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Research Article

A new alien snail *Ampullaceana balthica* for the Canadian fauna, with an overview of Transatlantic malacofaunal exchange in the Anthropocene

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Abstract

A survey of the exchange of freshwater gastropods mollusks between Europe and North America is provided. Several dozen species of snails migrated, during the last two centuries, in either direction across North Atlantic and this process is ongoing. The intensity of the faunal exchange is unequal since much more snail species have dispersed from North America to Europe than in the opposite direction. Two cases of “failed” invasions of North American lymnaeid snails to Europe are discussed. A species of pulmonate snails, *Ampullaceana balthica* (Linnaeus, 1758), is reported here as new for the malacofauna of Canada (and for the whole North America). This snail of European origin was found in June 2019 in a small lake in the vicinities of Rimouski Town (Québec, Canada). The taxonomic identification of the mollusks was confirmed by molecular analysis, with the studied specimens having two unique COI haplotypes, hitherto not found in Europe.

Key words: freshwater Gastropoda, biological invasion, invasive snails, Québec, faunal exchange

Introduction

Mollusks (Mollusca) are considered very successful invaders on a global scale, and some of the species of this phylum have appeared in the “100 of the World’s Worst Invasive Alien Species” list (Luque et al. 2014). For example, in Canada alone, for several decades, a number of non-indigenous terrestrial snails and slugs, introduced chiefly from Europe, were for the first time recorded (Forsyth 1999, 2008; Forsyth et al. 2001, 2016; Gerber 2014; Forsyth and Kamstra 2019), some of them are serious plant pests (Grimm et al. 2009). The inflow of adventive freshwater snails and bivalves to this country seems not to be equally intense, however, their potential negative impact, including the threat to the indigenous malacocoenoses, may be great (see, for example, Schueler and Martel 2009).

In this communication, we report the new alien species of freshwater snails, *Ampullaceana balthica* (Linnaeus, 1758) of the family Lymnaeidae Rafinesque, 1815, that was identified in a small lake near Rimouski Town, Québec, Canada. This finding prompted us to provide an overview of the malacofaunal exchange between Europe and North America during the Anthropocene, i.e. within the last several centuries marked by an intercontinental movement of people and goods, expanding of the global economy, as well as ongoing globalization. It allows us to put this finding into a broader context and to compare the newly discovered invasion with those studied previously. The overview is based both on literary data and on own work with malacological collections of various scientific repositories.

Snails discussed in this paper were collected by the authors or are part of the following museum collections (museums acronyms are given in bracket): Natural History Museum, London, UK (NHMUK), Hungarian Museum of Natural History, Budapest (HMNH), Senckenberg Museum, Frankfurt am Main, Germany (SMF), Zoological Museum of the Copenhagen University, Denmark (ZMUC), Natural History Museum in Vienna, Austria (NHMW), Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia (ZIN), Russian Museum of Biodiversity Hotspots, N. Laverov Federal Center for Integrated Arctic Research of the Ural Branch of the Russian Academy of Sciences, Arkhangelsk, Russia (RMBH), and Laboratory of Macroecology & Biogeography of Invertebrates, Saint-Petersburg State University, St. Petersburg, Russia (LMBI).

An overview of Transatlantic malacofaunal exchange in the Anthropocene

The recent fauna of Canadian freshwater mollusks is of relatively young age and formed after the last Ice Age (12–10 kya). Similar to the Siberian aquatic malacofauna, the malacofauna of Canada had two principal sources: 1) “longitudinal migration” of species from the south; and 2) “latitudinal migration” from Northern Asia via the Bering land bridge (see Vinarski et al. 2021 for review). The rise of globalization has opened the way for incidental and non-incidental introductions of freshwater Mollusca and other invertebrates from Europe to North America and vice versa (see Honigmann 1927; Schlesch 1930 for earlier discussions of this topic). The first scientific predictions on this subject were formulated in the mid-19th century (Forbes and Hanley 1853; Choules 1860; see Vinarski 2017 for details). The emblematic case of the Transatlantic faunal exchange with respect to freshwater snails is the story of *Physella acuta* (Draparnaud, 1805) invasion of Europe and its subsequent spread throughout the world (see Anderson 2003; Vinarski 2017 and references therein). Though the “natural” character of this invasion cannot be excluded, it seems more probable that *Ph. acuta* managed to cross the ocean through humans activities (Vinarski 2017).

Notably, the intensity of this interchange was unequal in both directions: to date, much more snail species moved from North America to Europe

than in the opposite direction (Table 1). It is remarkable since the Transpacific intercontinental exchange between Asia and North America via the Bering land bridge was of more or less similar intensity in both directions (Vinarski et al. 2021). One may suggest that the patterns of “natural” faunal exchanges have another underlying mechanism(s) as compared with the ongoing biota homogenization mediated by human activity. The “natural” ways of the long-distance dispersal of continental snails are diverse, ranging from the action of strong winds (Valvoglyi 1975; Kirschner et al. 1997; Özgo et al. 2016) to animal-mediated mechanisms (see, for example, Wesselingh et al. 1999; Haase et al. 2010).

