which increases the benefits of the completed adaptation to geothermal habitats. Another ecological and physiological benefit of being adapted to live under extremely hot temperatures is that these snails do not need to cope with thermal fluctuations characteristic for the zonal waterbodies and thus are not forced to develop special adaptations for overwintering, periodical food shortage, and so on [6,88]. From the point of view of the balance of ecological gains and losses, this seems to be a promising strategy. Within the three largest families of aquatic pulmonate snails (Lymnaeidae, Physidae, and Planorbidae), numerous examples of species capable to colonize hot springs and like habitats have been discovered (see Table 1). Wethington and Guralnick [5] discussed the taxonomic status and genetic divergence of the hot-water species of physid snails native to North America. In this study, we focused on another pulmonate family, Lymnaeidae.

The phylogeographic data obtained in the course of our study show that in all the studied lymnaeid species, colonization of geothermal waterbodies occurred repeatedly, and the snail population in almost every particular hot spring or lake arose independently and, most probably, from ancestors living in zonal habitats. No single source region for colonization of geothermal objects has been identified in any species. It is highly likely, for example, that the thermal populations of *A. balthica* in Iceland formed as a result of at least two independent introductions from the mainland Europe (see Bolotov et al. [7] for more information on the Icelandic *A. balthica*).

The terminal position of the vast majority of exclusively ‘hot’ haplotypes indicates that they are ‘imprisoned’ in their specific waterbodies with zero or very low possibility to go beyond and to colonize other waterbodies, either thermal or zonal. Possibly, it may be explained by the uttermost rarity of successful dispersal of snails and subsequent taking root outside their place of origin. After all, the short genetic distances between these haplotypes and the nearest ones (1–3 nucleotide substitutions in most instances) mean that they are evolutionary young; that provided them too little time to leave their thermal habitat and to form sustainable populations elsewhere.

There is, however, an alternative explanation. This is based on the assumption that the adaptation of snails to live in thermal habitats is irreversible, and, thus, makes them unable to return to their native zonal environments even when they retain the potential to physically escape from their ‘thermal prison’ (for example, using waterfowl as dispersal agents). Successful thermal acclimation and long existence under stable temperature regime leads to the reduction of thermal tolerance breadth. In this case, even small temperature anomalies may be stressful, which is often observed among animal species evolved in tropics [117–119]. Interestingly, some laboratory-reared populations of snails, whose founders were taken from thermal waterbodies, demonstrated inability to survive and reproduce under the ‘normal’ conditions [8,10,14,21].

If true, this explanation views the hot-water snails as victims of the so-called ‘phylogenetic immobilization’. This term was coined in the 1940s by the Russian evolutionary biologist Ivan Schmalhausen [120] and recently was discussed in modern theoretical context by Makhrov [121]. According to the latter author, phylogenetic immobilization is quite characteristic for animals inhabiting the ‘abnormal’ environments, including the geothermal waterbodies. A similar mechanism was recently invoked by Vinarski et al. [96] to explain the inability of *Tibetoradix* lymnaeids, evolved in the Tibetan Plateau, to leave their high-mountain cradle and to conquer the adjacent regions of Central Asia.

The ‘phylogenetic immobilization’ model does explain the uttermost rarity of ‘thermal’ haplotypes of lymnaeids in zonal habitats. The low intensity of the gene flow between the thermal populations of the same species may be better explained by the very low probability of successful dispersal of snails between spatially isolated waterbodies.

