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# Phylogeographic relationships of Baltic and Nordic populations of the Copse Snail *Arianta arbustorum*, with taxonomical implications

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**Abstract.** The Copse Snail, *Arianta arbustorum* (Linnaeus, 1758), is a common species in Europe, reaching from the Pyrenees in the south to the Arctic circle in northern Norway, and from the British Isles in the west to Russia in the east, with populations further afield in Iceland, Faroe Islands, and Canada. While its populations in Central Europe and the Alps have been widely studied, little is known about the Baltic coast and Nordic populations in Europe, including the Icelandic *A. a. pseudorudis* (Schlesch, 1924). We conducted a phylogeographic study focusing on the Baltic and Nordic populations of *A. arbustorum,* covering nearly all the species' distribution, including individuals from all recognized subspecies. Our analysis showed the existence of a monophyletic Baltic/Nordic clade that represents a recent expansion front of the copse snail towards northern latitudes. Moreover, there were likely multiple introduction events in Iceland, and *A. a. pseudorudis* is considered a synonym of *A. a. arbustorum*. The type locality of *A. arbustorum* is restricted to Sweden, based on original literature and reassessment of syntypes. *Arianta canigonensis* (Boubée, 1833) is considered a separate species and has nomenclatural priority over *A. xatartii* (Farines, 1834), resulting in new combinations: *A. canigonensis doriae* (Paulucci, 1878) comb. nov., *A. canigonensis gaillardi* (Germain, 1912) comb. nov., *A. canigonensis repellini* (Reeve, 1852) comb. nov., *A. canigonensis vareliensis* (Ripken & Falkner, 2000) comb. nov., and *A. canigonensis xatartii* (Farines, 1834) comb. nov. Only three subspecies remain in *A. arbustorum*: the nominate *A. a. arbustorum*, *A. a. stenzii* (Rossmässler, 1835), and *A. a. styriaca* (Frauenfeld, 1868); the other subspecific taxa (*alpicola*, *picea*, *pseudorudis*) cannot be maintained as distinct subspecies and are synonymised with nominate *arbustorum*.

**Key words.** Phylogenetics, Pleistocene, poleward range expansion, population genetics, Stylommatophora

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## Introduction

The Copse Snail, *Arianta arbustorum* (Linnaeus, 1758), is a common helicid species in many parts of Europe, being found from natural areas to urban settings in most of its range. It reaches from the Pyrenees in the south through the Alps and to the Arctic circle in northern Norway, and from the British Isles in the west to Russia in the east, with populations further afield in Iceland, the Faroe Islands, and Canada. Such wide distribution, both latitudinally and altitudinally, is multifaceted. Firstly, the species has been extending its range both (1) naturally (often indirectly benefiting from human action, such as the temperature increases in northern latitudes and more continental areas), and (2) through direct (albeit accidental) transport by humans (Bondareva *et al.* 2018; Mukhanov and Lisitsyn 2018; von Proschwitz *et al.* 2023). One of the potential reasons behind such wide geographical coverage could be its active dispersal ability, shown via behavioural tests to be the highest among common European Helicoidea (Dahirel *et al.* 2015).

*Arianta arbustorum* is reasonably variable in size, shell shape, shell colour, and soft body (head-foot) colour, leading to many localized morphs being described as forms, varieties, subspecies, and even full species throughout the past two centuries (Taylor 1914; Salvador *et al.* 2025). Most of these names have been synonymized through the years, but several remain commonly accepted in the literature to this day, mostly as subspecies, depending on the author and publication (e.g. Welter-Schultes 2012; Cadevall & Orozco 2016). Besides nominate *A. a. arbustorum*, the most common subspecies seen in the literature, either widely accepted or more occasionally used (e.g. Gittenberger *et al.* 2004; Groenenberg *et al.* 2016; Hausdorf & Walther 2021; MolluscaBase Eds 2026), are: *A. a. alpicola* (A. Férussac, 1821), *A. a. canigonensis* (Boubée, 1833), *A. a. doriae* (Paulucci, 1878), *A. a. gaillardi* (Germain, 1912), *A. a. picea* (Rossmässler, 1837), *A. a. pseudorudis* (Schlesch, 1924), *A. a. repellini* (Reeve, 1852), *A. a. stenzii* (Rossmässler, 1835), *A. a. styriaca* (Frauenfeld, 1868), *A. a. vareliensis* Ripken & Falkner, 2000, and *A. a. xatartii* (Farines, 1834). The latter subspecies, from the Pyrenees, is often considered a separate species, *A. xatartii*, in publications on the Spanish fauna (e.g. Verdú *et al.* 2011; Cadevall & Orozco 2016).

Previous phylogenetic and phylogeographic studies on the *arbustorum* complex based on mitochondrial markers (e.g. Gittenberger *et al.* 2004; Groenenberg *et al.* 2016; Hausdorf & Walther 2021) offered some hints about the species' relationships but were restricted to Central European snails, with a heavy focus on the Alpine forms. Thus, a significant portion of *A. arbustorum* populations in Europe remained unstudied, particularly the Baltic and Nordic ones, from Denmark and northern Germany to Estonia and Russia in the west, Fennoscandia in the north, and Iceland in the Atlantic.

Here we conduct a phylogeographic study of *A. arbustorum*, covering nearly the species' entire distribution (except for portions of eastern Europe), and including individuals from all the above-mentioned subspecies (including *A. xatartii*). In particular, we carried out an ample sampling of Baltic and Nordic populations, including the Icelandic *A. a. pseudorudis*, as well as samples from the introduced population in Canada. We also take the opportunity to revisit the fossil taxon *A. a. gaillardi* and to restrict the type locality of nominate *A. arbustorum*. Our analysis also has some implications for the classification of the involved taxa.

## MATERIAL AND METHODS

### Studied specimens

Specimens were selected to cover as much of the species' geographic distribution as possible, also including a large sampling from areas of interest in northern Europe. Attention was also paid to include specimens of all potential subspecies/species. A total of 117 specimens were sequenced and used in this study; the full list of specimens can be seen in Table 1 (including collection data and GenBank accession numbers).

The specimens (preserved in ethanol 70–96%) are deposited in the following natural history collections: GAMNH, "Grigore Antipa" National Museum of Natural History (Bucharest, Romania); KUO, Kuopio Natural History Museum (Finland); MNHN, Muséum national d'Histoire naturelle (Paris, France); MZB, Museu de Ciències Naturals de Barcelona (Spain); MZLU, Lund Museum of Zoology (Sweden); MZH, Finnish Museum of Natural History, Luomus (Helsinki, Finland); NHMD, Natural History Museum of Denmark (Copenhagen, Denmark); NHMW, Naturhistorisches Museum Wien (Vienna, Austria); NMS, National Museums Scotland (Edinburgh, Scotland); NSII (formerly IINR), Natural Science Institute of Iceland (Garðabær, Iceland); NTNU, University Museum, Norwegian University of Science and Technology (Trondheim, Norway); RMNH, Naturalis Biodiversity Center (Leiden, The Netherlands); TAMZ, Estonian Museum of Natural History (Tallinn, Estonia); ZMB, Museum für Naturkunde (Berlin, Germany).

Further comparative specimens (shells, including the type specimens we could trace, covering most but not all taxa) were studied for our taxonomic discussions, housed in the collections listed above as well as the following additional collections: LINN, The Linnean Society of London (London, UK); MDC, Musée des Confluences (Lyon, France); NHMUK, Natural History Museum (London, UK); RBINS, Royal Belgian Institute of Natural Sciences (Brussels, Belgium); SMF, Naturmuseum Senckenberg (Frankfurt a.M., Germany; UPSZTY, Zoological Museum of Uppsala (Uppsala, Sweden); ZSM, Zoologische Staatssammlung München (Munich, Germany).

### DNA extraction, amplification, and sequencing

A small tissue clip was obtained from each voucher specimen for DNA extraction at the Luomus DNA Lab (University of Helsinki). Extraction followed the standard protocol of the QIAGEN DNeasy® Blood & Tissue Kit but including a small modification of the final step in order to increase yield (i.e. using only one-quarter of suggested buffer AE amount, and repeating the step).

For this study, we targeted three molecular markers that are informative at the population level, two mitochondrial (the barcoding fragment of the COI gene and the 16S rRNA gene) and one nuclear (the non-coding ITS2 region). The COI marker (*c.* 650 bp) was amplified using invertebrate primers LCO/HCO (Folmer *et al.* 1994); for 16S (*c.* 450 bp), primers 16SarL/16SbrH (Simon *et al.* 1994) were used; ITS2 (*c.* 430–450 bp) was amplified using primers LSU-1/LSU-3 (Wade & Mordan 2000; Wade *et al.* 2006), which also includes the 3′ end of the 5.8S rRNA gene and the 5′ end of the 28S rRNA gene.

PCR amplification was conducted according to the following protocols. COI and 16S markers: 3 min initial denaturation at 96 °C; 35 cycles of denaturation at 95 °C (30 s), annealing at either 48 °C (COI) or 50 °C (16S) (1 min), and extension at 72 °C (2 min); 5 min final extension at 72 °C. ITS2/28S markers: 3 min initial denaturation at 95 °C; 40 cycles of denaturation at 95 °C (30 s), annealing at 50 °C (ITS2 section) (1 min), and extension at 72 °C (5 min); 4 min final extension at 72 °C. The success of PCR was assessed visually via agarose gel electrophoresis. The PCR products were cleaned with ExoSAP-IT™ (Affymetrix Inc.) following the manufacturer's protocol. All samples were sent to Macrogen Europe (Amsterdam, The Netherlands) for Sanger sequencing.

### Phylogenetic analysis

Resulting sequence data were quality-checked visually (using Phred Quality Score of bases) and *de novo* assembled in Geneious Prime (v. 2025.0.2, Biomatters Ltd). The consensus sequences were extracted and uploaded to GenBank (Table 1).

Further sequences of *Arianta* spp. from published studies, as well as of the outgroup (*Helicigona lapicida*), were obtained from GenBank (Table 2). Nearly all these additional terminals had sequences available for the COI and 16S markers only, so we used solely those specimens that covered gaps in our sampling to avoid including too much missing ITS2 data in the analysis. The locality of origin of the sequenced specimens and GenBank data used was mapped in Figure 1 to better illustrate our coverage (geographic coordinates can be found in Suppl. File Table S1). Most data available on GenBank is from the COI marker only, which were not included in the phylogeny but were used for the haplotype network (see below).

Sequence alignment was done in Geneious Prime via the MUSCLE plugin (Edgar 2004), optimized for accuracy (default settings). The resulting alignments of each marker were visually proofed for inconsistencies. The alignments of the three markers were then concatenated for the phylogenetic analysis.

A Bayesian inference phylogenetic analysis was done using MrBayes (v. 3.2.7, Ronquist *et al.* 2012) via the CIPRES Science Gateway (v. 3.3, Miller *et al.* 2015). Two concurrent analyses with 4 Markov chains each were run for 140 million generations using a generalized time reversible model, nst = 6, default priors, and rates set to "invgamma". The substitution model parameters were unlinked across the three markers. The first 20% trees were discarded as 'burn-in'. MCMC convergence was assessed by examining the standard deviation of split frequencies (~0.005) and the potential scale reduction factor (PSRF = 1.0), as well as trace plots (Ronquist *et al.* 2009).

### Haplotype networks

Haplotype networks were built to explore relationships that might not be immediately observable in the phylogenetic tree and, thus, provide additional insights into the group's evolution. Sequence alignment was done in Geneious Prime via the MUSCLE plugin (Edgar 2004), as above. A minimum-spanning ($\varepsilon = 0$) haplotype network for COI, 16S and concatenated COI+16S alignments were constructed in PopART (v. 1.7; Leigh & Bryant 2015), using the median-joining algorithm (Bandelt *et al.* 1999).

