First record of a *Semilimax pyrenaicus* population in the Benelux: insights into potential anthropogenic dispersal (Gastropoda: Vitrinidae)

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Abstract. *Semilimax pyrenaicus*, a terrestrial gastropod with a primarily Lusitanian distribution, is mainly confined to the Pyrenees and Ireland, with a few isolated populations in western France. It was first recorded in Schoten (Belgium) in February 2024. Further investigations confirmed the presence of a well-established, localized population, with different age classes, ranging from early juveniles to adults. The species identification was confirmed through genetic analysis. The occurrence of the population near two garden centers suggests a recent introduction via human-mediated pathways, such as the horticultural trade. This finding also highlights the significant role of citizen science in documenting new occurrences.

Key words. Introduction pathways, genetic identification, plant trade, citizen science

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Introduction

A photograph of a terrestrial semi-slug, previously unknown in the Belgian malacofauna, was taken on 17 February 2024 in Schoten (Belgium) and uploaded by the second author to Waarnemingen.be/Observations.be, the Belgian subportal of the citizen-science platform for biodiversity Observation.org (Fig. 1). The shape of the shell, relative size of the soft parts compared to the shell, the overall spotted coloration, and the yellowish hue of the gastric part that shows through the shell readily suggest *Semilimax pyrenaicus* (A. Férussac 1821) (Kerney & Cameron 1979; Bénéat 1999; Welter-Schultes 2012; Rowson *et al.* 2014b). The published range of this vitrinid covers the Pyrenees and northern Spain westwards up to Cantabria, northern, eastern, and southern Ireland, and scattered places in south-western France and Brittany (Welter-Schultes 2012; Cadevall & Orozco 2016; Bertrand 2018; Anderson 2024). *Semilimax pyrenaicus* is said to be very common in the French eastern Pyrenees (Bertrand 2020) and in expansion in Ireland (Kerney 1999; Rowson *et al.* 2014b). This species, typically associated with a Lusitanian distribution, was not expected in Belgium.

This study aims to verify the species identity and confirm the presence of an established population. The surveys also investigated the other mollusc species co-occurring with *S. pyrenaicus* at the study site.

Materials and Methods

Field searches

On 26 May 2024, the first and third authors conducted targeted visual searches around the residential plot in Schoten where the first individual was found (51.2931°N, 004.5388°E; Fig. 2). All sightings of molluscs were recorded. The slugs requiring the inspection of the genitalia for reliable identification (*Deroceras* Rafinesque, 1820 sp., and *Arion* A. Férussac, 1819 spp. (subgenera *Arion sensu stricto*, *Mesarion* P. Hesse, 1926, and *Kobeltia* Seibert, 1873)) were collected. The genitalia were compared to information in the literature (Jordaens *et al.* 2010; Rowson *et al.* 2014b).

Three immature specimens, tentatively identified as *S. pyrenaicus*, were collected and preserved in 99% ethanol. All empty shells that could be attributed to this species were also

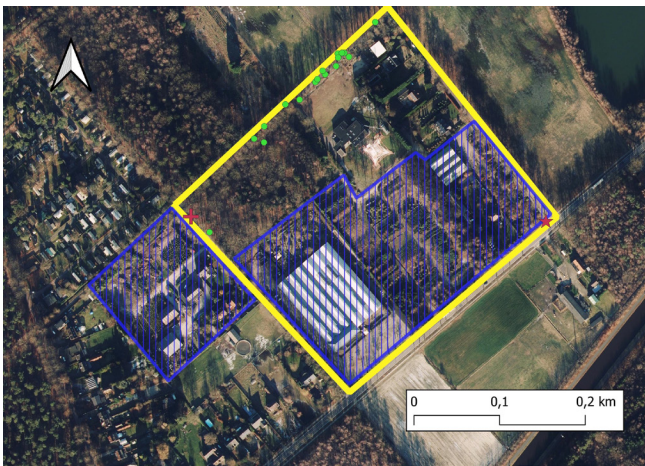**Figure 1.** The first individual pictured in Schoten. 17 February 2024.