4.2. The Probable Causes of Miniaturization in the Thermal Lymnaeids

Apart from the lymnaeid snails, examples of thermal miniaturization can be found in other groups of animals (e.g., freshwater fish; see [122–124]). Some available case studies suggest that the decrease in body size may be a usual ‘response’ of animal populations adapting to extreme, or generally unfavourable, aquatic habitats [125–132]. The world’s smallest vertebrate, the dwarf minnow *Paedocypris progenetica* Kottelat, Britz, Tan & Witte, 2006 (family Cyprinidae), was described from extremely acidic waterbodies of Sumatra (Indonesia) [130]. However, we are still unaware how widespread this phenomenon is among aquatic molluscs adapted to inhabit geothermal waterbodies. The effect of shell diminution found in all six lymnaeid species we studied, indicates that, in this family, there can constitute a common tendency observed in many thermal populations belonging to different species. What is more remarkable, the tendency of lymnaeid snails to become dwarfed was observed not only in geothermal sites [133–135]; it means that the miniaturization is a part of the adaptive plasticity repertoire of these molluscs. Different external conditions seem to drive the diminution of the lymnaeid body size, and a plausible explanation of the thermal dwarfism must include at least one of the potential triggers.

In our view, all possible hypotheses can be divided into three main categories:

- (a) A direct (modifying) influence of external conditions;
- (b) An outcome of some selective forces acting during the thermal acclimation;
- (c) Miniaturization as an inadaptive by-product of other adaptations that, probably, occur at physiological or biochemical levels.

Below, one may find a short discussion of all the three groups of explanations as applied to the studied case.

The first mechanism, that once was a signature of (neo-)Lamarckism, today gains some support from modern epigenetics [136, 137]. The diminutive body size of hot-water snails may be epigenetically encoded. High temperature may induce ‘thermal phenotypic plasticity’ via various epigenetic mechanisms such as DNA methylation [137].

One of the probable pathways of environmentally induced miniaturization is the shortage of dissolved oxygen in warmer aquatic habitats. Such a factor has repeatedly been used for explanation of the so-called ‘temperature-size rule’ that states that the higher ambient temperature is, the smaller aquatic organisms become (see [138–141] and references therein). The probable relationship between body size and oxygen concentration in aquatic ectotherms has become a matter of recent discussion (see [142–144]; and references therein).

We do not think that the hypothesis of the direct inhibiting action of high temperature on shell size of freshwater snails is a plausible explanation in the studied case. First and foremost, such an effect assumes the uniform effect on all snails, not only on lymnaeids. The epigenetic model predicts that ‘environment-directed epigenetic variation... is expected to show the same pattern in different individuals with the same genotype when exposed to the same environment’ [137]. In fact, the available literary data show that the miniaturization is not a universal phenomenon among the hot-water snails. As early as in 1881, the Hungarian amateur naturalist Hazay [44] studied conchological variability of snails lived in hot springs of Budapest at temperatures +20...+26 °C. The decreased shell size was found in three species: *Bithynia tentaculata*, *Planorbis planorbis*, and *Radix lagotis*. Another species, *Peregriana peregra*, however, did not exhibit any decrease in size [44]. A more striking example was provided by Boettger [145], who discovered in Central Europe a ‘thermal’ race of the invasive physid snail, *Physella acuta*. This local form, lived in an artificially heated arm of the Oder River, was characterized by unusually thick shell and large size (up to 21 mm). It is much higher than the size of *Ph. acuta* in the southern parts of its invasive range (for example, in Azores, the maximal size attained by this physid is 12.8 mm (see [146]).

Though these old reports lacked a proper statistical analysis, required by modern standards of scientific inference, at least one reliable instance of ‘thermal gigantism’ can be reported here. Namely, Elkarmi, & Ismail [56] found that snails *Melanoides tuberculata* from a hot spring, situated in Jordan, attain the definitive shell size, which is approx. 1.7 times larger than in their conspecifics from adjacent non-thermal ponds. Thus, thermal acclimation in freshwater Gastropods can be accompanied by both a decrease and an increase in body size; no universal pattern is discerned.

As concerns the oxygen limitation hypothesis, the lymnaeids belong to a group of lung-breathing snails (the former subclass Pulmonata) and are not highly dependent on the oxygen dissolved in the water.