For the COI-only haplotype analysis, we included many sequences in addition to the ones used in our phylogenetic analysis (Tables 1, 2), making use of the wealth of COI data of *A. arbustorum* sensu lato available on GenBank. Additional COI sequences came from the studies of Gittenberger *et al.* (2004), Haase (2003, 2013), Haase & Misof (2009), Bondareva *et al.* (2020), and Hausdorf & Walther (2021). However, not all their sequences were used. Bondareva *et al.* (2020) used mini barcodes in their study, which is a much shorter sequence; in our analysis, that results in plenty of 'missing data' points in the longer sequences that we and most previous studies used. Thus, we included only those sequences of Bondareva *et al.* (2020) that were relevant to our analysis according to our geographic coverage (Fig. 1). The datasets of Haase (2003, 2013) and Haase and Misof (2009) include sequences of multiple individuals collected in the exact same locality in a relatively small area. Including all of them would not bring much information to our analysis, so we simplified their datasets by leaving only one sequence per unique locality. The full list of sequences used here, alongside their locality data and GenBank accession numbers, can be found in the

**Table 1.** Specimens sequenced for the present study, with information on GenBank accession numbers, locality where the specimens were collected, and registration number of the voucher specimens in the respective collections (see Material and Methods). The asterisk (*) indicates specimens born in captivity (at UiT) from wild parents from the given locality. ITS2 sequences deposited in GenBank also contain the 3′ end of the 5.8S gene and the 5′ end of the 28S gene.

| Taxon | Country | Locality | GenBank accession numbers | | | Voucher code |
|---|---|---|---|---|---|---|
| | | | COI | 16S | ITS2 | |
| *arbustorum* | Austria | Carinthia, Mallnitz, Museum | PZ151373 | PZ151661 | PZ151460 | http://id.luomus.fi/HT.45153 |
| *arbustorum* | Austria | Kärnten, Gailtaler Alpen, Straße Bad Bleiburg | PZ151378 | PZ151613 | PZ151547 | NHMW ZOO-MO-109000-AL-732 |
| *arbustorum* | Austria | Kärnten, Spital an der Drau, Nockberge | PZ151369 | PZ151612 | PZ151466 | NHMW ZOO-MO-110425-ABOL-300 |
| *arbustorum* | Austria | Niederösterreich, Göller, Turmmauer | PZ151405 | PZ151611 | PZ151453 | NHMW ZOO-MO-103527 |
| *arbustorum* | Austria | Niederösterreich, Mödling, Wienerwald, Gruberau | PZ151371 | PZ151615 | PZ151550 | NHMW ZOO-MO-109000-AL-1551 |
| *arbustorum* | Austria | Salzburg, Saalbach, Kohlmaisalm, Bachbett | PZ151404 | PZ151607 | PZ157621 | NHMW ZOO-MO-79115 |
| *arbustorum* | Austria | Salzburg, Salzburg, Hochkönig Straße kurz nach Mühlbach | PZ151403 | PZ151605 | PZ151544 | NHMW ZOO-MO-74276 |
| *arbustorum* | Austria | Steiermark, Veitsch Aufgang von Sattel Niederalpl | PZ151376 | PZ151610 | PZ151545 | NHMW ZOO-MO-90398 |
| *arbustorum* | Austria | Tirol, Sankt Johann | PZ151367 | PZ151606 | PZ151472 | NHMW ZOO-MO-78273 |
| *arbustorum* | Austria | Tirol, Stripsenjoch, Wilder Kaiser | PZ151368 | PZ151608 | PZ151469 | NHMW ZOO-MO-79138 |
| *arbustorum* | Austria | Vienna, Vienna, Toter Grund (Donauinsel) | PZ151377 | PZ151622 | PZ151465 | NHMW ZOO-MO-101212 |
| *arbustorum* | Austria | Vorarlberg, Bregenzerwald, Kanisfluh | PZ151370 | PZ151614 | PZ151548 | NHMW ZOO-MO-109000-AL-990 |
| *arbustorum* | Austria | Vorarlberg, Rimsbach, Bregenzerwald | PZ151379 | PZ151620 | PZ151549 | NHMW ZOO-MO-109000-AL-1265 |
| *arbustorum* | Canada | New Brunswick, Saint John, Irving Nature Park | PZ151287 | PZ151562 | PZ151476 | http://id.luomus.fi/HT.47176 |
| *arbustorum* | Canada | New Brunswick, Saint John, Irving Nature Park | PZ151288 | PZ151563 | PZ151457 | http://id.luomus.fi/HT.47176 |
| *arbustorum* | Czechia | Brumov-Bylnice, Bylnička | PZ151324 | PZ151672 | PZ151519 | http://id.luomus.fi/HT.45993 |
| *arbustorum* | Denmark | Copenhagen, Fælledparken | PZ151289 | PZ151564 | PZ151477 | NHMD 1769507 |
| *arbustorum* | Denmark | Stevns, Gjorslev Forest, Skæppelund | PZ151386 | PZ151565 | PZ151458 | NHMD 1769580 |
| *arbustorum* | Denmark | Stevns, near Søholm | PZ151290 | PZ151566 | PZ151473 | NHMD 1769581 |
| *arbustorum* | Estonia | Haapsalu linn | PZ151362 | PZ151599 | PZ151538 | TAMZ 0270103 |
| *arbustorum* | Estonia | Hiiumaa vald | PZ151365 | PZ151602 | PZ151541 | TAMZ 0270112 |
| *arbustorum* | Estonia | Mulgi vald | PZ151401 | PZ151598 | PZ151537 | TAMZ 0270095 |
| *arbustorum* | Estonia | Otepää vald | PZ151363 | PZ151600 | PZ151539 | TAMZ 0270108 |
| *arbustorum* | Estonia | Pärnu, Kanaküla | PZ151315 | PZ151658 | PZ151507 | http://id.luomus.fi/HT.44730 |
| *arbustorum* | Estonia | Rapla vald | PZ151364 | PZ151601 | PZ151540 | TAMZ 0270109 |
| *arbustorum* | Estonia | Rõuge vald | PZ151402 | PZ151604 | PZ151543 | TAMZ 0270118 |
| *arbustorum* | Estonia | Toila vald | PZ151366 | PZ151603 | PZ151542 | TAMZ 0270113 |
| *arbustorum* | Finland | Lappi, Kilpisjärvi | — | PZ151624 | PZ157609 | http://id.luomus.fi/HT.47617 |
| *arbustorum* | Finland | North Savo, Kuopio | PZ151392 | PZ151589 | PZ151501 | KUO SML.633 |
| *arbustorum* | Finland | North Savo, Kuopio | PZ151393 | PZ151590 | PZ157610 | KUO SML.634 |
| *arbustorum* | Finland | Pirkanmaa, Tampere, Teisko, Viitapohjantie | PZ151316 | PZ151660 | PZ151509 | http://id.luomus.fi/HT.44951 |
| *arbustorum* | Finland | Uusimaa, Askola | PZ151308 | PZ151647 | PZ157611 | http://id.luomus.fi/HLA.20764 |
| *arbustorum* | Finland | Uusimaa, Espoo, Purotie | PZ151309 | PZ151648 | PZ151503 | http://id.luomus.fi/HLA.44795 |
| *arbustorum* | Finland | Uusimaa, Helsinki, Jollas | PZ151312 | PZ151655 | PZ151505 | http://id.luomus.fi/HLA.135494 |
| *arbustorum* | Finland | Uusimaa, Helsinki, Kurkimoisio | PZ151311 | PZ151654 | PZ151504 | http://id.luomus.fi/HLA.135403 |
| *arbustorum* | Finland | Uusimaa, Helsinki, Tuomarinkylä | PZ151313 | PZ151656 | PZ151506 | http://id.luomus.fi/HLA.135503 |
| *arbustorum* | Finland | Uusimaa, Porvoo, Pappilanmäki | PZ151329 | — | — | http://id.luomus.fi/KL.2009 |
| *arbustorum* | Finland | Uusimaa, Vantaa, Vaskipelto | PZ151310 | PZ151653 | — | http://id.luomus.fi/HLA.135377 |

**Table 1.** Continued.

| Taxon | Country | Locality | GenBank accession numbers | | | Voucher code |
|---|---|---|---|---|---|---|
| | | | COI | 16S | ITS2 | |
| *arbustorum* | Finland | Åland, Mariehamn, Östra Ytternäs | PZ151344 | PZ151619 | — | http://id.luomus.fi/KL.2051 |
| *arbustorum* | Finland | Åland, Sund | PZ151330 | PZ151625 | PZ157614 | http://id.luomus.fi/KL.2030 |
| *arbustorum* | France | Aine, Hirson, Blangy | PZ151349 | PZ151639 | PZ151528 | RMNH.5006705 |
| *arbustorum* | France | Bourgogne-Franche-Comté, Myennes, banks of the Loire | PZ151355 | PZ151621 | PZ151534 | MNHN-IM-2019-44202 |
| *arbustorum* | France | Bourgogne-Franche-Comté, Myennes, banks of the Loire | PZ151356 | PZ151647 | PZ151463 | MNHN-IM-2019-44203 |
| *arbustorum* | France | Bourgogne-Franche-Comté, Saint-Claude | PZ151399 | PZ151648 | PZ151464 | MNHN-IM-2019-44206 |
| *arbustorum* | France | Bourgogne-Franche-Comté, Saint-Claude | PZ151375 | PZ151649 | PZ151535 | MNHN-IM-2019-44207 |
| *arbustorum* | France | Doubs, Consolation | PZ151348 | PZ151635 | PZ157616 | RMNH.MOL.330341.b |
| *arbustorum* | France | Île-de-France, Montigny-sur-Loing | PZ151374 | PZ151646 | PZ151533 | MNHN-IM-2013-77899 |
| *arbustorum* | France | Savoie, Albertville, ca. 8 km S of town | — | PZ151636 | PZ151526 | RMNH.MOL.330355.b |
| *arbustorum* | Germany | Baden-Württemberg, Backnang, Maubachtal | PZ151325 | PZ151673 | — | http://id.luomus.fi/HT.46416 |
| *arbustorum* | Germany | Berlin, Berlin, Billerbecker Weg | PZ151372 | PZ151659 | PZ157612 | http://id.luomus.fi/HT.44869 |
| *arbustorum* | Germany | Berlin, Humboldt Flakbunker | PZ151286 | PZ151559 | PZ151474 | MZB 2008-0069-A |
| *arbustorum* | Germany | Berlin, Humboldt Flakbunker | PZ151384 | PZ151560 | PZ157607 | MZB 2008-0069-B |
| *arbustorum* | Italy | Veneto, Cortina d'Ampezzo, Pecol, Gavon Picol | PZ151318 | PZ151663 | PZ157613 | http://id.luomus.fi/HT.45155 |
| *arbustorum* | Latvia | Riga, Līči, Mazā Jugla river floodplain | PZ151320 | PZ151667 | PZ151514 | http://id.luomus.fi/HT.45602 |
| *arbustorum* | Netherlands | Flevoland, Leystad, Oostvaarderplassen | PZ151333 | PZ151631 | PZ157615 | http://id.luomus.fi/HT.47616 |
| *arbustorum* | Netherlands | Gelderland, Wageningen, Bornsesteeg | PZ151396 | PZ151637 | PZ151527 | RMNH.MOL.330408.b |
| *arbustorum* | Norway | Nordland, Rana, SW Moen - S Litl-Nilsmobekken | PZ151304 | PZ151586 | PZ151494 | http://id.luomus.fi/HT.46896 |
| *arbustorum* | Norway | Nordland, Værøy, Sandtjønna | PZ151305 | PZ151587 | PZ151495 | http://id.luomus.fi/HT.46898 |
| *arbustorum* | Norway | Rogaland, Finnøy, Marmorplassen-Saltstut | PZ151302 | PZ151583 | PZ151491 | http://id.luomus.fi/HT.46876 |
| *arbustorum* | Norway | Troms og Finnmark, , Nordreisa, Gjøvarden SW | PZ151303 | PZ151585 | PZ151493 | http://id.luomus.fi/HT.46877 |
| *arbustorum* | Norway | Troms og Finnmark, Tromsø* | PZ151318 | PZ151665 | PZ151512 | http://id.luomus.fi/HT.45157 |
| *arbustorum* | Norway | Troms og Finnmark, Tromsø* | PZ151394 | PZ151666 | PZ151513 | http://id.luomus.fi/HT.45158 |
| *arbustorum* | Norway | Trøndelag, Trondheim | PZ151351 | PZ151642 | PZ157619 | NTNU-VM-WET-46375 |
| *arbustorum* | Norway | Trøndelag, Trondheim | PZ151352 | PZ151643 | PZ151530 | NTNU-VM-WET-46375 |
| *arbustorum* | Norway | Trøndelag, Trondheim, Bakkaunet | PZ151314 | PZ151657 | PZ151507 | http://id.luomus.fi/HT.44616 |
| *arbustorum* | Norway | Trøndelag, Trondheim, Dalen Hageby | PZ151353 | PZ151644 | PZ151531 | NTNU-VM-WET-46376 |
| *arbustorum* | Norway | Trøndelag, Trondheim, Dalen Hageby | PZ151354 | PZ151645 | PZ151532 | NTNU-VM-WET-46376 |
| *arbustorum* | Norway | Vestland, Ullensvang, Ullensvang | PZ151391 | PZ151584 | PZ151492 | http://id.luomus.fi/HT.46878 |
| *arbustorum* | Norway | Østlandet, Bærum, Hagabråten | PZ151306 | PZ151588 | PZ151496 | http://id.luomus.fi/HT.46897 |
| *arbustorum* | Norway | Østlandet, Oslo, Ekeberg* | PZ151395 | PZ151676 | PZ151521 | http://id.luomus.fi/HT.46816 |
| *arbustorum* | Norway | Østlandet, Oslo, Ekeberg* | PZ151328 | PZ151677 | PZ151522 | http://id.luomus.fi/HT.46817 |
| *arbustorum* | Romania | Cheile Tătarului | PZ151400 | PZ151596 | PZ151468 | GAMNH#5 |
| *arbustorum* | Romania | Cheile Tătarului | PZ151361 | PZ151597 | PZ151536 | GAMNH#6 |
| *arbustorum* | Romania | Ic Ponor, Cheile Somesului Cald | PZ151359 | PZ151594 | PZ151470 | GAMNH#3 |
| *arbustorum* | Romania | Prahova, Buşteni, Valea Cerbului | PZ151357 | PZ151592 | PZ151467 | GAMNH#1 |
| *arbustorum* | Romania | Rodna Mountains | PZ151358 | PZ151593 | PZ157620 | GAMNH#2 |
| *arbustorum* | Romania | Stanciu Valley, Cascada Valul Miresei | PZ151360 | PZ151595 | PZ151471 | GAMNH#4 |
| *arbustorum* | Russia | Karelia, Martsialnye Vody | PZ151347 | PZ151634 | PZ151462 | http://id.luomus.fi/HT.47177 |