Figure 2. Aerial photograph of the residential plot in Schoten (MercatorNet 2024). Yellow line: route followed for the visual searches on 26 May 2024. Blue hash: garden centres. Green dots: live specimens and shells of *Semilimax pyrenaicus*. Red: live specimen of the flatworms *Marionfyfea adventor* (cross) and *Parakontikia ventrolineata* (star).

collected. The shells and one alcohol specimen have been put in collection in the Royal Belgian Institute of Natural Sciences (RBINS, Brussels): I.G. 34928, INV324022–23.

DNA extraction

The two other collected specimens were brought to the GeCoLab (Liège, Belgium), which extracted the CO1 sequences using the following protocol. DNA was extracted using the QiaAmp® DNA Mini Kit following the manufacturer's instructions (Qiagen 2017). A fragment of the mitochondrial CO1 (LCO1490 and HCO2198) gene was amplified via polymerase chain reaction (PCR). The PCR

protocol was as follows: an initial heating period of 5 min at 95 °C, followed by 35 cycles with the following steps: a denaturation phase of 40 seconds at 95 °C, an annealing phase of 45 s at 45 °C, and an extension phase of 1 min at 72 °C. A final extension of 10 min at 72 °C was performed. Sanger sequencing was performed by Macrogen.

Molecular bioinformatics

CO1 sequences were generated via Sanger sequencing and subsequently assembled at the GeCoLab using CodonCode Aligner v. 11 (CodonCode Corporation, Centerville, Massachusetts, USA; http://www.codoncode.com). The resulting contigs were deposited in GenBank (accession numbers: PQ772174, PQ772175). For all downstream analyses, only the 663 nucleotide positions retained by the GenBank submission engine were considered.

The assembled sequences were aligned with additional CO1 data from European Vitrinidae retrieved from GenBank (Clark *et al.* 2016) and the BOLD database (Ratnasingham & Hebert 2013), as well as with sequences provided by Ben Rowson and Olivier Gargominy (corresponding to material cited by Rowson *et al.* (2014b) and specimen MNHN-IM-2013-77013 from the Muséum national d'Histoire naturelle (MNHN), Paris, France; Table 1). Aligning was conducted using MUSCLE (Edgar 2004) as included in MEGA 11 (Tamura *et al.* 2021) with default parameters. Following alignment, all positions containing gaps were trimmed. Subsequently, the best-fit substitution model was selected in MEGA based on both AICc and BIC criteria.

We reconstructed the maximum-likelihood (ML) phylogenetics using MEGA under the HKY model with 5 gamma categories. The initial trees were generated using both original neighbour-joining (NJ) and BioNJ algorithms, followed by branch swapping to optimize the topology. After we obtained the best ML tree, we assessed the branch support using 10,000 bootstrap replicates.

We calculated the pairwise genetic distances using the Kimura 2-parameter (K2P) method (Kimura 1980) to compare the differences among sequences.

Distribution map

The distribution map for Ireland and Spain is derived from published data (Welter-Schultes 2012; Cadevall & Orozco 2016; Anderson 2024). In France, the recent significant extension of the published range (Bertrand 2018), combined with the coexistence of other vitrinid species that are easily misidentified by field naturalists, prompted a review of the original records. We analyzed records cited in recent literature (Charles & Gréaume 2010; Vrignaud 2012; Ber-

Table 1. CO1 sequences used in the molecular analyze. Accession numbers refer to GenBank, except for those beginning with "MO", which refer to BOLD Systems, and those with three characters, which correspond to sequences provided by Ben Rowson. Country codes follow ISO 3166-1.