Another remarkable detail of this story is that invasive species of North American origin are seemingly much more successful in their spread over new lands than the European freshwater snails in North America. Among the first group, at least four species are now distributed in Europe and far beyond—*Ferrissia californica* (Rowell, 1863), *Gyraulus parvus* (Say, 1817), *Physella acuta*, and *Pseudosuccinea columella* (Say, 1817)—and the two latter species are subcosmopolitan (Lounnas et al. 2017; Vinarski 2017; Vinarski et al. 2019). On the other hand, of the three European snail species that colonized North America [*Ampullaceana balthica*, *Bithynia tentaculata* (Linnaeus, 1758), *Radix auricularia* (Linnaeus, 1758)], only *R. auricularia* is found in various parts of the continent. Burch (1989: 176) characterizes the distribution of this species in North America as “spotty”. Judging from the patchy distribution of *R. auricularia*, multiple independent introductions of this Palearctic species may have taken place (Mills et al. 1993). The slow rate and spotty distribution pattern of the European snails may possibly be explained by high intraspecific competition in molluscan communities in North America. The number of aquatic snail species in this continent is remarkably higher than that in Europe, especially in the subarctic and temperate parts (Johnson et al. 2013).

Two of the invasive snail species included in Table 1, *Hebetancylus excentricus* (Morelet, 1851) and *Galba cubensis* (L. Pfeiffer, 1839), are broadly distributed in the southern part of North America; their native ranges cover the southern part of North America as well as the Caribbean Region and Central America. To date, the sources of their invasion into Europe are not ascertained, and their origin from North America remains hypothetical, albeit rather probable. We conditionally included them in the list of North American invasive species (see Table 1).

At least three cases of Transatlantic migration of snails, possibly mediated by human activity, may be classified as unfinished or failed invasions (see Table 1). Two of them have not been considered in the recent literature and we would like to discuss these cases here:

1. *Ladislavella catascopium* (Say, 1817). The native range of this species includes the North American mainland, Greenland, and the extreme northeast of Asia (Vinarski et al. 2017). To the best of our knowledge, the

Table 1. A summary of Transatlantic invasions of freshwater snails in the historical time (only cases of migration from Europe to North America and vice versa are included).

Species [family]	Direction of migration*	Invasive range	Reference(s)
<i>Ampullaceana balthica</i> (Linnaeus, 1758) [Lymnaeidae]	E→NA	Canada, Quebec	This study**
<i>Bithynia tentaculata</i> (Linnaeus, 1758) [Bithyniidae]	E→NA	Mainly the Great Lakes region	Dundee 1974; Clarke 1981; Mills et al. 1993; Perez et al. 2016
<i>Ferrissia californica</i> (Rowell, 1863) [Planorbidae]	NA→E	The entire Europe save the northern parts of the continent	Glöer 2002, 2019
<i>Galba cubensis</i> (L. Pfeiffer, 1839) [Lymnaeidae]	NA→E**	Spain; greenhouses of Austria and Germany	Schniebs et al. 2018
<i>Gyraulus parvus</i> (Say, 1817) [Planorbidae]	NA→E**	Central Europe***	Glöer 2002, 2019; Lorencová et al. 2021
<i>Hebetancylus excentricus</i> (Morelet, 1851) [Planorbidae]	NA→E	Hungary	Domokos 1992
<i>Helisoma anceps</i> (Menke, 1830) [Planorbidae]	NA→E	Southern Europe; the Urals (in artificial waterbodies)	Khokhutkin and Vinarski 2013; Glöer 2019
<i>Planorbella duryi</i> (Wetherby, 1879) [Planorbidae]	NA→E	In various countries of Western, Central, Eastern, and Southern Europe	Domokos 1992; Glöer 2002, 2019
<i>P. scalaris</i> (Jay, 1839) [Planorbidae]	NA→E	Known from some places in Germany, Italy, and Spain	Glöer 2019
<i>P. trivolvis</i> (Say, 1817) [Planorbidae]	NA→E	Reported from Austria (in thermal waterbodies) and Malta	Hafner et al. 1986; Glöer 2019
<i>Menetus dilatatus</i> (Gould, 1841) [Planorbidae]	NA→E	Distributed throughout Europe, Portugal to Poland, except the northern regions	Glöer 2002, 2019
<i>Physella acuta</i> (Draparnaud, 1805) [Physidae]	NA→E	Almost entire Europe except the north latitudes; eastward to Western Siberia	Vinarski et al. 2015; Lydeard et al. 2016; Vinarski 2017; Glöer 2019
<i>Pseudosuccinea columella</i> (Say, 1817) [Lymnaeidae]	NA→E	Reported from various countries of Europe but mainly from greenhouses and botanical gardens	Glöer 2019
<i>Radix auricularia</i> (Linnaeus, 1758) [Lymnaeidae]	E→NA	Patchily distributed through much of the US; reported from Mexico	Baker 1911; Dundee 1974; Burch 1989; Naranjo-García and Castillo-Rodríguez 2017
Unsuccessful invasions			
<i>Ladislavella catascopium</i> (Say, 1817) [Lymnaeidae]	NA→E	England***	Kevan 1941, 1943
<i>Stagnicola reflexa</i> (Say, 1821) = <i>Ladislavella elodes</i> [Lymnaeidae]	NA→E	Hungary****	This study**
<i>Viviparus viviparus</i> (Linnaeus, 1758) [Viviparidae]	E→NA	Northeastern USA	Dundee 1974; U.S. Geological Survey 2009****