The second group of hypotheses explains miniaturization as a consequence of natural selection for reduced body size. This suggests that in geothermal habitats, for some reason, small size gives snails some selective advantages. Though differences in shell morphology in freshwater gastropods may have some adaptive values (see, for example, [147]), in each particular instance, it is rather difficult to propose a reliable selectionist explanation of a given shell character. Indeed, it is hardly possible to imagine why it may be ‘smaller is better’ for lymnaeids conquering thermal waterbodies.

In the course of the diversification of this family, there seems to have been no uniform trend in the body size evolution, and the ecological consequences of being small (or large) for the lymnaeids are unclear for us. The lymnaeids are represented by a plethora of clades, including some groups demonstrating very large (*Bulimnea*, *Lymnaea*) or even giant (extinct *Valenciennius*) sizes. The small-sized genera (*Galba*, *Kamtschaticana*, *Orientogalba*) are known in this family as well. It seems, that, within each clade, a certain ‘optimal’ body

size has evolved, which is depending on the mode of life and life cycles of species belonging to it.

The literary evidence concerning the direct selection on miniaturization in aquatic animals is contradictory. There are some experimental data, obtained on freshwater fish, that body size could have a role in thermotolerance, with smaller individuals being more thermotolerant [148]. However, it is unclear, if one may extrapolate these data on a phylogenetically distant group, the gastropods. In addition, a recent study, based on a phylogenetically broad meta-analysis, did not bring any evidence of the negative selection on body size under warmer temperatures across several groups of higher metazoans, including both ecto- and endothermic taxa [149].

To conclude, we remain unconvinced that the directional selection on body size had taken place within lymnaeid populations during the process of their adaptation to thermal habitats.

The third explanation, which seems to us the most reliable, relates the observed ‘thermal dwarfism’ with the adaptive changes in the life-histories of lymnaeid snails adapting to live in thermal waterbodies. It is known that the adult size in snails is determined by the rates of their growth and development [150], and the changes in these parameters can effectively alter the final dimensions attained by the molluscs. Another critical parameter of the life cycle of snails is the age at maturity, which is a rather flexible value, varying greatly under natural conditions [137,151–153]. Moreover, when aquatic ectotherms are reared under cool conditions, they grow slowly and mature at a larger body size than under warm conditions [154], which suggests the negative relationship between the ambient temperature and the tempo of maturation.

The effect of the thermal regime on the life-cycle parameters of molluscs was demonstrated in a number of case studies, involved not only freshwater snails [8,153,155–158], but even such ‘exotic’ groups as extinct belemnite cephalopods [159]. The lymnaeids, as well as other freshwater invertebrates (e.g., rotifers; see [160]), are able to adjust the key parameters of their life cycles to cope with environmental challenges, including the thermal stresses. We hypothesize that the increased rate of development and, consequently, the maturation at an earlier age, may be a main component of the non-morphological adaptation of lymnaeid snails to thermal habitats. This phenomenon is by no means unique to the hot-water lymnaeids. As Walter [136] observed, even in zonal populations of these snails, ‘typically, some individuals mature at a much smaller size than others’ (see also [156]). In the thermal habitats, this tendency to reach the adulthood earlier can become dominant. The underlying mechanism of this is the increased rate of metabolism and development observed in warmer habitats. For example, in lymnaeids, the maximal rate of embryonic development is attained at temperatures above 30 °C. This was found in laboratory experiments, when lymnaeid snails taken from non-thermal populations were grown under different temperatures [161].

The thermal dwarfism in the studied lymnaeid populations is, highly likely, a mere by-product of their precocious sexual maturation. The growth rate in lymnaeid snails, as in the vast majority of other ectothermic invertebrates, reaches its peak before maturation and slows down (if not stops altogether) after that, since virtually all available resources are allotted from somatic growth to reproduction. Thus, the definitive body size becomes much smaller than in their cold-water conspecifics that are growing slowly. Gustafson et al. [162] proposed a similar model for explanation of the decrease in shell size in physid snails under laboratory rearing. More technically, it may be called *progenesis* [40,163], a particular case of heterochrony—a mechanism that has played an important role in the evolution of various animals [164–166], including gastropods [167,168].