Accession no.	Associated species	Source	Country
I38	*Semilimax pyrenaicus*	Ben Rowson; picture in Rowson *et al.* 2014b: 109	IE
MF983499.1	*Semilimax* sp.	Gómez-Rodríguez *et al.* 2018	SP
MOLCA177-19	*Semilimax pyrenaicus*	Museu de Ciències Naturals de Barcelona	SP
MOLCA176-19	*Semilimax pyrenaicus*	Museu de Ciències Naturals de Barcelona	SP
MOLFR168-22	*Semilimax* sp.	Olivier Gargominy, Muséum National d'Histoire Naturelle	FR
MOSK152-23	*Semilimax semilimax*	Slovak National Museum-Natural History Museum	SK
MOSK177-23	*Semilimax semilimax*	Slovak National Museum-Natural History Museum	SK
MT181520	*Vitrinobrachium breve*	Pfarrer *et al.* 2021	CH
MT181521	*Vitrinobrachium breve*	Pfarrer *et al.* 2021	CH
OK393874	*Vitrina pellucida*	Pfarrer B., Nekola J.C. & Neubert E. (unpublished)	RU
OK393873	*Vitrina pellucida*	Pfarrer B., Nekola J.C. & Neubert E. (unpublished)	RU
Y18	*Vitrina pellucida*	Ben Rowson; picture in Rowson *et al.* 2014b: 109	UK
WV1	*Phenacolimax major*	Ben Rowson; picture in Rowson *et al.* 2014b: 109	UK
MT181505	*Limax maximus*	Pfarrer *et al.* 2021	CH
MOLCA283-22	*Semilimax pyrenaicus*	Museu de Ciències Naturals de Barcelona	SP
KT371424	*Vitrinobrachium breve*	Schmera *et al.* 2016	CH
MT181516	*Hesselimax kotulae*	Pfarrer *et al.* 2021	CH
MT181502	*Eucobresia diaphana*	Pfarrer *et al.* 2021	CH
MT181515	*Hesselimax kotulae*	Pfarrer *et al.* 2021	CH
MT181518	*Vitrina pellucida*	Pfarrer *et al.* 2021	CH
MT181517	*Vitrina pellucida*	Pfarrer *et al.* 2021	CH
OK043840	*Boettgerilla pallens*	Schallenberg V.M., Heim R., Schneppat U.E. & Neubert E. (unpublished)	CH
OK393819	*Limax maximus*	Pfarrer B., Nekola J.C. & Neubert E. (unpublished)	CH

trand 2018) as well as those available on the Global Biodiversity Information Facility (GBIF).

The GBIF database aggregates records from international platforms (e.g. iNaturalist, Observation.org) and local citizen-science portals, which are numerous in France. It also notably includes data from the MNHN. Only records dated from 1990 onward were considered. For records lacking directly linked photograph, we conducted an active search for associated images online (e.g. via Google Search using the observer's name and "Semilimax").

RESULTS

Field searches

Live immatures and adult empty shells of *Semilimax pyrenaicus* were found in the litter and under pieces of wood on the verges of the ditches along both sides of a beech tree-

lined avenue and in a connected acidic woodland (planted with beeches *Fagus sylvatica* L., oaks *Quercus* L. sp., elders *Alnus glutinosa* (L.) Gaertn., rhododendron *Rhododendron ponticum* L., etc.) (Figs 2–5). Two adjoining sides of the woodland are bordered by garden centres with nurseries installed between 1989 and 1994 (MercatorNet 2013; Cartesius 2024).

The other gastropods found on 26 May 2024 around the residential plot in Schoten are listed in Table 2. No additional species had been previously reported around this plot on Waarnemingen.be / Observations.be.

Molecular research

The final dataset comprised 576 nucleotide positions. The calculated K2P genetic distance between the CO1 sequences (Table 3) reveals a close relationship between the Belgian specimens and Irish one, with a distance of
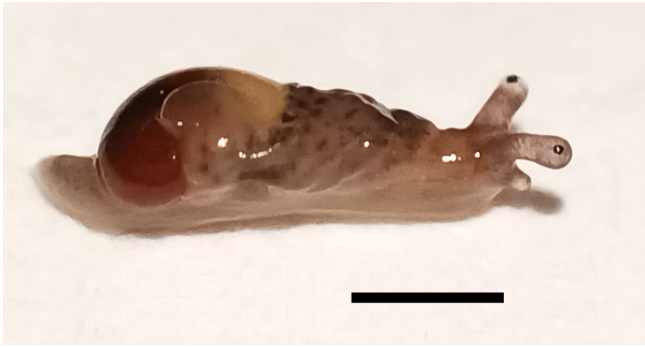
Figure 3. Juvenile individual captured in Schoten on 26 May 2024. Scale bar: 1mm.

only 1.23%. K2P distances between the Belgian and Irish sequences, on one side, and the Spanish sequences, on the other, range between 4.15 and 5.09%. Similarly, the K2P distances from the French sequence to the Spanish sequences are in the same range (4.86–4.87%), although they all come from the Pyrenees. The distances from Irish and Belgian sequences to the French one are even higher (6.96–7.75%).