*E→NA – Europe to North America, and NA→E – North America to Europe;

**See Discussion in the text;

***There is a possibility that this species entered Europe through Siberia during the Ice Age (see Lorencová et al. 2021);

****Possibly, the invasive populations have become extinct for now.

occurrence of *L. catascopium* in Europe was only reported in Leith, Scotland, where it was first discovered in 1929 in a warm engine pond at 27 °C and remained viable at least until 1940 (Kevan 1941, 1943). Kevan believed that the snails were “introduced to the timber yard at Leith with logs of birch and elm imported from Eastern Canada, for these on arrival are immediately floated in the engine-pond” (Kevan 1943: 431). Images of the shells and the generative system of this mollusk provided by Kevan (1943)

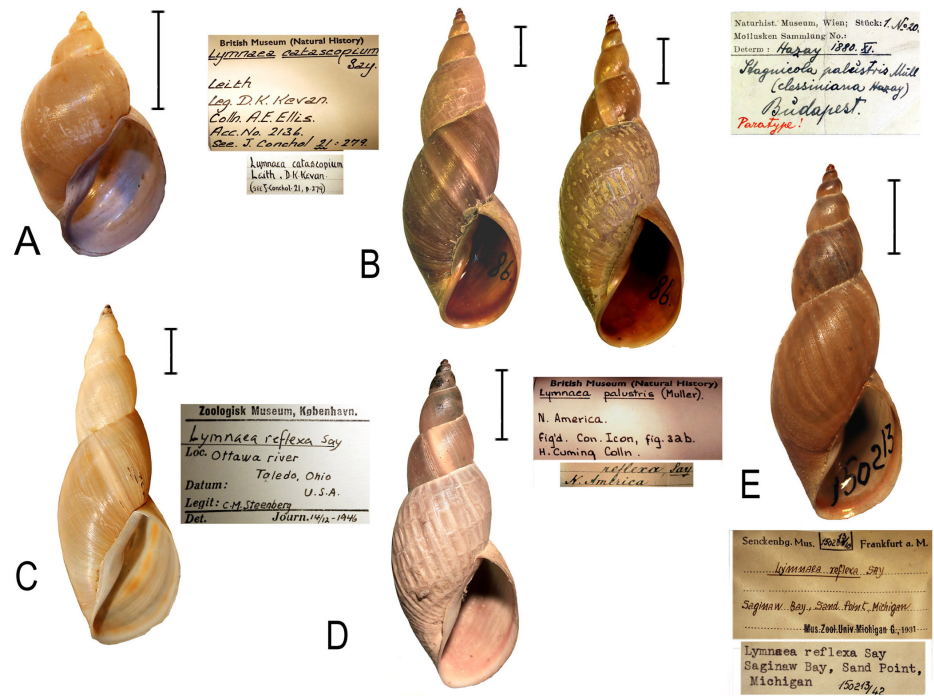


Figure 1. Shells of Nearctic stagnicoline snails from their native and invasive ranges. A. *Ladislavella catascopium*, a pond in Leith, Scotland [NHMUK]. B–C. *Stagnicola palustris* var. *clessiniana*, paratypes [NHMW]. D. *Stagnicola reflexa*, USA, Ohio, Ottawa River [ZMUC]. E. *S. reflexa*, “North America”, without a precise locality [NHMUK]. F. *S. reflexa*, USA, Michigan, Saginaw Bay of the Huron Lake, Sand Point [SMF]. Scale bars 5 mm. Photo by Maxim V. Vinarski.

seem to confirm the correctness of the species identification. We were able to examine some specimens (dried shells) of Kevan’s sample from NHMUK (Figure 1A). The later authors, including those written about the malacofauna of the UK (Kerney 1976; Anderson 2005), did not mention this species (except Macan 1949); it is absent from the recent pan-European check-lists (Falkner et al. 2001) and atlases (Glöer 2002, 2019; Welter-Schultes 2012). Thus, this event of invasion may be classified as “failed”, and Kevan’s data gives some hints on the probable causes of this failure. On the basis of the author’s information, the pond in Leith was “repopulated annually after cleaning by the emergence of snails from the overflow pipes” (Kevan 1943: 459). It means that, besides the high water temperature in the pond, this population was highly dependent on human activity and, probably, could not sustain without it. One may hypothesize that changes in the water regime of this habitat caused the disappearance of *L. catascopium* from the pond.