**Table 1.** Continued.

| Taxon | Country | Locality | GenBank accession numbers | | | Voucher code |
|---|---|---|---|---|---|---|
| | | | COI | 16S | ITS2 | |
| *arbustorum* | Russia | Saint Petersburg, Saint Petersburg, Moskovskiy Avenue | PZ151345 | PZ151632 | PZ151523 | http://id.luomus.fi/HT.47178 |
| *arbustorum* | Russia | Saint Petersburg, Saint Petersburg, Peterhof, Sergievka Park | PZ151346 | PZ151633 | PZ151524 | http://id.luomus.fi/HT.47179 |
| *arbustorum* | Scotland | East Lothian, Haddington | PZ151398 | PZ151640 | PZ151529 | NMS Z.2024.89.1 |
| *arbustorum* | Scotland | East Lothian, Pencaitland | PZ151350 | PZ151641 | PZ157618 | NMS Z.2024.89.2 |
| *arbustorum* | Sweden | Lycksele Lappmark, , Holme | — | PZ151591 | PZ151502 | MZLU L962/6525 |
| *arbustorum* | Sweden | Värmland, Älgå Parish | PZ151327 | PZ151675 | PZ151461 | http://id.luomus.fi/HT.46537 |
| *arbustorum* | Sweden | Västerbotten, Umeå, Holmsund, Sahakallio | PZ151331 | PZ151629 | — | http://id.luomus.fi/KN.13800 |
| *arbustorum* | Sweden | Västergötland, Kinnekulle, Madelpiana Parish | PZ151326 | PZ151674 | PZ151520 | http://id.luomus.fi/HT.46536 |
| *canigonensis* | Spain | Catalonia, Queralbs, Bastiments peak | PZ151385 | PZ151561 | PZ151475 | MZB 2018-0556 |
| *chamaeleon* | Slovenia | Bohinj, Stara Fužina, Rudno Polje, below Debeli peak | PZ151321 | PZ151669 | PZ151515 | http://id.luomus.fi/HT.45887 |
| *pseudorudis* | Iceland | Akranes (Smiðjuvellir), Borg | PZ151291 | PZ151568 | PZ151478 | IINR 44837 |
| *pseudorudis* | Iceland | Akureyri (Heiðarlundur) | PZ151292 | PZ151569 | PZ151479 | IINR 47991 |
| *pseudorudis* | Iceland | Akureyri (Smáratún) | PZ151300 | PZ151579 | PZ151487 | IINR 114527 |
| *pseudorudis* | Iceland | Austurland, Egilsstaðir, Þjóðvegur Bridge | PZ151317 | PZ151662 | PZ151510 | http://id.luomus.fi/HT.45154 |
| *pseudorudis* | Iceland | Austurland, Hlíðarvegur | PZ151323 | PZ151671 | PZ151518 | http://id.luomus.fi/HT.45991 |
| *pseudorudis* | Iceland | Einifell, Stafholtstungum, Mýr | PZ151390 | PZ151581 | PZ151489 | IINR 114548 |
| *pseudorudis* | Iceland | Gunnarsholt, Rangárvöllum, Rang | PZ151298 | PZ151577 | PZ151486 | IINR 68063 |
| *pseudorudis* | Iceland | Hveragerði (Heiðmörk), Árn | PZ151294 | PZ151572 | PZ151481 | IINR 53441 |
| *pseudorudis* | Iceland | Mógilsá, Kjalarnesi, Kjós | PZ151301 | PZ151582 | PZ151490 | IINR 114549 |
| *pseudorudis* | Iceland | Mógilsá, Kjalarnesi, Kjós | PZ151295 | PZ151573 | PZ151482 | IINR 56789 |
| *pseudorudis* | Iceland | Reyðarfjörður, S-Múl. | PZ151389 | PZ151580 | PZ151488 | IINR 114547 |
| *pseudorudis* | Iceland | Reykholt (Skógarstígur), Reykholtsdal, Borg | PZ151299 | PZ151578 | PZ157608 | IINR 114503 |
| *pseudorudis* | Iceland | Reykjavík (Fossvogur) | PZ151296 | PZ151575 | PZ151484 | IINR 65910 |
| *pseudorudis* | Iceland | Reykjavík (Gufuneskirkjugarður) | PZ151387 | PZ151570 | PZ151480 | IINR 52158 |
| *pseudorudis* | Iceland | Seltjarnarnes (Lindarbraut) | PZ151297 | PZ151576 | PZ151485 | IINR 68051 |
| *pseudorudis* | Iceland | Vorsabær, Flóa, Selfoss | PZ151293 | PZ151571 | PZ151459 | IINR 52729 |
| *pseudorudis* | Iceland | Ytri-Kambar, Djúpavogi, S-Múl | PZ151388 | PZ151574 | PZ151483 | IINR 56845 |
| *stenzii* | Italy | Trentino-Alto Adige, Corvara, Colfoaco, Passo Gardena | PZ151283 | PZ151617 | — | http://id.luomus.fi/HT.45979 |
| *stenzii* | Italy | Trentino-Alto Adige, Saltria, Forcella Denti di Terrarossa | PZ151285 | PZ151668 | PZ151516 | http://id.luomus.fi/HT.45978 |
| *stenzii* | Italy | Trentino-Alto Adige, Selva di Val Gardena, Val de Chedul | PZ151282 | PZ151664 | PZ151511 | http://id.luomus.fi/HT.45156 |
| *styriaca* | Austria | Oberösterreich, Gmunden, Großer Priel, Großer Priel Gipfel | PZ151380 | PZ151638 | PZ151551 | NHMW ZOO-MO-109000-AL-1554 |
| *styriaca* | Austria | Oberösterreich, Gmunden, Höllengebirge, Großer Steinkogel | PZ151406 | PZ151618 | PZ151546 | NHMW ZOO-MO-109000-AL-499 |
| *styriaca* | Austria | Steiermark, Gesäuse, Neuburg Alm | PZ151284 | PZ151609 | PZ151452 | NHMW ZOO-MO-89970 |
| *styriaca* | Austria | Steiermark, Johnsbach | PZ151397 | PZ151623 | PZ157617 | RMNH.5006704 |
| *xatartii* | Spain | Catalonia, Coll de Nou Fonts, Pod Coll de Noufonts | PZ151322 | PZ151670 | PZ151517 | http://id.luomus.fi/HT.45989 |

**Table 2.** Further genetic sequences used in the phylogenetic analysis, with information on GenBank registration numbers, provenance of the sampled animals, voucher information, and reference to the original publications.

| Taxon | Country | Locality | GenBank accession numbers | | | Voucher code | Source |
|---|---|---|---|---|---|---|---|
| | | | COI | 16S | ITS2 | | |
| *arbustorum* | Austria | Oberösterreich, Hallstatt | AF296925 | JX156945 | — | ST 440 | Gittenberger *et al.* 2004 ; Groenenberg *et al.* 2016 |
| *arbustorum* | Austria | Kärnten, Trögern, 11.6 km W of Bad Eisenkappel | KJ095033 | KJ095080 | — | ST 4526 | Groenenberg *et al.* 2016 |
| *arbustorum* | England | Derbyshire | AF296946 | — | AY014136 | EG735 / — | Gittenberger *et al.* 2004 ; Wade *et al.* 2001 |
| *arbustorum* | France | Aude, Gorges du Rébenty | AF296945 | JF717810 | — | ST 726 | Gittenberger *et al.* 2004 ; Groenenberg *et al.* 2016 |
| *arbustorum* | Germany | Pleß forest near Eddigehausen, Wittenberg (mountain) | KR705022 | KR704982 | KR705059 | MN 2552-Hel-036 | Neiber & Hausdorf 2015 |
| *arbustorum* | Netherlands | Zuid-Holland, Hoogmade, banks of the Wijde Aa river | AF296924 | JX156946 | — | ST 144 | Gittenberger *et al.* 2004 ; Groenenberg *et al.* 2016 |
| *arbustorum* | Netherlands | Zuid-Holland, Hoogmade, banks of the Wijde Aa river | AF296940 | JF717809 | — | ST 603 | Gittenberger *et al.* 2004 ; Groenenberg *et al.* 2016 |
| *arbustorum* | Slovenia | Kamniske Alpe, S-slope Grintavec | KJ095035 | KJ095082 | — | ST 4519 | Groenenberg *et al.* 2016 |
| *arbustorum* | Sweden | Stockholms Län, S of Uppsala in forest | AF538294 | JX156947 | — | ST 1239 | Gittenberger *et al.* 2004 ; Groenenberg *et al.* 2016 |
| *canigonensis* | France | Aude, Massif du Canigou, Pla Guillem | AF538288 | JX156948 | — | ST 1054 | Gittenberger *et al.* 2004 ; Groenenberg *et al.* 2016 |
| *chamaeleon* | Austria | Kärnten, Karawanken, Bärental, Johannsenruhe | AF296994 | JX156952 | — | ST 839 | Gittenberger *et al.* 2004; Groenenberg *et al.* 2016 |
| *doriae* | Italy | Piemonte, Biella, Monte Mucrone, E of Bocchetta del Lago | MW633242 | — | — | ZMH 143668-5576 | Hausdorf & Walther 2021 |
| *repellini* | France | Hautes-Alpes | AF296948 | — | — | FPW703 | Gittenberger *et al.* 2004 |
| *repellini* | France | Hautes-Alpes, Pic des Chalances, Queyras | AF296947 | — | — | ST 361 | Groenenberg *et al.* 2016 |
| *schmidtii* | Austria | Kärnten, Karawanken, S-side of Natschacher Sattel (N of Bielschitza) | AF538286 | JX156953 | — | ST 725 | Gittenberger *et al.* 2004; Groenenberg *et al.* 2016 |
| *schmidtii* | Slovenia | Kamnisko-Savinjske Alps | KF596872 | KF596825 | — | NHMW 90401 | Cadahía *et al.* 2014 |
| *styriaca* | Austria | Oberösterreich, Johnsbach, 2.8 km N of Hesshütte | KJ095034 | KJ095081 | — | ST 4528 | Groenenberg *et al.* 2016 |
| *vareliensis* | France | Alpes-Maritimes, near D64 to St.Etienne de Tinée (W of Bouseyas) | JX156780 | JX156950 | — | ST 1631 | Groenenberg *et al.* 2016 |
| *vareliensis* | France | Alpes-Maritimes, near D64 to St.Etienne de Tinée (W of Bouseyas) | JX156781 | — | — | ST 1632 | Groenenberg *et al.* 2016 |
| *xatartii* | Spain | Catalunya, Ripollès, 3 km NE of Núria | AF296993 | JX156951 | — | ST 145 | Gittenberger *et al.* 2004; Groenenberg *et al.* 2016 |