The consensus tree with corresponding bootstrap support values is presented in Figure 6. With the exception of

a few samples (MOLCA283-22, KT371424), the clustering is congruent with the taxonomic identifications given by providers of the sequences. All genera represented by more than two samples were recovered as monophyletic with full support (100% bootstrap), with the sole exception of the genus *Semilimax*. *Semilimax semilimax* (J.B. Férussac, 1802) is sister to *Vitrinobrachium breve* (A. Férussac, 1821), indicating non-monophyly for *Semilimax*.

In the *S. pyrenaicus* lineage, the Belgian specimens clustered with the Irish and Central Pyrenean Spanish samples of *S. pyrenaicus*, forming a well-supported lineage (95% bootstrap; Figs 6, 7). Additionally, *S. pyrenaicus* from the French Western Pyrenean region is the sister group to the Belgian, Irish, and Spanish lineage with low support (64% bootstrap).

Distribution map

In France, outside the Pyrenean departments, we identified very few records of *S. pyrenaicus* accompanied by photographs or descriptions consistent with a *Semilimax* species. These include records from Ille-et-Vilaine (Bénéat 1999), Creuse (Margry 2020) and Landes (https://www.
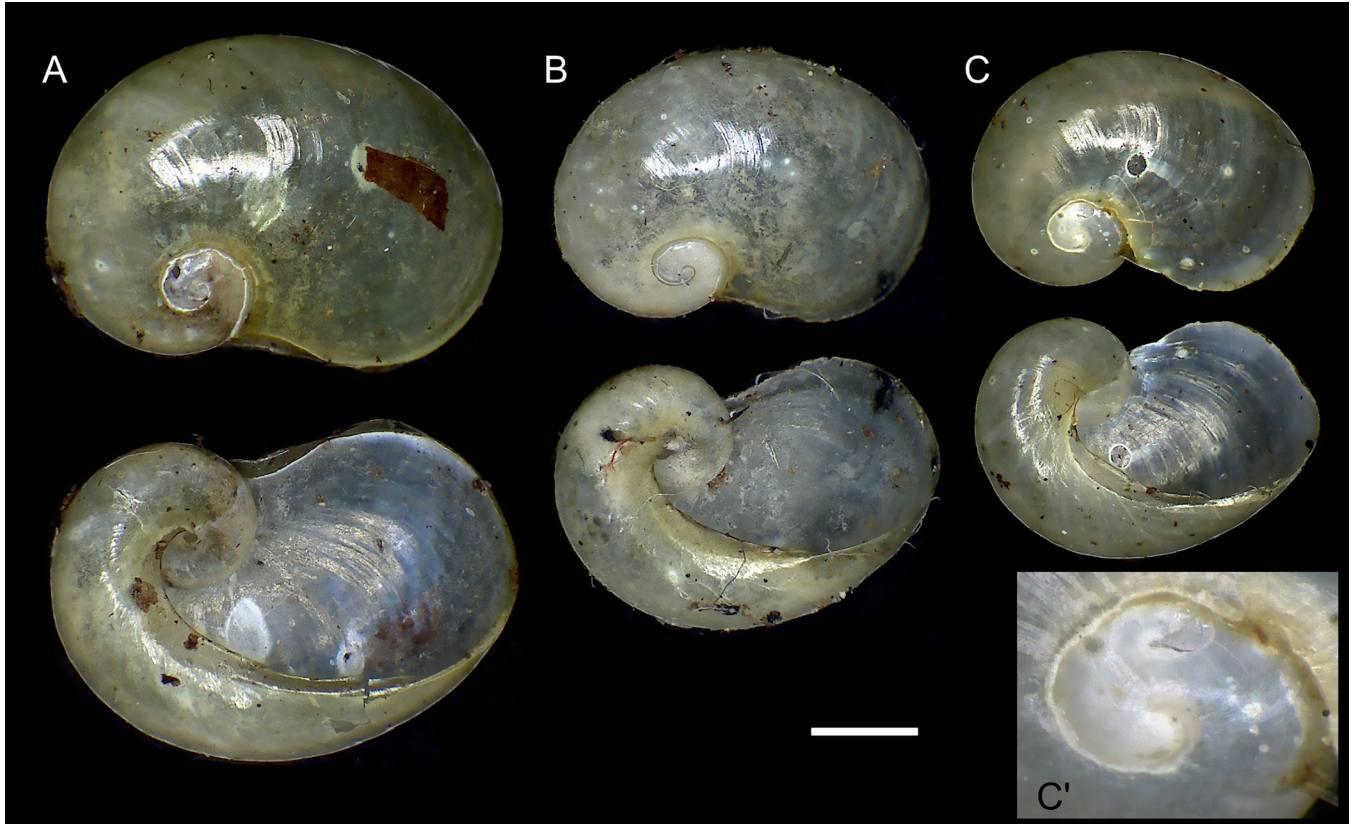