2. A more mysterious case is that of *Stagnicola palustris* var. *clessiniana* (Hazay, 1880), described in the late 19th century from the pond of the Budapest Botanical Garden in Hungary (Hazay 1880). This variety is distinguishable from the typical one in the much larger (up to 45 mm height; see Clessin 1887–1890) and thick-walled shell, with a very long and slender spire (see Figure 1). Though the internal anatomy of this snail was not studied, its conchological characters distinguish it from the rest of *Stagnicola* species of Europe (reviewed and illustrated by Glöer 2002, 2019). The taxonomic identity of this taxon has remained unclear, and the most recent publications

on stagnicoline snails of Eastern Europe do not mention its occurrence in either Hungary or neighboring countries (Glöer 2002, 2019; Horsák et al. 2013; Piechocki and Wawrzyniak-Wydrowska 2016; Vinarski 2020).

We examined the paratypes of this variety kept in NHMW (see Figure 1B, C) and also studied the entire collection of *Stagnicola* from Hungary in HNHM. Conchologically, specimens described by Hazay (1880) look almost identical to shells of the North American species “*Stagnicola*” *reflexa* (Say, 1821) [= *Ladislavella elodes* (Say, 1821) of current nomenclature]. Actually, Hazay himself noted this resemblance though he listed some slight conchological differences between his *S. palustris* var. *clessiniana* and the North American species (Hazay 1880: 164).

Botanical gardens were often places for the first findings of exotic species of aquatic snails in Europe (e.g. *Physella acuta*, see Vinarski 2017; *Pseudosuccinea columella*, see Schlesch 1930). Could it be that the snails described by Hazay (1880) as a new aboriginal variety, represented, in fact, an invasive population of a Nearctic lymnaeid, which already existed in the Botanical garden? The apparent way of snail transportation, in this case, was their import from North America with water plants.

Unfortunately, the area of the former Botanical Garden in Budapest is today occupied by city buildings, and the waterbodies studied by Hazay exist no longer (Z. Feher 2020, *pers. comm.*). We failed to find shells of this variety in the extensive collection of Hungarian mollusks kept in HNMH, and it is reasonable to suggest that this invasive population failed to colonize other localities and went extinct as a consequence of habitat destruction. However, the true identity of Hazay’s snails remains unclear owing to the total absence of anatomical and/or molecular data.

To conclude, almost 20 species of freshwater snails, belonging to two subclasses (Caenogastropoda and Heterobranchia) and five families, have been involved in the faunal exchange between Europe and North America (see Table 1), and the case of *A. balthica*, discussed in this paper, shows that this process is ongoing.

Materials and methods

Material examined in the present section is from two sources. Soft tissues and shells of fifty-five snails preserved with 96% ethanol were found in museum collections. Particularly, 33 specimens of *A. balthica* were collected in August 2012 from Pirenga Lake, Murmansk Region, Russia; coordinates 67.703056 N; 32.070278 E, leg. I.O. Nekhaev (LMBI); 25 snails were collected in July 2013 from a brook in Reykjavik City, Iceland; coordinates 64.128941N; -21.788737W, leg. O.V. Aksenova (RMBH).

Forty living individuals of *A. balthica* were collected in June 2019 in Québec Province (Canada) by MZ (in a course for a PhD thesis preparation) with the assistance of MVV. Animals were collected by hand from the