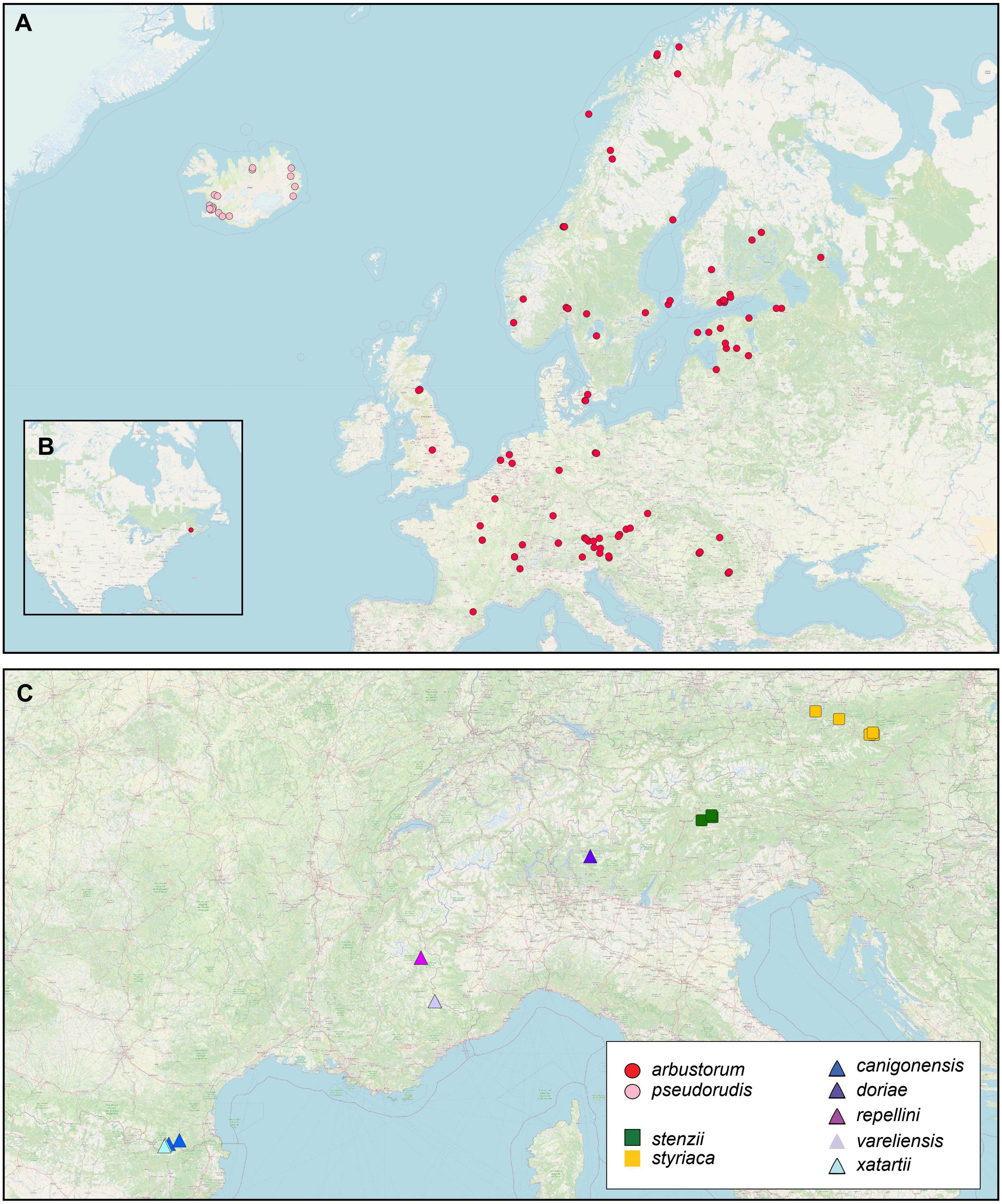


**Figure 1.** Map showing the origin of sequenced specimens and GenBank data used in the phylogenetic analysis (outgroup not shown). Base map source: Open Street Map (public domain). **A,** *Arianta arbustorum arbustorum*; synonymized Icelandic *A. a. pseudorudis* is shown in a different colour. **B,** inset showing the introduced population of *A. arbustorum* in Canada. **C,** *A. canigonensis* and Alpine subspecies of *A. arbustorum*.

Supplementary File (Table S2).

The 16S haplotype analysis was done using the same sequences as the phylogeny, as there was no additional data available locality-wise (Tables 1, 2). Similarly, the concatenated COI+16S analysis was done with the same sequences as the phylogenetic analysis, though in this case, we removed from the analysis the four specimens that were missing one of the markers (Tables 1, 2).

### Distribution maps

Maps were created with QGIS v. 3.30 (QGIS 2026) using Open Street Map (OSM) as the base layer map for plotting the points.

To illustrate the distribution of *A. arbustorum*, focusing on the Nordic region, distribution data was obtained from GBIF on 16 March 2025 (download file identifier: doi: 10.15468/dl.fn35fp). The raw GBIF data were cleaned by downloading only georeferenced data; removing records with "absent" status; removing records that are based on fossil specimens; removing machine observation records; removing records with uncertainty greater than 50 km.

A note of caution is needed when using GBIF data, which is an automatic aggregator that unselectively draws data from primary sources such as museum collection databases, online community science platforms (e.g. iNaturalist), and national observation databases (e.g. LAJI, Artsdatabanken). Variation in shell morphology and coloration of *A. arbustorum* (both adult and juveniles) often confounds identification and the species can be mistaken for other helicoids, notably with common species like *Cepaea hortensis*, *Cepaea nemoralis*, *Fruticicola fruticum*, and even with snails of different size categories such as *Perforatella incarnata* and *Cornu aspersum*. While these species are quite different in external morphology, such confusion is not uncommon, particularly with juvenile specimens; anecdotally, around 3–5% of cases had wrong identifications on iNaturalist and also among specimens deposited in natural history collections. The majority of records from observation databases other than iNaturalist lack photographs or voucher specimens and thus, cannot be assessed, though a similar error rate could be expected. As *A. arbustorum* is a well-known and conspicuous species in Europe, this is likely not a serious problem. Still, the distribution map presented here is only meant to illustrate the general distribution pattern of *A. arbustorum* and not to be a completely accurate representation of it; in particular, records from the edge of the species' distribution should be taken with a grain of salt.

## RESULTS

### Phylogenetic analysis

The multi-marker phylogenetic analysis comprised 133 terminals, and the concatenated sequence was 1587 bp long (COI = 658, 16S = 425, ITS2 = 504).

The resulting tree (shown in two parts in Figs 2 and 3), recovered *Arianta schmidtii* (Rossmässler, 1836) as the sister to *A. arbustorum* "sensu lato" (i.e. including *A. xatartii*). Several clades were recovered inside the latter and we will explore each in order of branching (i.e. from bottom to top of Fig. 2).

The first clade (Fig. 2) is made of snails from the Pyrenees (both French and Spanish) and the Western Alps (France and Italy) (posterior probability, PP = 1); it is the sister group of the remainder *A. arbustorum* (Fig. 1). Within this clade, the subspecies *doriae* (from Italy) is sister to the rest (PP = 0.99), which are divided in two branches: one French Alpine (PP = 1) including subspecies *repellini* and *vareliensis* (each PP = 1); and another from the Pyrenees (PP = 1), including French subspecies *canigonensis* (PP = 1) and Spanish species *A. xatartii* (PP = 0.98).

The clades of *A. arbustorum* sensu stricto are designated by numbers of 1 to 4 to make discussion easier (Fig. 2). The *A. arbustorum* Clade 1 (PP = 1) is made up of eastern Alpine snails and is sister to nominate *A. arbustorum* (Clades 2–4, Fig. 2). It is divided in two branches: one Italian (PP = 1) representing subspecies *stenzii*; and another Austrian (PP = 0.86 on base, but higher support internally) representing subspecies *styriaca* but containing one individual identified as nominate *arbustorum* from the study by Groenenberg *et al.* (2016).

The nominate *A. arbustorum* clade has borderline strong support (PP = 0.94) and can be divided in Clades 2 to 4 (Fig. 2). Clade 2 (Fig. 2) has moderate support (PP = 0.93), likely due to the basalmost English representative, which lacks information for the 16S marker (Table 2). Its more internal trichotomous clade has strong support (PP = 1) and contains specimens from France, central Germany, Austria, Romania, and Slovenia; the latter two countries include forms traditionally considered as subspecies *picea*. Clade 2 is sister to a clade with low support (PP = 0.66) containing Clades 3 and 4; the low support means that a different arrangement of these clades is not unlikely.

Clade 3 has moderate support (PP = 0.93) and is composed of two main sub-clades with strong (PP = 1) and moderate (PP = 0.92) support (Fig. 2). The latter contains specimens from Italy, Czechia, and Romania, as well as specimens from Austria, both Alpine and "lowland", including

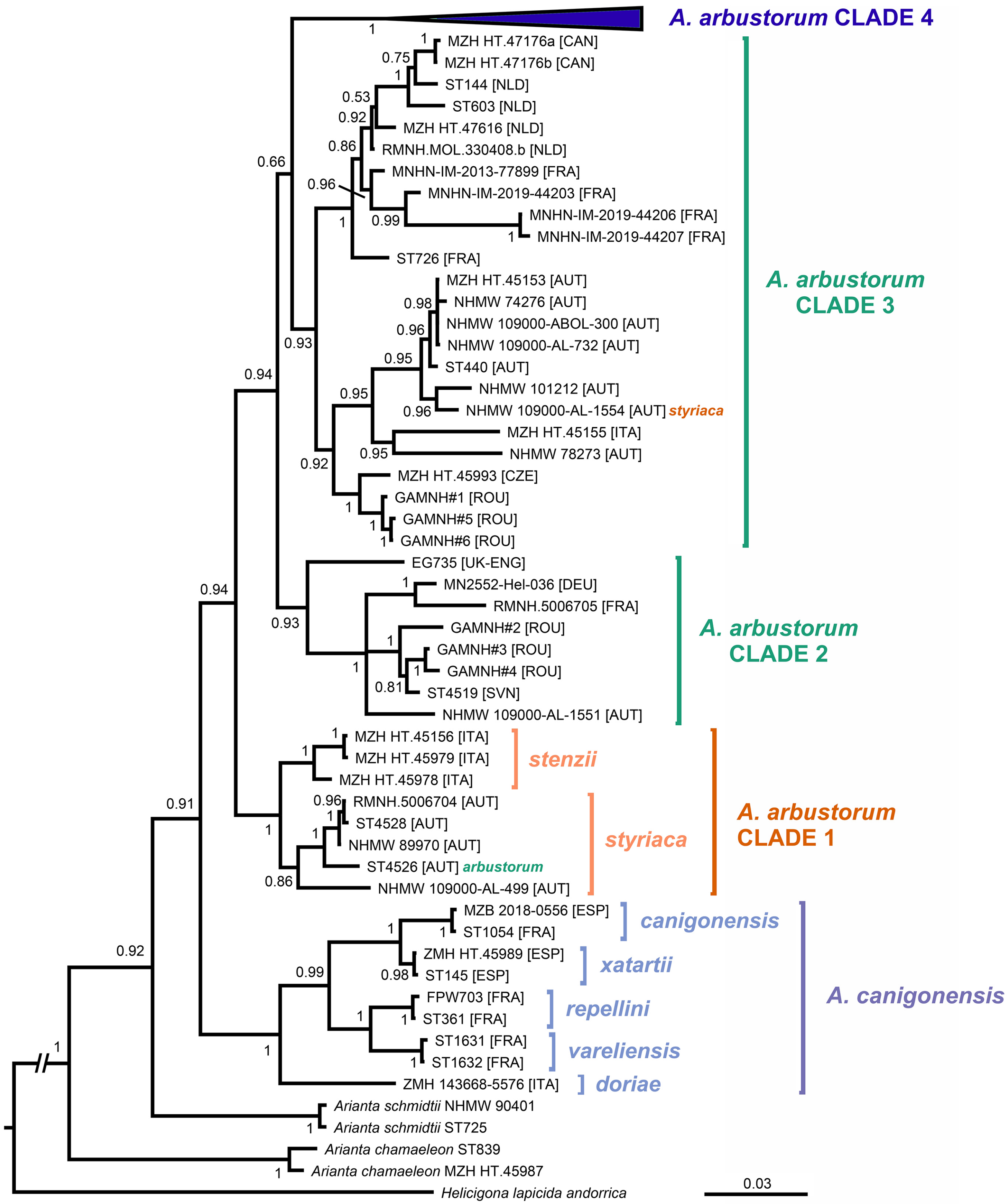


**Figure 2.** Bayesian inference phylogenetic tree (50% majority-rule consensus) based on the three concatenated markers (COI, 16S, ITS2). The species-level clades are shown in different colours and the crown "Baltic/Nordic" *A. arbustorum* Clade 4 is collapsed (see Fig. 3). Posterior probabilities are shown on nodes. Scale bar represents substitutions per site. See Tables 1 and 2 for more specific information on each terminal/specimen.