Figure 4. Empty shells collected in Schoten on 26 May 2024. Scale bar: 1mm. **C'**, detail of the protoconch of shell C.

Figure 5. Places where the empty shells and live immatures were found. **A**, beech line-treed avenue. **B**, woodland. Schoten, 26 May 2024.

Table 2. Gastropods found around the residential spot in Schoten (Fig. 2).

Alinda biplicata (Montagu, 1803)
Ambigolimax valentianus (A. Férussac, 1821)
Arion fuscus (O.F. Müller, 1774)
Arion hortensis A. Férussac, 1819
Arion intermedius Normand, 1852
Arion vulgaris Moquin-Tandon, 1855
Boettgerilla pallens Simroth, 1912
Cepaea nemoralis (Linnaeus, 1758)
Cochlicopa lubrica (O.F. Müller, 1774)
Cornu aspersum (O.F. Müller, 1774)
Deroceras invadens Reise, Hutchinson, Schunack & Schlitt, 2011
Deroceras reticulatum (O.F. Müller, 1774)
Euconulus fulvus (O.F. Müller, 1774)
Gonyodiscus rotundatus (O.F. Müller, 1774)
Hygromia cinctella (Draparnaud, 1801)
Lehmannia marginata (O.F. Müller, 1774)
Limax maximus Linnaeus, 1758
Oxychilus alliarius (J.S. Miller, 1822)
Oxychilus draparnaudi (H. Beck, 1837)
Paralaoma servilis (Shuttleworth, 1852)
Trochulus hispidus (Linnaeus, 1758)
Vitrina pellucida (O.F. Müller, 1774)

inaturalist.org/observations/194293263). In the Puy-de-Dôme (Auvergne), the analysis of the genitalia of a *Semilimax* sp. specimen does not exclude *S. pyrenaicus* as a possibility (Vrignaud 2012).

Administrative districts with these records are represented on the map (Fig. 7) using the same colour as the (historic) range in the Pyrenees, northern Spain, and Ireland. Another colour has been used for the districts with records of *S. pyrenaicus* reported firsthand by Alain Bertrand (2018), or reported by observers whose published photographs labelled as this taxon were all consistent with a *Semilimax* species.

All other sightings are classified as "doubtful". These include documented records of *S. pyrenaicus* that are illustrated with photographs of *Phenacolimax major* (A. Férussac, 1807) (Charles & Gréaume 2010; local citizen-science portals), particularly north of the River Loire. Undocumented records from central France (Loir-et-Cher, Indre-et-Loire, Indre) often originate from observers who have also published photographs of *P. major* under the name *S. pyrenaicus* or from individuals closely affiliated with these observers (e.g. members of the same association or co-authors of publications).