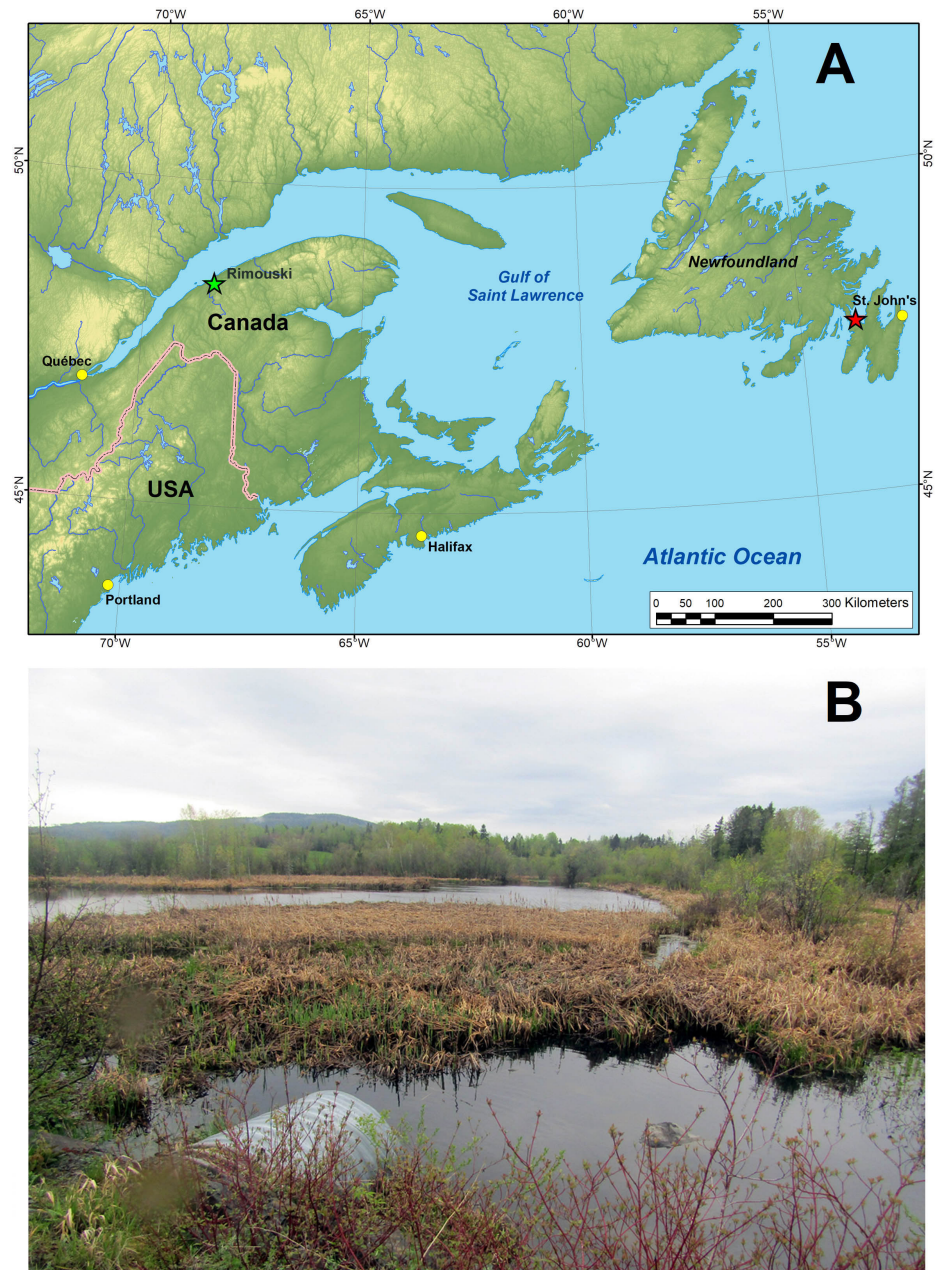


Figure 2. Records of *A. balthica* in Canada. (A) Map of Eastern Canada, with the two locations of *A. balthica* discussed in this article. The red star indicates the first occurrence on Newfoundland; the green star indicates our new record in Québec. (B) The southern part of Lake d'Anguille, separated by a dam from the main area of the lake. The photo was taken from the dam. Photo by Maxim V. Vinarski.

surface of leaves of submerged water plants over which they were crawling, from an artificial waterbody created by a dam built in the southern part of the d'Anguille Lake, situated east of Rimouski Town (Figure 2); coordinates 48.422222N; -68.427543W. After narcotization, soft tissues were removed from the shells. Twelve individuals were dissected and examined by MVV; small tissues samples from eight animals were preserved with 96% ethanol for subsequent DNA analysis.

Measurements of shells (Figure 3) and dissections of the soft bodies were carried out following the standard protocols applied in lymnaeid studies