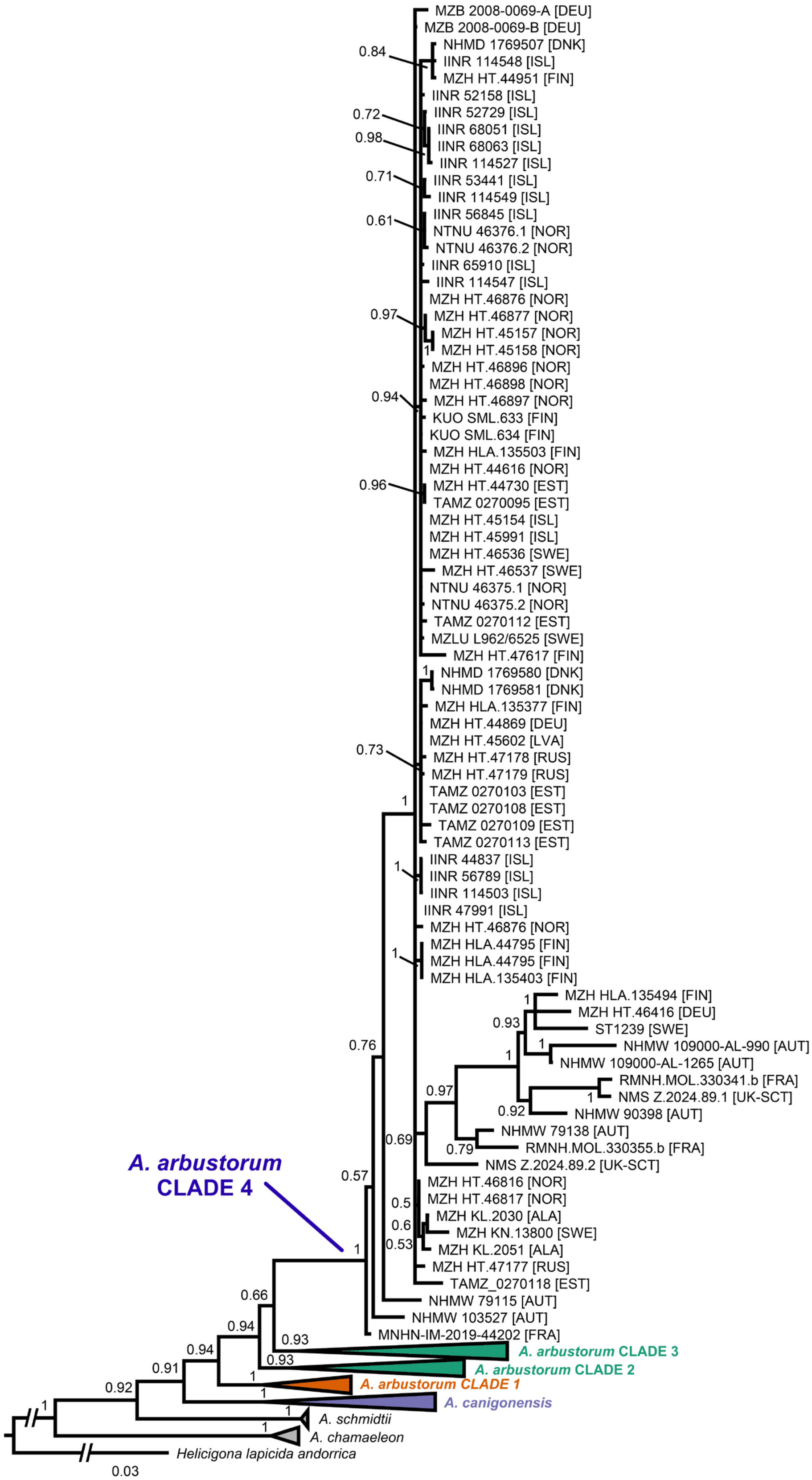


**Figure 3.** The crown "Baltic/Nordic" *A. arbustorum* Clade 4 from Fig. 2. Other clades are shown collapsed. Posterior probabilities are shown on nodes. Scale bar represents substitutions per site.

one specimen typically identified as *styriaca* based on its locality of occurrence in the Alps (Großer Priel; cf. Haase 2003, 2013; Haase & Misof 2009) but genetically (comparing both mDNA and nDNA) akin to nominate *arbustorum*. The other sub-clade contains specimens from France and the Netherlands, as well as individuals from the population that was established in Canada; the latter are more closely related to specimens from the Netherlands. Clades 2 and 3 also contain specimens often referred to subspecies *alpicola* (typically from France) and *picea* (typically from Eastern Europe) in the literature (e.g. Gittenberger *et al.* 2004; Groenenberg *et al.* 2016; Hausdorf & Walther 2021).

Finally, Clade 4 has a strong support (PP = 1) and mostly represent the Baltic/Nordic populations (Fig. 3). The first isolate branches of this clade are from France and Austria and then there is a 12-fold polytomy (PP = 1) containing six isolated terminals from: Russia (Karelia), Estonia, southern Norway, Iceland, and northern Germany; three small sub-clades, one unsupported (PP = 0.5) with specimens from southern Norway, Sweden and Åland, one (PP = 1) exclusively Finnish, and one exclusively Icelandic; two medium-sized sub-clades (see below); and one large sub-clade. The first of the medium-sized clades has low support (P = 0.69) and high internal distances between terminals, hinting that its position inside crown Clade 3 might be erroneous and an artifact introduced by the ITS2 marker (this clade is more basally positioned in the mitochondrial DNA only tree; Suppl. File Fig. S1). It contains specimens from France, Austria, Scotland, Germany, Sweden, and Finland. The other medium-sized clade has low support (PP = 0.73) but is clearly Baltic in scope, containing specimens from Denmark, northern Germany, Latvia, Estonia, Russia (St. Petersburg), and southern Finland.

The large sub-clade has borderline strong support (PP = 0.94) and contains specimens mostly with virtually no genetic distance, coming from Denmark, Iceland, Norway, Sweden, Finland and Estonia. The specimens from Norway and Finland include individuals from the northernmost populations in Troms and Lapland. Notably, the specimens from Troms form a strongly supported (PP = 0.97) sub-clade with some genetic distance from the others.

The mitochondrial markers are discussed in greater detail in the following section. The non-coding ITS2 marker shows marked genetic differences between species: circa 85.5–88.5% identity between *xatartii*/*canigonensis* and both *stenzii*/*styriaca* and *arbustorum*; and 92.0–100% between *stenzii*/*styriaca* and *arbustorum*. Even so, by itself, it provided an uninformative tree, with large polytomies, which we consider to be an artefact of having too many terminals from the Baltic/Nordic populations, which have little to no variation in the ITS2 marker, biasing the analysis. Still, the inclusion of the ITS2 marker (in comparison to the mitochondrial DNA only tree; Suppl. File Fig. S1) seems to have been important in solving the relationships within the non-Nordic *A. arbustorum* clades (especially in Clades 2 and 3); though it seemingly introduced a small artifact in the crown Clade 4, as mentioned above.

### Haplotype analysis

A total of 301 sequences was used in the COI analysis, 127 in the 16S analysis, and 108 in the concatenated COI+16S analysis. There are a few groupings of nodes/haplotypes that can be immediately recognized in the haplotype networks (Fig. 4, Suppl. File Figs S2, S3). First, two isolated groups represent the species-level clades formed by (1) *vareliensis* + *canigonensis* + *xatartii* (*doriae* and *repellini* were excluded in the concatenated analysis as there were no 16S data available), and (2) *stenzii* + *styriaca*. Nominate *A. arbustorum* has multiple groups: (1) Baltic/Nordic; (2) Alpine (Austria) (observable only in the COI network; Suppl. File Fig. S2); (3) and (4) two small eastern European groups (Romania/Czechia and Romania/Slovenia); (5) and (6) two Central European clades, one of each is more closely linked to the Eastern European groups (a large central network), while the other is closer to the Baltic/Nordic group (more isolated). There were no significant differences between COI, 16S, and concatenated analyses except for an Austrian Alpine *arbustorum* clade that is only identified as a distinct group in the COI network due to the larger number of sequences (COI data from the literature).

Similarly to what was observed in the phylogenetic analysis results described above: (1) specimens from England and Scotland belong to each of the two Central European haplotype groups; (2) specimens from Canada are close to those from the Netherlands; (3) Icelandic *pseudorudis* is included in, and thus indistinct, from the larger Baltic/Nordic *arbustorum* haplotype group. Furthermore, some new information can be gleaned from the haplotype analyses in comparison to the phylogenetic one: (1) the COI-only analysis was able to capture a larger distinction within the Baltic/Nordic group, more clearly separating the Baltic (e.g. Denmark, northern Germany, Estonia, Saint Petersburg) from the Nordic (Fennoscandia and Iceland); and (2) a Finnish specimen clustering with the central network of Central European specimens.

Finally, genetic distances of the COI barcoding markers across specimens are often used to indicate species-level taxa. While in many animal taxa a 3–4% threshold is often adopted, in stylommatophoran snails that "rule" cannot be

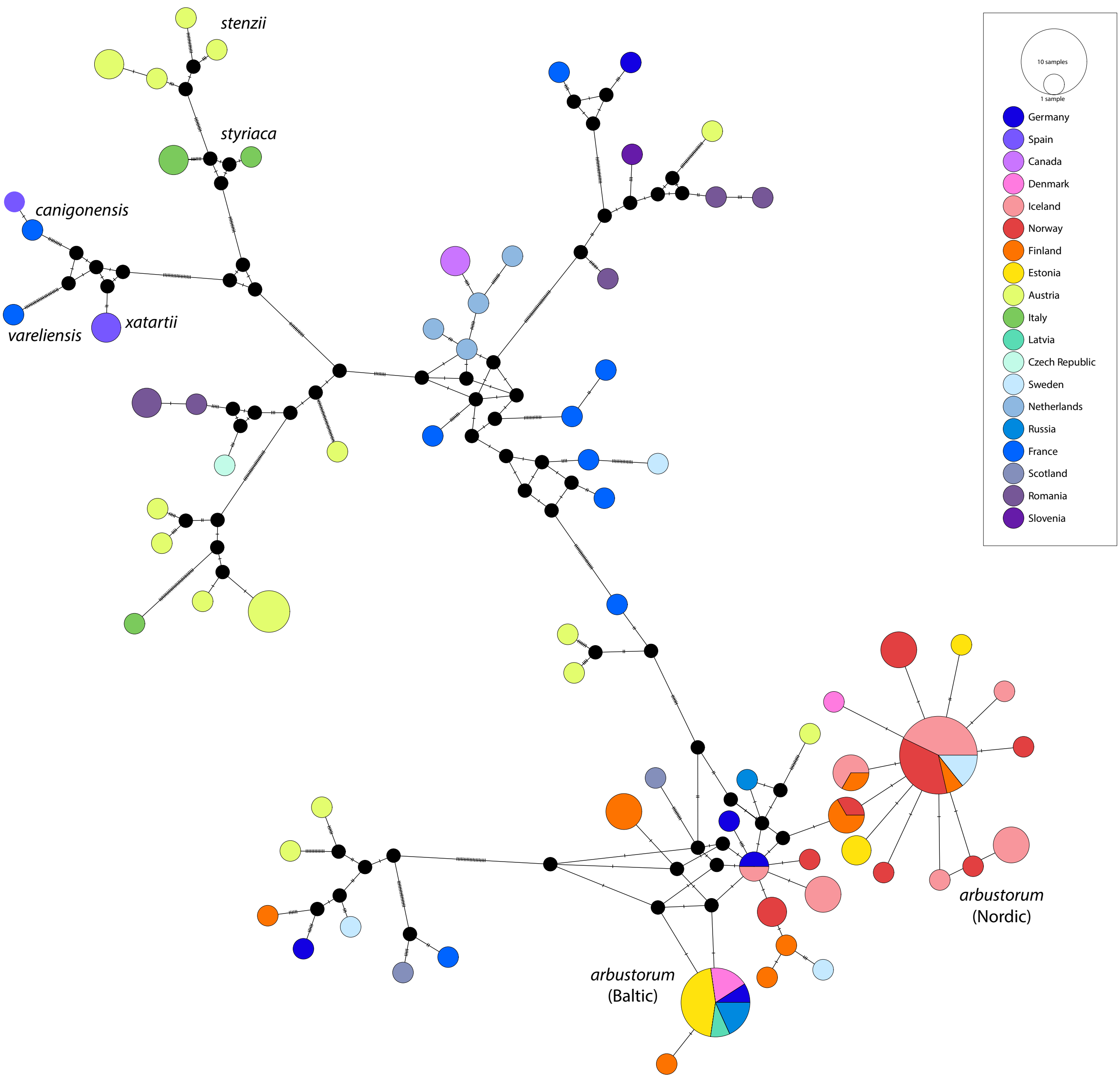


**Figure 4.** Haplotype network of concatenated mitochondrial markers COI and 16S, with colour scheme representing the specimen's country of origin.

applied, because differences might reach over 10% between populations of a single species (e.g. Davison *et al.* 2009), as it is easy for a mitochondrial lineage of slow-dispersing animals to form geographic clusters (e.g. Nekola *et al.* 2015). Such distances are reported here between all analysed subspecies taxa (Table 3), considering the 522 positions of the COI marker for which we had data for all specimens used in the phylogeny (excluding the short sequences of Bondareva *et al.* 2018). Sequence identity of COI goes from 93 to 98.5% between the subspecies of the *canigonensis* clade (*doriae* + *repellini* + *vareliensis* + *canigonensis* + *xatartii*); from 96.5 to 97% between the subspecies of Clade 1 (*stenzii* + *styriaca*) clade; and from 90.5 to 100% within the individuals belonging to the nominate *arbustorum* clade (Clades 2–4), in which the Baltic/Nordic specimens (Clade 4, including *pseudorudis*) show 99–100% identity among themselves. Sequence identity between the *canigonensis* clade and Clade 1 goes from 88 to 94%, and between each of them and *arbus-*

*torum* (Clades 2–4), from 88 to 92% and from 89 to 93%, respectively.