Discussion

Identification

The specific identification of the Belgian population as *Semilimax pyrenaicus* is suggested by the external features of the pictured animals and shells (Figs 1, 3, 4). This hypothesis is further supported by the K2P genetic distance between the Belgian and Irish sequences (1.23%; Table 3), which is below the 3% threshold typically considered as optimal for species delimitation in CO1 barcode-based studies (Hebert *et al.* 2003a, b). The higher K2P distances to the Spanish sequences (up to 5.09%) may still be con-
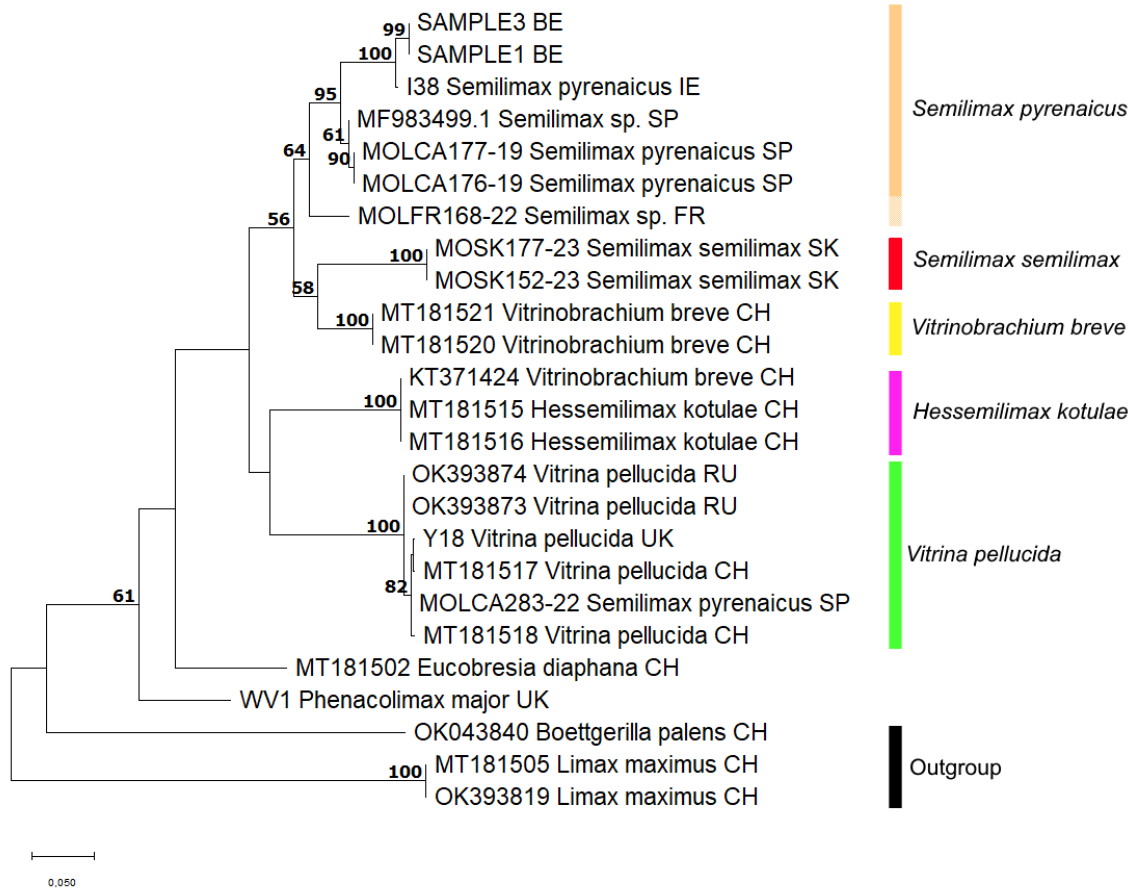
Table 3. Estimates of evolutionary divergence between CO1 sequences obtained using Kimura 2-parameter method. To lighten the table, we randomly selected one sequence per cluster, except for *S. pyrenaicus*.

	SAMPLE1	SAMPLE3	I38	MOLCA177-19	MOLCA176-19	MF983499.1	MOLFR168-22	MT181521	MOSK177-23	Y18	MT181516	WV1	MT181502	MT181505
SAMPLE1 BE														
SAMPLE3 BE	.0000													
I38 *Semilimax pyrenaicus* IE	.0123	.0123												
MOLCA177-19 *Semilimax pyrenaicus* SP	.0509	.0509	.0452											
MOLCA176-19 *Semilimax pyrenaicus* SP	.0509	.0509	.0452	.0000										
MF983499.1 *Semilimax* sp. SP	.0472	.0472	.0415	.0035	.0035									
MOLFR168-22 *Semilimax* sp. FR	.0775	.0775	.0696	.0486	.0486	.0487								
MT181521 *Vitrinobrachium breve* CH	.0830	.0830	.0811	.0616	.0616	.0617	.0711							
MOSK177-23 *Semilimax semilimax* SK	.1153	.1153	.1153	.0948	.0948	.0929	.0926	.0910						
Y18 *Vitrina pellucida* UK	.1230	.1230	.1230	.1044	.1044	.1046	.1064	.1207	.1436					
MT181516 *Hessemilimax kotulae* CH	.1226	.1226	.1205	.1123	.1123	.1126	.1084	.1023	.1315	.1252				
WV1 *Phenacolimax major* UK	.1395	.1395	.1460	.1268	.1268	.1271	.1247	.1374	.1329	.1546	.1360			
MT181502 *Eucobresia diaphana* CH	.1393	.1393	.1393	.1246	.1246	.1248	.1244	.1285	.1286	.1438	.1291	.1194		
MT181505 *Limax maximus* CH	.1865	.1865	.1887	.1731	.1731	.1756	.1755	.1775	.1937	.2116	.1799	.1962	.1867	
OK043840 *Boettgerilla palens* CH	.2006	.2006	.2006	.1914	.1914	.1895	.1806	.1802	.1870	.2247	.1852	.1920	.1964	.2284