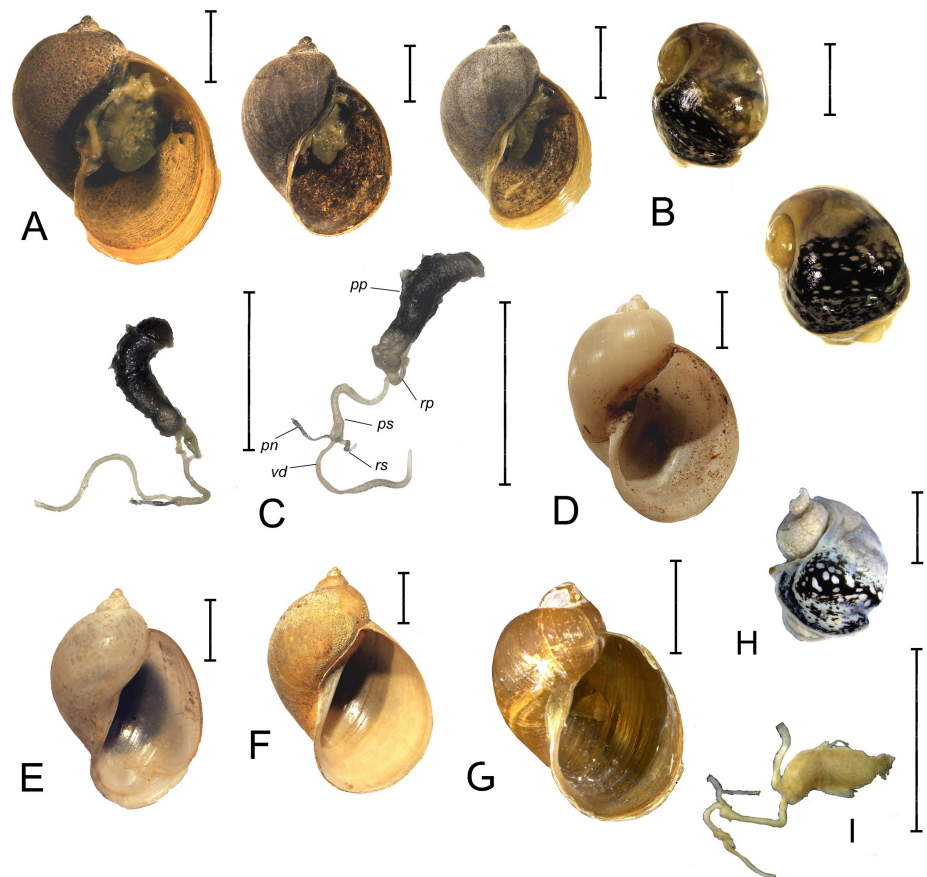


Figure 3. Shells (A, D–G), mantle pigmentation (B, H), and copulatory apparatuses (C, I) of *Ampullaceana balthica* from Canada and Europe. A–C. Canada, Québec, d’Anguille Lake, 02.06.2019. D. Iceland, without a precise locality, collected in 1876 [ZMUC]. E. France, Rhône River, sampling date unknown [SMF]. F. Denmark, Lødderup Kær, sampling date unknown [ZMUC]. G–I. Iceland, a brook in Reykjavik [RMBH]. Scale bars 5 mm. Abbreviations: pn – nerve of the penis; pp – praeputium; ps – penis sheath; rp – retractor of the praeputium; rs – retractor of the penis sheath; vd – vas deferens. Photos by Maxim V. Vinarski (A–F), Olga V. Aksenova (G–I).

(Kruglov 2005; Andreyeva et al. 2010; Vinarski et al. 2020). Particularly, the praeputium: penis sheath ratio (PP:PS) is used as the main characteristic of the proportions of the copulatory apparatus, which has widely been applied in the lymnaeid taxonomy (Kruglov 2005; Vinarski 2011; Vinarski et al. 2020). In total, 88 shells (Table 2) were measured with an accuracy of ± 0.1 mm. Subadult shells were excluded from the measurements. The voucher specimens are housed in the museums, RMBH and LMBI.

New sequences of the mitochondrial cytochrome *c* oxidase subunit I (COI) gene fragment were generated from fourteen *A. balthica* specimens, including three from Québec (Supplementary material Table S1). The DNA extraction, PCR, and sequencing of new samples followed protocols described previously (Aksenova et al. 2017, 2018). Additionally, we obtained 159 COI sequences of *A. balthica* from NCBI’s GenBank (Table S1). The alignment of the COI sequences was performed using the ClustalW algorithm implemented in MEGA7 (Kumar et al. 2016).

To estimate the phylogeographic relationship between haplotypes of *A. balthica*, a network-based approach was applied using Network ver. 4.6.1.3

Table 2. A morphometric comparison of *A. balthica* from Canada and several native range populations.

Character / index	Locality		
	Québec, d'Anguille Lake	Iceland, a brook in Reykjavik	Russia, Murmansk Region, Pirenga Lake
Repository	LMBI	RMBH	LMBI
Number of specimens measured (dissected)	33 (12)	25 (12)	33 (13)
Whorls number	<u>3.00–4.00*</u> 3.39±0.20	<u>2.50–3.75</u> 3.00±0.40	<u>3.00–4.25</u> 3.51±0.40
Shell height, mm (SH)	<u>11.0–15.9</u> 12.8±1.0	<u>7.1–10.2</u> 8.6±1.3	<u>11.6–17.2</u> 14.2±1.3
Shell width, mm (SW)	<u>8.6–10.9</u> 9.9±0.9	<u>4.5–7.0</u> 5.8±0.7	<u>8.0–12.8</u> 9.9±1.1
Spire height, mm (SpH)	<u>1.9–3.7</u> 2.9±0.4	<u>1.5–3.4</u> 2.4±0.7	<u>2.8–5.3</u> 4.2±0.6
Body whorl height, mm (BWH)	<u>10.1–13.7</u> 11.7±0.8	<u>6.2–9.5</u> 7.6±1.1	<u>12.3–15.4</u> 12.8±1.2
Aperture height, mm (AH)	<u>8.5–13.1</u> 10.1±0.9	<u>5.0–7.7</u> 6.3±0.8	<u>9.4–12.1</u> 10.2±1.0
Aperture width, mm (AW)	<u>5.6–8.6</u> 7.1±0.5	<u>3.3–5.2</u> 4.2±0.5	<u>6.0–9.4</u> 7.2±1.1
Praeputium length, mm (PP)	<u>4.4–6.5</u> 5.8±0.9	<u>1.9–2.6</u> 2.2±0.2	<u>2.1–3.7</u> 2.8±0.8
Penis sheath length, mm (PS)	<u>4.5–7.5</u> 6.0±0.9	<u>1.4–2.4</u> 1.7±0.3	<u>2.0–3.1</u> 2.5±0.6
SW/SH	<u>0.70–0.84</u> 0.78±0.04	<u>0.62–0.74</u> 0.68±0.04	<u>0.63–0.82</u> 0.70±0.06
SpH/SH	<u>0.16–0.28</u> 0.23±0.03	<u>0.28–0.34</u> 0.28±0.04	<u>0.24–0.35</u> 0.29±0.03
BWH/SH	<u>0.83–0.96</u> 0.92±0.02	<u>0.85–0.93</u> 0.89±0.02	<u>0.85–0.93</u> 0.90±0.02
AH/SH	<u>0.72–0.85</u> 0.79±0.34	<u>0.66–0.79</u> 0.73±0.04	<u>0.65–0.76</u> 0.72±0.03
AW/AH	<u>0.60–0.79</u> 0.71±0.04	<u>0.62–0.73</u> 0.68±0.03	<u>0.58–0.81</u> 0.71±0.06
PP/PS	<u>0.76–1.22</u> 0.97±0.13	<u>1.03–1.52</u> 1.26±0.15	<u>0.81–1.54</u> 1.15±0.22