Virtually all mollusc communities of geothermal springs and swamps consist of a single or two species [10,15,47,66], which makes the interspecific competition highly relaxed in such habitats. As a result, the lymnaeid populations can reach extreme densities, up to several thousand individuals per square meter [47,169]). Under such circumstances, the precocious maturation may have an adaptive value, helping animals to win in the

intrapopulation competition. The earlier reproduction onset secures faster generation turnover under conditions of thermally stable environment, where the lymnaeid snails are able to reproduce all year round (as it is observed in hot springs of Kamchatka; see [47]). These advantages may suggest that, after some preliminary stages of acclimation, the precocious maturation turns into a heritable trait in a lymnaeid population, becoming a part of a more complex process of thermal adaptation.

The clear speculativeness of the progenetic model of thermal dwarfism proposed above is its main shortcoming. Indeed, we do not have empirical data on the life cycles parameters of most lymnaeid populations studied during this research, except for those of Kamchatka's (see [47] for more details). We lack any direct evidence of the heritable character of the earlier maturation in the studied populations. Therefore, only indirect evidence supporting our explanation may be briefly discussed here.

The case of Lake Troinoye (Kamchatka, the Valley of Geysers) is of special interest. This formerly hot (and recently cooled) lake maintains a population of *Kamtschaticana kamtschatica*, whose shells exhibit normal (i.e., relatively large) size, but their shell shape is typically 'thermal' (see Results for more details). In our opinion, it may be interpreted as a sign of heritability of shell morphology evolved in hot waterbodies.

This 'thermal morphology' is remarkable in itself. In four species out of the six studied (*K. kamtschaticana*, *L. catascopium*, *R. auricularia*, and *R. alticola*), the thermal populations are clearly different in their shell shape from the conspecifics inhabiting non-thermal waterbodies (see Results). In all the four cases, the shells of thermal snails may be characterized as 'juvenilized', i.e., their appearance corresponds to that of subadult snails of the same species living in zonal habitats. For example, shells of juvenile individuals of *R. auricularia* are typically taller and slenderer, as compared with the adults (see Figure 7), and they are lacking a broad ear-like aperture, characteristic of the full-grown individuals of this species [107,170]. In *L. catascopium*, shells of the thermal individuals retain proportions typical for subadult specimens of this species from cold waterbodies (see Figure 8).

It is useful to compare the shell growth trajectories of conspecific populations taken from waterbodies with contrasting thermal regime. A morphometric study of shell growth in four thermal populations of *R. auricularia* has shown that the line approximating the ontogenetic relationships between shell height and shell width is virtually identical with that describing shell growth in zonal populations of this snail (Figure 12). Specimens of thermal populations of *R. auricularia* occupy the left half of the graph, which corresponds both to their miniature size and earlier cessation of shell growth compared to conspecifics from non-thermal habitats.