## Discussion

We conducted a phylogeographic analysis of *Arianta arbustorum* with samples covering nearly the species' entire distribution (except for some areas of eastern Europe) and including all currently accepted infraspecific taxa, with a particular focus on the Baltic and Nordic populations of the species. Our analysis builds upon the previous works of Gittenberger *et al.* (2004) and Hausdorf & Walther (2021), complementing their dataset with a much broader sampling from outside the Central European nucleus of the species' distribution. We have obtained similar results in part, as well as new insights into the involved taxa, which also allowed us to address some taxonomic issues.

As suggested by Hausdorf & Walther (2021) (but also visible in Gittenberger *et al.* 2004), the first clades to branch off ("basalmost" clades) represent (1) a western and (2) an eastern branch of Alpine forms (Fig. 2). The 'western clade', as named by Hausdorf & Walther (2021), contains the taxa from the Pyrenees (*canigonensis*, *xatartii*) and from the western Alps in France and Italy (*repellini*, *doriae*, *vareliensis*). The 'eastern clade' *sensu* Hausdorf & Walther (2021) contains the taxa from the eastern Alps in Italy and Austria (*stenzii*, *styriaca*).

The "western clade" is genetically (see also Table 3), morphologically (see discussion below), and geographically well defined, and no hybridisation with other forms has been reported (but see mentions of supposed intermediate forms by Gittenberger *et al.* 2004). Thus, we recognize it as a distinct species, *A. canigonensis* (the name has priority over *xatartii*; see below). The "eastern clade" is more complex; despite presenting considerable genetic distance from nominate *arbustorum* and being geographically isolated, there are various reports of hybridisation and introgression between *stenzii*/*styriaca* and nominate *arbustorum* (e.g. Baumgartner 1997; Gittenberger *et al.* 2004; Hausdorf & Walther 2021). Due to that, we maintain *stenzii* and *styriaca* as subspecies of *A. arbustorum* for now, until more studies are conducted to clarify this issue.

The nominate *arbustorum* clade of Gittenberger *et al.* (2004) and Hausdorf & Walther (2021) contained specimens from Central Europe, as well as (in the case of the latter study) a few specimens from England, Romania, and Slovenia. There were no representatives of the Baltic area or Nordic countries in those studies; thus, their *arbustorum* clade corresponds to our Clades 2 and 3 (Fig. 2). These clades also include forms that are typically assigned to *alpicola* and *picea* (see discussion below), which are spread throughout the tree and thus, are not genetically distinct from nominate *arbustorum*. It also includes one Austrian individual belonging to *styriaca*, which could signify hybridisation and introgression as previously reported (Gittenberger *et al.* 2004; Hausdorf & Walther 2021). Also, Clade 3 includes the introduced population in Canada.

Finally, our Clade 4 is well supported (Figs 2, 3) and represents a novel result; i.e. it was absent from the phylogenies of Gittenberger *et al.* (2004) and Hausdorf & Walther (2021). This newly recognized clade brings in valuable new information. While its "basalmost" branches consist in a few individuals from Central Europe, the crown clade contains representatives from all around the Baltic and Fennoscandia, namely: northern Germany, Denmark, Latvia, Estonia, Russia, Finland, Åland, Sweden, and Norway. It also contains all specimens from Iceland.

**Table 3.** COI sequence identity between subspecies-level taxa, with values rounded to closest 0.5% to facilitate visualization. Comparison is restricted to the 522 positions of the COI marker for which we had data for all specimens used in the phylogeny (also excluding the short sequences of Bondareva *et al.* 2018).

| Taxon | *canigonensis* | *xatartii* | *repellini* | *vareliensis* | *doriae* | *styriaca* | *stenzii* | *arbustorum* | *pseudorudis* |
|---|---|---|---|---|---|---|---|---|---|
| *canigonensis* | — | 98.5% | 94.5–95.0% | 94,00% | 93.0–93.5% | 92.0–92.5% | 93.5–94.0% | 88.5–91.5% | 89.5–90.0% |
| *xatartii* | 98.5% | — | 95.5% | 94.5% | 94.0% | 93.0% | 94.0% | 89.0–92.0% | 90.5% |
| *repellini* | 94.5–95.0% | 95.5% | — | 96.5% | 93.0% | 91.0–92.0% | 92.5% | 88.0–92.0% | 89.5–90.0% |
| *vareliensis* | 94.0% | 94.5% | 96.5% | — | 92.5% | 91.5–92.0% | 92.5–93.0% | 89.5–91.0% | 89.5–90.0% |
| *doriae* | 93.0–93.5% | 94.0% | 93.0% | 92.5% | — | 92.5–93.5% | 93.0% | 88.5–91.5% | 89.0–89.5% |
| *styriaca* | 92.0–92.5% | 93.0% | 91.0–92.0% | 91.5–92.0% | 92.5–93.5% | — | 96.5–97.0% | 89.5–91.0% | 89.5–90.0% |
| *stenzii* | 93.5–94.0% | 94.0% | 92.5% | 92.5–93.0% | 93.0% | 96.5–97.0% | — | 89.0–93.0% | 90.5–91.5% |
| *arbustorum* | 88.5–91.5% | 89.0–92.0% | 88.0–92.0% | 89.5–91.0% | 88.5–91.5% | 89.5–91.0% | 89.0–93.0% | — | 90.5–100% |
| *pseudorudis* | 89.5–90.0% | 90.5% | 89.5–90.0% | 89.5–90.0% | 89.0–89.5% | 89.5–90.0% | 90.5–91.5% | 90.5–100% | — |

Thus, Clade 4 contains all the Nordic forms, including the typical *arbustorum*, as we argue below, and the Iceland-endemic *pseudorudis*. It also evidences that the Central and Eastern European Clades 2 and 3 are "paraphyletic" in relation to Clade 4, with much more genetically distant terminals, showing that the populations in those regions are much older than the Baltic/Nordic ones. The structure of Clade 4 by itself (polytomy with short horizontal branches) and in relation to Clades 2 and 3 is typical of fringe populations, which represent the expanding borders of a species' distribution that only had a short period of divergence (e.g. Suzuki *et al.* 2016; Shimizu *et al.* 2018).

Our results have some taxonomic implications that we explore in more detail below, including a few modifications to the systematic classification of the studied taxa. Finally, we discuss in greater depth the Nordic populations of *A. arbustorum*.

### *Arianta canigonensis*

The "western clade" *sensu* Hausdorf & Walther (2021) containing populations from the Pyrenees and western Alps is recognized here as a distinct species, for which the oldest name available is *A. canigonensis*, described from the base of Canigou mountain (Boubée 1833). Three strongly supported subclades can be recognized in this group (Fig. 2), the Italian *doriae*, the French *repellini* + *vareliensis*, and the French/Spanish Pyrenean *canigonensis* + *xatartii*; each subclade forms a distributional cluster (Fig. 1). As the subspecific taxa named above represent clearly geographically isolated populations (Fig. 1; see also Hausdorf & Walther 2021) and have significant genetic differences (Table 3), they can be thus recognized as subspecies.

The members of the pair *canigonensis* and *xatartii* have low genetic difference between them (COI distinction is only 1.5%; Table 3) and proximate distribution in the Pyrenees. Conchological differences between them are relatively small, pertaining to more globular or discoid shells and a variability in the covering of the umbilicus. On the other hand, difference in COI between *repellini* and *vareliensis* amounts to 3.5% (Table 3); morphological differences are more pronounced between this species pair, and the populations are more distant and likely isolated from one another.

Nomenclaturally, *canigonensis* has priority over *xatartii*, resulting in the following four subspecies: *A. canigonensis canigonensis* (Boubée, 1833), *A. canigonensis doriae* (Paulucci, 1878) **comb. nov.**, *A. canigonensis repellini* (Reeve, 1852) **comb. nov.**, *A. canigonensis vareliensis* (Ripken & Falkner, 2000) **comb. nov.**, *A. canigonensis xatartii* (Farines, 1834) **comb. nov.**

It is interesting to note that *A. xatartii* has sometimes been treated as a distinct species from *A. arbustorum* in the literature (mostly in works from the Iberian Peninsula) but, curiously, *canigonensis* has always been treated as a synonym or subspecies of *A. arbustorum*, not of *A. xatartii* (e.g. Verdú *et al.* 2011; Cadevall & Orozco 2016). As expected from a biogeographic standpoint, here we show that these two taxa are closely related.

In general, *A. canigonensis canigonensis* and *A. canigonensis xatartii* have a rounder and more elevated shell (Fig. 5A), with an almost entirely covered umbilicus, of light brown to yellowish brown colour, with the spiral band just slightly darker than the base colour, with very few to no white "flecks". Boubée (1833) had already discussed such conchological differences, as well as the distinct habitat in the Pyrenees, as supporting evidence for his decision to describe *canigonensis* as a separate species from *A. arbustorum*. There are individuals with a more discoid shape, with a lower spire, and a larger, more open umbilicus (e.g. Cadevall & Orozco 2016), which is the same type of overall variation in shell shape observed in *A. arbustorum*. While *A. arbustorum* is typically darker and flecked, we can find individuals that are lighter in colour and have fewer to no flecks throughout the species' entire distribution (e.g. Grime & Blythe 1969; von Proschwitz *et al.* 2023).

*Arianta canigonensis doriae* is similar to nominate *canigonensis* in most regards (overall shell shape and size, closed umbilicus, lack of flecks), its shell is typically of a much darker tone of brown, albeit still with a low contrast difference between the base colour and the spiral band (see Hausdorf & Walther 2021). *Arianta canigonensis repellini* has typically more discoid shells and a partially open umbilicus, while *A. canigonensis vareliensis* has globular shells with a closed umbilicus (Fig. 5B). There is a report of intermediate forms between *arbustorum* and *repellini* occurring in the narrow contact zone of the two populations (Gittenberger *et al.* 2004), although these animals have not been studied in detail so far.

Finally, it is worthwhile noting that, while the Alps have long been considered a glacial refugium for snails, the importance of the Pyrenees as such has only been recently recognized (Horsák *et al.* 2025). *Arianta canigonensis* is interesting for having relict populations in both the Alps and the Pyrenees.

### The Pleistocene *gaillardi*

*Helix* (*Arianta*) *arbustorum* var. *gaillardi* Germain, 1912 is a fossil described from Pleistocene loess deposits in Île-Barbe, Lyon (Germain 1912). It has been later considered a subspecies of *A. arbustorum* and is currently noted as a *taxon inquirendum* (MolluscaBase Eds 2026).


**Figure 5.** *Arianta canigonensis*; scale bar = 5 mm. **A,** syntype of *Helix xatartii* Farines, 1834, RBINS MT.3560. **B,** syntype of *Helix repellini* Reeve, 1852, NHMUK 1953.1.19.355. **C,** holotype of *Helix* (*Arianta*) *arbustorum* var. *gaillardi* Germain, 1912, MDC 20402020.

The holotype (and single known specimen) of *gaillardi* has a more discoid shell, with a lower and step-like spire, a faint angulation on the body whorl immediately below the coloured spiral band, and a partially covered umbilicus (Fig. 5C). It is thus, much closer in shape to the French Alpine forms *repellini* and *vareliensis* than to *A. arbustorum* proper, though it is significantly larger than them. In later studies, Germain (1929) also considered this proximity to be the case and synonymized his *gaillardi* with *repellini*, though this has not been widely noted or adopted by later literature.

Thus, considering the new classification scheme proposed above, and following Germain (1929), we reclassify *A. a. gaillardi* as *A. canigonensis gaillardi* (Germain, 1912) **comb. nov.** Its significantly larger, more discoid and angulated shell, alongside its Pleistocene age and occurrence outside the Alps, favour its treatment as a distinct subspecies within *A. canigonensis*. Thus, this fossil represents the oldest known record of the species, though it is not currently possible to assign it an age more specific than "Pleistocene" (D. Berthet pers. comm.).