Above lines – limits of variation (min–max), below lines – mean value ± SD

software with default settings (Bandelt et al. 1999). This approach revealed minute genetic differences between haplotype sequences.

The ZIN repository holds the neotype of *A. balthica* designated by Kruglov and Starobogatov (1983) and examined during this study.

Results

Identification and morphology

To date, field observations and experimental sampling (2018–2019) in over 40 localities in Québec and Ontario showed that *A. balthica* only occurs in the d'Anguille Lake, QC. Its preliminary identification has been carried out by analysis of shell and soft tissues structures using the recent atlases and keys (Glöer 2002, 2009; Kruglov 2005; Andreyeva et al. 2010; Vinarski et al. 2020). This morphological-based identification was confirmed later by the data of molecular analysis.

Three different COI haplotypes exist for the snails from d'Anguille Lake: two unique (i.e. absent from the available databases) and one found also in Western and Northern Europe (Figure 4). These two unique haplotypes are

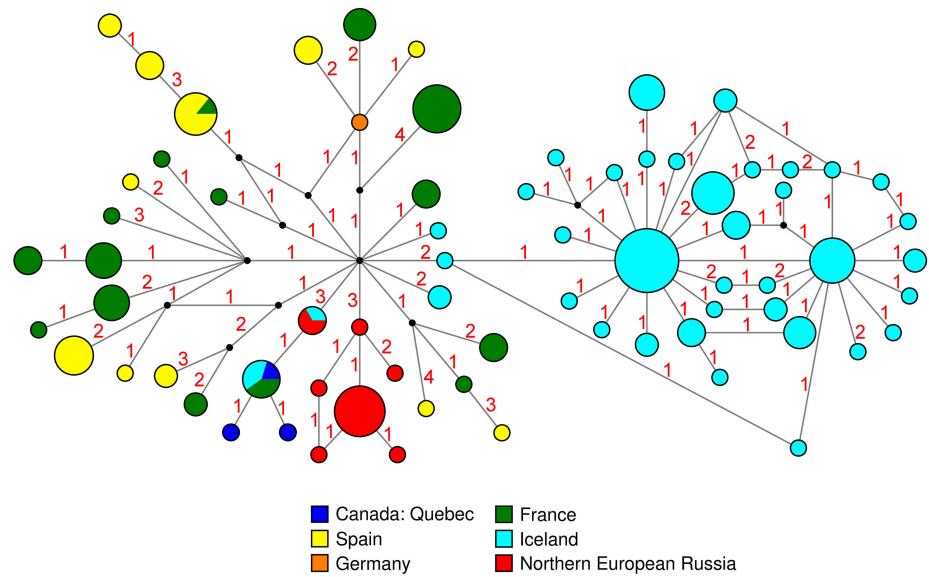


Figure 4. Median-joining network of the COI sequences of *Ampullaceana balthica* ($N = 171$). The red numbers near branches indicate the numbers of nucleotide substitutions between haplotypes. Size of circles corresponds to the number of available sequences for each haplotype (smallest circle = 1 sequence).

very close to the third one and separated from the latter by a single mutational step only (see Figure 4). The nearest Western European haplotype represented also in the studied sample from Québec, has a rather broad distribution; it occurs in France as well as in Iceland (introduced from continental Europe; see Bolotov et al. 2017 for details). One cannot exclude, however, that the two other haplotypes found in Québec are also distributed in Europe but, being quite rare, still have not been detected in the native range populations. The emergence of these haplotypes in Canada seems unlikely, given the very recent introduction of these mollusks into North America (see Discussion).

Phenotypically, the snails collected from Lake d’Anguille are similar to the European *A. balthica* described in the recent taxonomic publications (Glöer 2002, 2019; Andreyeva et al. 2010; Schniebs et al. 2011; Vinarski et al. 2020) as well as to the neotype of this species [see Schniebs et al. 2011 for the neotype image]. They possess ovoid shells with small depressed spire and relatively inflated body whorl and aperture (Figure 2). Table 2 gives a morphometric comparison of shells of *A. balthica* from Lake d’Anguille and selected native range populations.

The mantle pigmentation pattern of Canadian *A. balthica* (see Figure 3B) corresponds to the third type of Schniebs et al. (2011) classification, i.e. “mantle black, grey-black, or grey-yellow with few or numerous roundish distinct spots of white or rarely grey-green or grey-yellow, that are very variable in size; mantle collar white or bluish-white with numerous irregular small patches of black; mantle edge white or rarely yellowish” (Schniebs et al. 2011: 667).