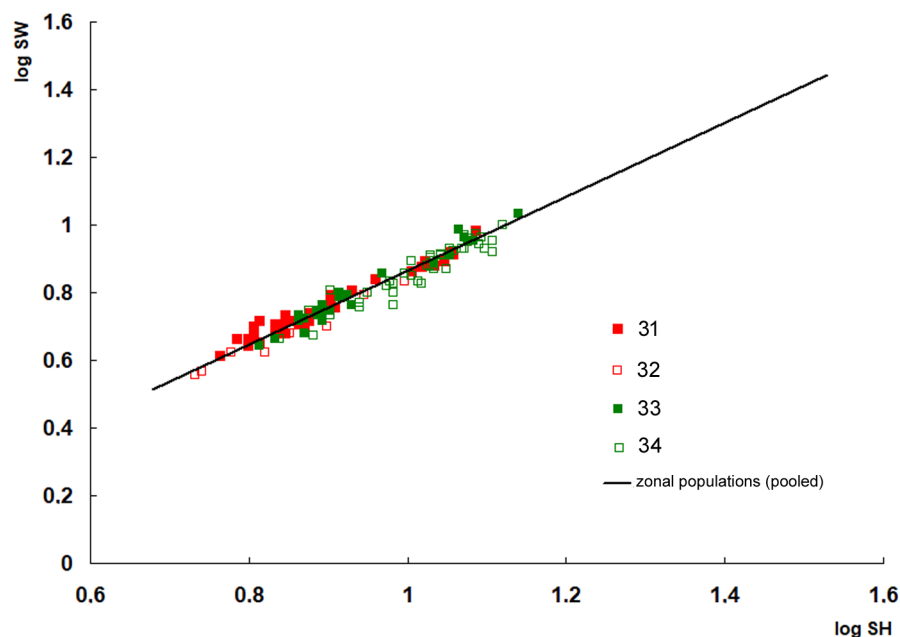


Figure 12. The relationship between shell height (SH) and shell width (SW) in four thermal populations of *Radix auricularia* as contrasted with the analogous data obtained from zonal populations of the same snail. The numbers correspond to numbers of localities in Table 2.

The juvenilization of thermal lymnaeids is, thus, a product of the cessation of shell growth at an earlier stage, with the subadult phenotype being fixed at the moment of maturation. The two exceptions to this rule, *A. balthica* and *A. lagotis*, are simple to explain. In both these species, no drastic changes in shell shape occur during growth under zonal conditions, and, thus, the precocious maturation has no effect on the final shell shape of these species in thermal habitats.

According to Khmeleva et al. [47], the duration of the life cycle in thermal *Radix* species of Kamchatka is significantly shorter than in the zonal conditions, and does not exceed 70–80 days. Probably, this is characteristic also for other thermal races of Palearctic lymnaeids. The reduced life span is obviously connected with the earlier maturation and cessation of growth.

We must acknowledge that there is at least one potential bias to our results in the case of *Radix auricularia*. This is a broadly distributed species, whose range covers the major part of the Palearctic as well as Nearctic [13,17,106,108]. The number of samples of *R. auricularia* used in this study and the number of sampled areas seem to be negligible as compared to this species' huge range. However, as Table 1 shows, the thermal populations of this mollusc are known from a limited number of regions, and, for some countries (Afghanistan, Austria), these populations are known from literature sources only. We included into our analyses all available samples from two regions (Kamchatka and the Baikal Lake basin), where *R. auricularia* forms numerous populations in geothermal sites. What is even more important, the goal of our study was to check the hypothesis of convergent evolution, which is driven by similar environment, not geography. Therefore, we do not think that the limited number of samples/regions studied could significantly bias our results in the case of the ear-shaped pond snail.

In our opinion, the factor of 'geography' has not played any significant role in the formation of the reported trends, with the possible exclusion of only *A. balthica*, discussed in Section 3.1. In all other species studied by us, neither latitude nor altitude contributed to the formation of the 'thermal phenotype'. For example, shells of 'thermal' *A. lagotis* from the Polar part of Northeast Europe (Vashutkiny Lakes) are more similar to 'thermal' *A. lagotis* from East Kazakhstan (Central Asia) than the latter sample to another Central Asian

(but non-thermal) sample from Pamir Mts (see Figure S3 in Supplementary Materials). Shell miniaturization was observed in all ‘thermal’ samples, irrespective of their location and species identity.

4.3. ‘Ecological Race’ vs. ‘Incipient Speciation’ (a Conclusion)

In general, the empirical findings of the present study, save a few exceptions, conform to the hypothesis of phenotypic repeatability in lymnaeid snails inhabiting the geothermal waterbodies. This repeatability can be observed at both the intra- and interspecific (*Radix alticola*, *R. auricularia*) levels. The ‘ecological races’ which have been formed within a widespread species (*A. balthica*, *R. auricularia*, and the like) are characterized by diminutive shell size and, in many cases, demonstrate the ‘juvenilized’ phenotype, which we are inclined to relate to the life-cycle re-adjustment following the penetration of molluscs to thermal habitats. In other terms, these intraspecific races exhibit, to a great extent, evolutionary predictability (= convergent evolution; = parallelisms). However, one should not overgeneralize this conclusion. Though the ‘thermal miniaturization’ was found not only among snails but also in other aquatic animals, it does not constitute a strict law. Cases of the body size increase in thermal environments are known (*Physella acuta* var. *thermalis*).