Further fossils identified as *repellini* and thus, potentially similar to *A. c. gaillardi*, were reported from the Geneva Basin (Favre 1927; Germain 1929). Their identity needs to be reassessed, as they could shed new light into the history of the clade.

### The Eastern Alps clade

The "eastern clade" (our *A. arbustorum* Clade 1) contains populations from the eastern Alps (Italy and Austria) typically assigned to *stenzii* and *styriaca* (Hausdorf & Walther 2021). The subspecies *stenzii*, however, has sometimes been considered a separate species from *A. arbustorum*, based on its distinctive shell morphology and reddish-brown head-foot (e.g. Welter-Schultes 2012).

Our analysis recovered two subclades within Clade 1 (Fig. 2), one strongly supported and corresponding to Italian *stenzii* and another with weaker support corresponding to Austrian *styriaca* (also containing one individual previously identified as nominate *arbustorum*). Still, Gittenberger *et al.* (2004) and Hausdorf & Walther (2021) recovered both as mutually non-monophyletic. The *styriaca* clade indeed has low support in our analysis (Fig. 2), which could indicate a different arrangement. Furthermore, there is only 3.0–3.5% difference between their COI markers (Table 3). Thus, the matter of these subspecies' monophyly must be studied in greater depth in the future.

In addition, as seen here and in previous studies, specimens identified as *styriaca* are sometimes recovered within the nominate *arbustorum* clade and vice-versa (Fig. 2; see also Gittenberger *et al.* 2004; Hausdorf & Walther 2021). This complication arises from hybridisation and introgression between *arbustorum* populations living in contact with Alpine *stenzii*/*styriaca* (e.g. Thorson, 1931; Venmans 1954; Baumgartner 1997; Haase *et al.* 2013; Hausdorf & Walther 2021). In any event, there is ample genetic distance in general between the two Alpine subspecies and nominate *arbustorum* (Table 3); this could argue in favour of them being treated as full species separate from *arbustorum*, which could be supported by the recognized morphological differences and their restricted geographic distribution in Alpine habitats. The existence of hybrids and morphologically intermediate forms has likely been the factor responsible for keeping them as subspecies of *A. arbustorum*, even though some hybridisation in contact zones should not by itself preclude the recognition of separate species if largely distinct gene pools are maintained in the core populations (e.g. Mallet 2008; Harrison & Larson 2014).

Finally, it has been a somewhat common practice to assign any specimen with a darker and less-calcified shell to *picea* (e.g. Haase *et al.* 2003). This is incorrect, as discussed in more detail further below, but it is worthwhile to note that it could have led to "*picea*" specimens being recovered inside the *stenzii* clade in previous studies (Hausdorf & Walther 2021).

### The subgenus *Altarianta*

*Arianta* (*Altarianta*) Schileyko, 2013 was described based on tenuous differences of the penis, and it was proposed as monotypic, containing only *A. stenzii*. This subgenus has largely been ignored in the literature since. Still, it is worthwhile to reiterate that stance based on phylogenetic studies (Fig. 2; Gittenberger *et al.* 2004; Groenenberg *et al.* 2016; Hausdorf & Walther 2021): *Altarianta* is "lodged" in the midst of all other *Arianta*, which would render the nominate subgenus paraphyletic. Thus, we can consider *Altarianta* superfluous and a junior synonym of *Arianta*.

### *Arianta arbustorum arbustorum*

Nominate *arbustorum* can be divided into three clades (Figs 2, 3: Clades 2–4). Clade 2 contains specimens from England, France, central Germany, Austria, Slovenia, and Romania. Clade 3 contains two subclades: (3a) specimens from Italy, Czechia, Romania, and Austria (including Alpine specimens); (3b) France, The Netherlands, and the introduced population of Canada. Clade 4 mostly represents the Baltic/Nordic populations.

Clades 2 and 3 also contain some individuals typically referred to *alpicola* and *picea*. These have been shown to be synonymous with nominate *arbustorum* in earlier studies (e.g. Gittenberger *et al.* 2004), and our results further corroborate that. While most of the current literature already does not recognize such subspecies (e.g. Kerney *et al.* 1983; Turner *et al.* 1998; Welter-Schultes 2012), names such as *alpicola* and *picea* can still be found in some studies and faunal lists, including MolluscaBase (MolluscaBase Eds 2026).

A further clarification regarding *picea* is needed. Various authors have considered *picea* as meaning different things: often, any dark pigmented and/or weakly calcified shell is assigned to *picea* (e.g. Haase *et al.* 2003); else, *picea* is simply considered an eastern European subspecies (e.g. Grossu 1955). Its type locality is Volhynia (Rossmässler 1837), a historic region between southeastern Poland, southwestern Belarus, and northwestern Ukraine. Although we could not obtain representatives from Volhynia for our analysis, a Slovenian specimen typically referred to *picea* forms a small clade with Romanian specimens (Fig. 2) nested inside Clade 2. Still, there are further Romanian specimens forming another small clade with a Czech specimen inside Clade 3 (Fig. 2). Therefore, a geographically defined *picea* likely does not represent a monophyletic lineage either and cannot be ranked as subspecies. It should be considered a junior synonym of nominate *arbustorum* and its dark shell (Fig. 6A) is deemed part of the species' range of morphological variation, as seen elsewhere (e.g. Iceland, see below).

The haplotype networks are useful to illustrate the relationships between Clades 2 and 3 (Fig. 4, Suppl. File Figs S2,S3), showing large genetic variation consistent with its wide distribution (e.g. in contrast to the smaller variation seen in the geographically restricted *A. canigonensis* and Alpine *stenzii*/*styriaca*, and to the minimal variation seen


**Figure 6.** *Arianta arbustorum*; scale bar = 5 mm. **A,** holotype of *Helix picea* Rossmässler, 1837, SMF 5991. **B,** probable syntype of *Helix arbustorum* Linnaeus, 1758, LINN 594 (syntype series contains seven shells). **C,** paratype of *Helicigona arbustorum* var. *pseudorudis* Schlesch, 1924; ZSM.Mol.20050187.

in the widely distributed Baltic/Nordic Clade 4). One interesting result, more immediately visible in the COI-only haplotype analysis (Suppl. File Fig. S2), is an Austrian Alpine *arbustorum* group, indicating some degree of isolation. Furthermore, it would be interesting for future studies to analyse in more detail the pattern of "double origin" of Romanian populations.

In conclusion, the present evidence does not support the recognition of further subspecies within *A. arbustorum* besides the nominate one and the two eastern Alps taxa mentioned above (see also discussion on *pseudorudis* below). It is worthwhile to mention that snails in the expanding front of the species' distribution (Clade 4) apparently have a small degree of premating isolation in relation to snails from the "core" European distribution, as shown by experiments with captive animals from Sweden and Switzerland (Baur & Baur 1992; Baur 1993). Still, pairs from the same populations and across populations did not differ in number of clutches produced, clutch size, or hatching success, indicating a high degree of reproductive compatibility between geographically distant populations (Baur & Baur 1992; Baur 1993).

It has been long argued that the Alpine areas acted as refugia for *A. arbustorum* during the Pleistocene glaciations (e.g. Haase *et al.* 2003, 2013; Haase & Misof 2009; Hausdorf & Walther 2021). While *A. a. stenzii* and *A. a. styriaca* remain restricted to their mountain homes, *A. a. arbustorum* underwent a postglacial expansion in distribution (e.g. Bondareva *et al.* 2020), recently reaching Fennoscandia.

### Type locality

The type locality of *A. arbustorum* is understood to be simply "European forests" (Linnaeus 1758: "Europæ arbustis"). In the original description in *Systema Naturae* (Linnaeus 1758), the first reference given by Linnaeus is from his *Fauna Svecica* (Linnaeus 1746), which is a compendium on the animal species of Sweden. The second entry is Lister (1678, 1685), from England; the third is a mistaken reference of d'Argenville (1742) that figures and describes a yellow shell with five brown bands and, hence, it is what later became known as either *Cepaea nemoralis* (Linnaeus, 1758) or *Cepaea hortensis* (O. F. Müller, 1774).

Like most gastropod entries in *Systema Naturae*, the original description is very generic and vague, mentioning only the rough shape of the shell and its aperture (Linnaeus 1758). The description in *Fauna Svecica*, albeit brief, is a bit more complete, including mentions to the shell pale-brown colour, coloured spiral band, and whitish flecks (Linnaeus 1746). More attenuated pale brown to yellowish tones is most prevalent in Nordic individuals of *A. arbustorum*. Moreover, the series of seven potential syntypes in the collection of the Linnean Society (LINN 549; Fig. 6B), though lacking locality data, are consistent with Nordic animals in size and colouration.

Therefore, considering the morphological description of the species, its syntype series, and its original primary reference to the Swedish fauna, we propose restricting the type locality of *Arianta arbustorum* (Linnaeus, 1758) to Sweden.

Furthermore, under the light of our phylogenetic analysis (Fig. 3: Clade 4), we reiterate here that old varieties of *arbustorum* that represent Nordic phenotypes and were described from Nordic countries, are all considered synonymous with nominate *arbustorum*: *Helix arbustorum* var. *septentrionalis* Clessin, 1879 (type locality: Sweden, Medelpad); *Helix* (*Arionta*) *arbustorum* var. *gotlandica* Westerlund, 1894 (type locality: Sweden, Gotland, Rosendal; *Helix* (*Arionta*) *arbustorum* var. *oelandica* Westerlund, 1894 (type locality: Sweden, Öland, Borgholm); *Arianta arbustorum* var. *roseolabiata* Schlesch, 1908 (type locality: Denmark, Rungsted). The same is true for the Icelandic *Helicigona arbustorum* var. *pseudorudis* Schlesch, 1924, which is discussed in detail below.

### The Icelandic *pseudorudis*

*Helicigona arbustorum* var. *pseudorudis* Schlesch, 1924 was described from Seyðisfjörður, in Iceland (Schlesch 1924). Morphologically, specimens of *pseudorudis* have smaller and more globose shells (Fig. 6C), with adult shells often being smaller than even the arctic Fennoscandian snails. There seems to be minimal variation in shell shape (e.g. umbilicus entirely closed or only partially so; cf. paratype series ZSM.Mol.20050187). The shells can go from the typical light northern morph to being more uniformly coloured with darker tones of brown, to an extent that the contrast between the base colour of the shell and the darker brown spiral band can become quite faint. This led to the naming of *A. a. pseudorudis* as a distinct variety (Schlesch 1924), which was considered an endemic Icelandic subspecies and was never revised since its description.

Investigating the status of this subspecies was an important goal of our study, so we included specimens of both dark and light morphs, covering virtually all the distribution of *A. a. arbustorum* in Iceland (Table 1), including specimen IINR 114547 from a place close to the type locality. Considering the results of our analysis (Fig. 3), *pseudorudis* is virtually genetically identical to Fennoscandian *A. a. arbustorum* regarding the sequenced markers. Thus, we can consider it a junior synonym of nominate *arbustorum*.

### Introduction to Canada

*Arianta arbustorum* has been repeatedly imported into Canada with various garden plants (McAlpine *et al.* 2009). The first record is an 1885 observation from Newfoundland (Whiteaves 1904), though the species was though to not have managed to establish itself then (Pilsbry 1939). McAlpine *et al.* (2009) considered that *A. arbustorum* only became established around 65 years ago. Today, the species is present in eastern Canada in the provinces of Ontario (in Toronto), Quebec (in Montreal), Newfoundland and Labrador (on the Island of Newfoundland), New Brunswick, and Prince Edward Island (McAlpine *et al.* 2009; McAlpine & Forsyth 2014; Picard *et al.* 2017). So far, the species has not been reported from neighbouring areas in the United States. Considering its habitat requirements and sensitivity to desiccation, it is considered unlikely to become widespread or a pest in this region (Cowie *et al.* 2009; McAlpine & Forsyth 2014), despite their success in urbanized environments across Europe.