There are no serious differences between *A. balthica* from Québec and Europe in the male reproductive system, being a significant source of

taxonomic signal in the Lymnaeidae. The structure of the copulatory apparatus (see Figure 3C) is identical to that of the European populations of this species (see Schniebs et al. 2011 for a full morphological account of *A. balthica* from Europe). PP:PS ratio in the sample from Lake d'Anguille was equal to 0.97 ± 0.13 (see Table 2). This value corresponds to the PP:PS variation in *A. balthica* of Europe, which ranges from 0.70 to 2.30 (Schniebs et al. 2011). Some differences between the Canadian and North European (Icelandic) populations in the mantle pigmentation and the praeputium coloration (compare Figures 3B and 3H, and Figures 3C and 3I) may be explained by an interpopulation variability. These slight differences fall within the range of the morphological variability of *A. balthica* reported for Europe (Schniebs et al. 2011).

Discussion

The first data on the malacofauna in the environs of Rimouski was published as early as 1859 (Bell 1859), and the studied species was absent from Bell's list. The subsequent surveys and check-lists (Baker 1911; Clarke 1973; Burch 1982, 1989; Johnson et al. 2013) did not mention *A. balthica* as a member of the malacofauna of North America. However, Clarke (1981) reported the presence of the European species *Radix peregra* (O.F. Müller, 1774) in "a few localities in Newfoundland". The shell photos of this species provided by the author correspond to the shells of *A. balthica* rather than to *Peregriana peregra* (see Lawton et al. 2015; Vinarski et al. 2020 for discussion of the taxonomic status of the latter species). Although Clarke (1981) reported the occurrence of *A. balthica* in North America, the author's finding was never confirmed by anatomical nor by molecular genetic studies, and the authors of the succeeding malacofaunal overviews (Burch 1989; Johnson et al. 2013) ignored (if not overlooked) this record. Hence, Clarke (1981) has remained the only source for the probable presence of *A. balthica* in North America. The exact date of introduction of *A. balthica* to Newfoundland remains unknown, though, most probably, it has happened rather recently, perhaps in the mid-20th century.

The distance between Bellevue, the locality of *A. balthica* in Newfoundland mentioned by Clarke (1981), and Rimouski exceeds slightly 1100 kilometers. One can hypothesize that, probably, between the mid-1970s and 2019, the snails moved westward and cover this distance, using, for example, the waterfowl as vectors of their transportation.

However, the fact of the relatively high genetic diversity of the Lake d'Anguille population, harboring at least 3 different, albeit similar haplotypes, as well as the absence of other reliable findings of *A. balthica* between Newfoundland and Quebec allows us to propose an alternative explanation. In our opinion, it is more reasonable that Rimouski (or another point on the shores of the Gulf of Saint Lawrence) is an independent source of invasion of *A. balthica* to Canada, another landing point of this

species, maybe of quite a recent origin. Indeed, one may hypothesize that at the time of the invasion, a group of individuals from the same locality with several close haplotypes came to Canada. It helps to explain the increased genetic diversity in a relatively confined habitat.

The occurrence of the species in Iceland suggests that the oceanic island might have served as a “stepping stone” for the Baltic pond snail in its intercontinental journey (see Vinarski 2017 for the discussion of the possibility of such dispersal for freshwater gastropods). Continental Europe (France) seems the most probable source of invasion of this mitochondrial lineage of *A. balthica* to Québec and Iceland, and human transportation means – the most likely transportation mode of the snail dispersal (see Bolotov et al. 2017). The findings of *A. balthica* in Newfoundland and Québec along the sea coast suggest that its transportation via ships was the most probable mode of transportation. The aquarium trade as the origin of its dispersal, though repeatedly discussed in the context of molluscan invasions (Mackie 1999; Duggan 2010; Patoka et al. 2017), seems unlikely in the studied case, as *A. balthica* does not belong to snail species popular among aquarists.

Conclusions

To our best knowledge, *A. balthica* from the province of Québec is the only known representative of the genus in North America. Owing to the rather broad distribution of the probable ancestral haplotype of the Canadian *A. balthica*, from France to Iceland it is impossible to determine the precise origin of the adventive Canadian populations. Since phenotypically similar species are absent in Canada, shell morphology allows *A. balthica* identification. However, we recommend confirming morphological-based identification with genetic methods, because the lymnaeid shell is prone to high intraspecific variations.

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Authors’ contribution

M. Vinarski – field and museum study, laboratory study, conceptualization, writing and editing the manuscript, funding acquisition; O. Aksenova – laboratory study, conceptualization, writing and editing the manuscript; I. Bolotov – conceptualization, writing and editing the manuscript; A. Kondakov, I. Khrebtova – molecular research, bioinformatics, software; M. Gofarov – visualization of results; M. Schindler – funding acquisition, writing and editing the manuscript; M. Zuykov – field and museum study, conceptualization, writing and editing the manuscript.

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Supplementary material

The following supplementary material is available for this article:

Table S1. List of present and additional COI sequences of *Ampullaceana balthica* obtained from NCBI’s GenBank.