The short genetic distances between zonal and thermal populations, the existence of haplotypes shared by the two types of habitats, and the lack of the full hiatuses between shell traits of snails living under different thermal conditions vote for the status of ecological (or thermal) local races for populations found in geothermal sites. In our previous works [15–19], we already doubted the species status of most nominal species of the Lymnaeidae restricted ecologically to thermal habitats. Meier-Brook [14], in his monograph on the genus *Gyraulus*, came to the same conclusion. According to him, the species *Gyraulus thermalis*, described from Austria, is preferable to be considered simply as an ecological form, not a subspecies, let alone a ‘good’ species.

An alternative approach, developed in publications of some Russian authors [10,21,66,109], is to classify at least some thermal populations of widespread snail species as ‘independent young species’ [10], still not significantly diverged, both morphologically and genetically, from their alleged ‘zonal’ ancestors. To view these local forms as instances of incipient speciation allows one to explain the short genetic distance separating them from the ancestral population(s) and the lack of morphological hiatus.

It seems that there is no straightforward solution to this dilemma, since the answer depends on which species concept one prefers. The clear reproductive isolation of thermal snails from their non-thermal counterparts, and their inability to survive the zonal condition, found in some laboratory experiments [8,10,14,21], give some support for their species status, since it is possible to treat these populations as independently evolving lineages. On the other hand, the molecular approaches to species delineation, becoming standard in the modern lymnaeid taxonomy [19,171], invariably deny the species status for all nominal forms of the hot-water snails subjected to integrative revisions [15,16,18,19].

At last, we wish to stress that the results of our study are not of only academic interest. As it is well known, in temperate regions, the artificially warmed habitats have long been used by exotic species of snails and other invasive invertebrates as the ‘stepping stones’ on their penetration to the recipient areas. In many countries, cooling reservoirs and like habitats serve as sources of dispersal of alien species, including the harmful ones. Since the thermal optimum in geothermally adapted populations of temperate snails may shift to the higher temperature [171], they may therefore be considered as potential candidates for biological invasions to subtropical and tropical areas. It is well known that some tropical snail taxa could successfully invade temperate geothermal springs, e.g., *Melanoides tuberculata* in the USA [58,172, 173], but a reverse immigration of the temperate ‘hot snails’ to the southern regions also cannot be excluded.

Thus, the more profound knowledge of factors and trends accompanying adaptation of freshwater snails to extreme habitats can be useful for the understanding, forecast, and monitoring molluscan invasions both in temperate and tropical regions.

Supplementary Materials: The following supporting information can be downloaded at: www.mdpi.com/article/d15040548/s1, Table S1. List of Lymnaeidae COI sequences used in this study. Tables S2–S5. Intraspecific Mahalanobis distances (D^2) separating samples of studied lymnaeids taken from habitats with different thermal regime. Figure S1. Mean shell size in 26 populations of *A. balthica* in Iceland. Figures S2–S4. Dendrograms visualizing overall similarity (based on Mahalanobis distances) between thermal and non-thermal populations of the studied snail species. Table S5. The Mahalanobis distances (D^2) separating samples of *Radix alticola* and *R. auricularia* from habitats with different thermal regime (thermal populations are marked red; zonal populations—blue). The numbers correspond to the numbers of populations in Table 2.

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Data Availability Statement: The primary materials (gastropod samples) for this study are placed in some public repositories (ZIN, RMBH, LMBI). The new sequences, obtained during this research, have been made available through GenBank. Original data, used and collected during this research, are available (with reservations) upon request from the authors.

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