Our sequenced specimens from Canada come from the New Brunswick population and are nested well inside Clade 3, within a sub-clade formed otherwise exclusively by Dutch snails (Figs 2, 4, Suppl. File Figs S2, S3). Thus, we can assume that the origin of the specimens that led to this established Canadian population lies in The Netherlands. This is in line with McAlpine *et al.* (2009), who reported

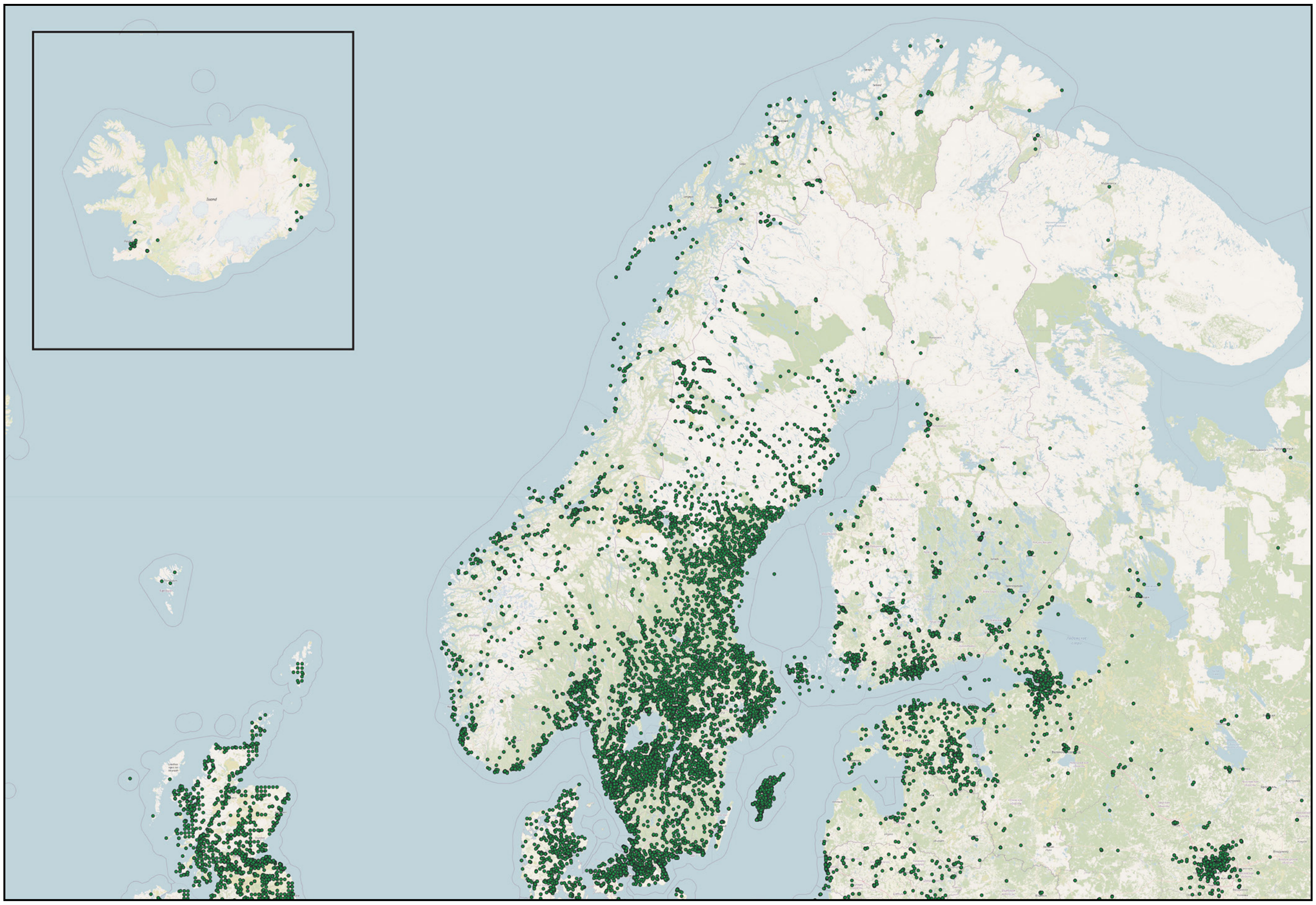

**Figure 7.** Distribution map of *Arianta arbustorum* in northern Europe using data extracted from GBIF. Inset map (not to scale) shows the distribution in Iceland. Please refer to the Materials and Methods section to read about the caveats of using GBIF data. Base map source: Open Street Map (public domain).

that most (73%) interceptions of incoming *A. arbustorum* in Canada were related to imported plants from The Netherlands. Nevertheless, considering the distribution of the species in isolated "bubbles" in Canada, multiple introductions are a likely scenario, be it from the Netherlands or elsewhere in Europe (McAlpine *et al.* 2009).

### Nordic populations

Our Clade 4 (Fig. 3) represents the Baltic/Nordic clade of *A. a. arbustorum*, containing a few individuals from Central Europe in its base, but with a crown clade containing representatives from all along the Baltic and the Nordic countries (see Fig. 7 for a summary of its distribution). Importantly, Clade 4 includes all specimens from the newly restricted type locality (Sweden).

The general structure of Clade 4, with a large polytomy and short horizontal branches showing little genetic distances (see also haplotype networks: Fig. 4, Suppl. File Figs S2, S3), is typical of fringe populations (e.g. Suzuki *et al.* 2016; Shimizu *et al.* 2018). This means that this clade is the expanding front of the species' distribution, with little time to accumulate genetic differences, signifying the expansion into Fennoscandia is quite recent in evolutionary terms, likely happening after the end Last Glacial Period, as modelled by Bondareva *et al.* (2020). For now, we have refrained from calculating divergence times based on our genetic data and intend to address this matter in greater depth in the future using genomic data and reassessing Holocene subfossils from Nordic countries (e.g. Kjellmark 1904; Odhner 1910; Steenberg 1911; Taylor 1914).

Furthermore, during historical times the populations have been expanding northwards as temperatures have increased, as supported by both historical records (e.g. Schrenk 1848; Nordenskiöld & Nylander 1856; Luther 1901; Økland 1925; Suomalainen 1939) and ecological niche modelling (Bondareva *et al.* 2020).

Considering the typical fringe population status of Clade 4 (Fig. 3), not much can be said from its inner structure.:

We could not identify any clusters expected based on history and geography, such as a Norwegian/Swedish clade, for instance (except for a small Arctic clade from Troms in northern Norway). Still, the COI-only haplotype analysis (Suppl. File Fig. S2) showed a larger distinction within the Baltic/Nordic group, more clearly separating the Baltic (e.g. Denmark, northern Germany, Estonia, St. Petersburg) from the Nordic (Fennoscandia and Iceland) populations.

As of now, we cannot ascertain whether this is (1) an issue with the markers used, that although generally suitable for population genetics, might not have captured enough variation; or and/or (2) a more complex pattern with multiple introduction/colonization events and introgression across populations. Further studies should address this topic in more detail, and one particularly interesting case is Finland. In the late 19th and early 20th centuries, *A. a. arbustorum* was only present along the coast in the south and in the northern part of the country and absent from most central areas and from Lapland (Nordenskiöld & Nylander 1856; Luther 1901; Suomalainen 1939). It has been hypothesized that the northern population arrived from Sweden or Norway, while the southern population arrived from southern Sweden or other places in Europe, perhaps via Åland or even Estonia. Today, *A. a. arbustorum* is widely distributed in Finland (except for Lapland, where it is mostly restricted to the Baltic coast and areas closer to Sweden and Norway) (Koivunen *et al.* 2014; LAJI 2026) and it is expected that these two populations of different origins will meet up as they expand their range.

Finally, a curious result observed in Clade 4 are the two Scottish specimens, which are very far removed from the English specimen of Clade 2 (Figs 2–4, Suppl. File Figs S1–3). We can postulate that these populations have different origins, arriving from different parts of mainland Europe, either naturally or aided by humans.

### Iceland

*Arianta arbustorum* was already present in Iceland when malacological studies started on the island (Mörch 1869a). Still, it was likely inadvertently introduced there centuries ago by human action, similarly to what is postulated for *Cepaea hortensis*, a species with similar body size, shell shape and habits (Bengston *et al.* 1976, 1979; Jensen *et al.* 2014). The initial records of *A. arbustorum* are from Reykjavik (Mörch 1869a), with further reports from the eastern coast from 1884 (Seyðisfjörður; the type locality of *pseudorudis*) and 1912 (Norðfjörður, formerly Norðisfjörður) (Taylor 1914). Later in the 20th century, there were only reports from the eastern part of the country, with seemingly no surviving populations in the west according to Einarsson (1977). Presently, the species is more widespread throughout the country.

In our analysis, Icelandic specimens, instead of forming a single clade as predicted if they all belonged to an endemic subspecies (*pseudorudis*), are "scattered" throughout the Baltic/Nordic Clade 4 (Fig. 3), belonging to various sub-clades, either by themselves (e.g. specimen IINR 114547 from a place close to the species' type locality) or together with specimens from Fennoscandia. Besides verifying the little differentiation between Nordic populations (see also the haplotype networks: Fig. 4, Suppl. File Figs S2, S3), this result also allows us to postulate more than one introduction event of *A. a. arbustorum* to Iceland.

### Faroe Islands

There has been more than one "attempt" by *A. a. arbustorum* to live in the Faroe Islands. The earliest record is from a single specimen found in a garden in Tórshavn (Mörch 1869b), though the species failed to establish itself until after 2003 (Jensen *et al.* 2014). This is likely due to recent changes in climate and increase in anthropically altered habitats in the past decades. These snails are thought to have been imported along building and gardening materials (Jensen *et al.* 2014), though their exact place of origin remains unknow, as we could not include Faroese specimens in our analysis.

### Russia

It is also worthwhile to highlight that distinct processes can be identified in Russian populations of *A. a. arbustorum* (Mukhanov & Lisitsyn 2018). The population of Kaliningrad is likely native (Ehrmann 1933), while that around St. Petersburg likely established itself during the 20th century. Notably, the species was already present on the island Ostrov Malyy in the Gulf of Finland back in the 1930s (the island was then part of Finland and called Peninsaari) (Suomalainen 1939). It was also already present on the Finnish island of Suursaari, *c.* 50 km to the west, in mid-19th century (Schrenk 1848; Luther 1901). Its expansion to Moscow and beyond started in the mid-20th century with the transportation of plants (Mukhanov & Lisitsyn 2018). While we could not procure specimens from Kaliningrad, other Russian specimens all belong to the Baltic/Arctic clade (Clade 4).

More recently, the species has been introduced to places far inland in Russia, close to the border with Kazakhstan and Mongolia, as visible through records in the community science platform iNaturalist (http://www.inaturalist.org). Introduction to such remote places in relation to the species' regular range is likely due to human action. The modelling of future distributions of Bondareva *et al.* (2020) did not take such introduced populations into account and thus, could not provide predictions for the Asian part of Russia. Investigating a potential spread of *A. a. arbustorum* into Asia would be an interesting avenue for future studies.

## Conclusion

Our phylogenetic analysis of *Arianta arbustorum* and related forms is the most complete to date. While offering support to previous assessments, it also brought new insights, particularly regarding the so far ignored Nordic populations. We restricted the type locality of *A. arbustorum* to Sweden, and consider the subgenus *Arianta* (*Altarianta*) Schileyko, 2013 a synonym of *Arianta* Turton, 1831. Finally, we propose the following revised classification for the studied taxa:

***Arianta arbustorum* (Linnaeus, 1758)**
- *Arianta arbustorum arbustorum* (Linnaeus, 1758)
  [synonyms: *Helix sylvatica* var. *alpicola* A. Férussac, 1821; *Helix picea* Rossmässler, 1837; *Helicigona arbustorum* var. *pseudorudis* Schlesch, 1924]
- *Arianta arbustorum stenzii* (Rossmässler, 1835)
- *Arianta arbustorum styriaca* (Frauenfeld, 1868)

***Arianta canigonensis* (Boubée, 1833)**
- *Arianta canigonensis canigonensis* (Boubée, 1833)
- *Arianta canigonensis doriae* (Paulucci, 1878) **comb. nov.**
- *Arianta canigonensis gaillardi* (Germain, 1912) **comb. nov.**
- *Arianta canigonensis repellini* (Reeve, 1852) **comb. nov.**
- *Arianta canigonensis vareliensis* (Ripken & Falkner, 2000) **comb. nov.**
- *Arianta canigonensis xatartii* (Farines, 1834) **comb. nov.**

Note that only the subspecific taxon names in current use are listed above as synonyms. The multiple older synonyms (including the Nordic varieties mentioned in the Discussion) are not listed here for brevity; for those, please refer to Tryon (1888), Pilsbry (1894), Taylor (1914), Wenz (1923), and Germain (1929). See also Salvador *et al.* (2025) for three recently rediscovered names from Switzerland that are junior synonyms of *A. a. arbustorum*.

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## Supplemental Materials

Supplementary file (doi: 10.61733/jconch/4571s) containing additional figures and tables:

**Figure S1.** Phylogenetic tree with mitochondrial markers only

**Figure S2.** COI haplotype network

**Figure S3.** 16S haplotype network

**Table S1.** Coordinates used in Fig. 1.

**Table S2.** Additional sequences used in COI haplotype network.

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