Figure 6. Consensus tree with bootstrap support based on CO1 sequences. The percentages indicated next to the branches represent the proportion of bootstrap replicates (out of 10,000) supporting the sequence groupings (clusters). Only percentages above 50% are indicated. The sequences SAMPLE1 and SAMPLE3 come from Schoten; other sequences are listed in Table 1. The two trailing capitalized letters indicate country code (ISO 3166-1). Clusters likely corresponding to species-level associations are labeled with their respective species names and displayed on the right-hand side.

sistent with conspecificity, as it is well documented that stylommatophoran land snails often exhibit extreme divergence in their mtDNA. For instance, maximum K2P intraspecific distances have been reported at 7.6% for 600 bp CO1 sequences in *Monacha samsunensis* (L. Pfeiffer, 1868) (Pieńkowska *et al.* 2022), 12.7% for 655 bp CO1 sequences in *Theba pisana* (O.F. Müller, 1774) (Vendetti *et al.* 2021), and up to 20% for 650 bp CO1 in Testacellidae (Rowson *et al.* 2014a). A broad study covering 97 species and 381 bp of CO1 sequences reported a maximum intraspecific K2P distance of 28% (Davison *et al.* 2009). Interestingly, Davidson *et al.* (2009) also found cases where the mean interspecific K2P distance was lower than the mean intraspecific K2P distance, highlighting potential overlap between intra- and interspecific variability. These results underline the complexity of using CO1 divergence as a sole marker for species delimitation.

Nonetheless, the specific identification of the Belgian animals is strongly supported by their clustering with *S. pyrenaicus* specimens from Ireland and Spain (Fig. 6).

Uncertainties in taxonomy

The clustering of the French specimen with other *S. pyrenaicus* specimens is not supported, suggesting it may not necessarily belong to the same species. Altonaga (pers. comm. cited by Bénéat 1999) suggested that Irish and Spanish populations may represent distinct species, based on unspecified conchological and anatomical differences. The present results even cast doubt on the conspecificity within the Pyrenees. However, the genitalia of the French specimen have not yet been checked (Gargominy pers. comm., December 2024). These doubts echo the uncertainty that Vrignaud (2012) had concerning the *Semilimax* specimen found in Puy-de-Dôme, whose inspection of the genitalia did not

lead to a specific identification. Further studies incorporating other genetic markers and detailed anatomic research are then necessary to clarify the relation between the populations now labelled as *S. pyrenaicus*.

The non-monophyly of the genus *Semilimax* (Fig. 6) requires further clarification. Misidentifications would offer a simple explanation; however, the CO1 sequences of *Vitrinobrachium breve* come from a study (Pfarrer *et al.* 2021) that implemented rigorous measures to ensure correct identification. Additionally, the *Semilimax semilimax* specimens considered in our study come from Slovakia, which lies outside of the currently known range of *Vitrinobrachium* Künkel, 1929 species (Welter-Schultes 2012). Nonetheless, the photographs of specimens and the habitats at the locations publicly available on BOLD Systems do not appear inconsistent with *V. breve*. Moreover, the possibility that actual eastern range of *V. breve* is larger than previously thought cannot be excluded, as was recently demonstrated for its western distribution (Bronne *et al.* 2022).

Anatomical phylogenetic analyses have consistently treated *Semilimax* and *Vitrinobrachium* as separate genera, while the taxonomic status of *Hessemilimax* Schileyko, 1986 remains debated, being considered either a synonym of *Semilimax*, a subgenus of *Semilimax*, or a distinct genus by Hausdorf (2002), Schileyko (2003), and Giusti *et al.* (2011), respectively.

The bootstrap support values in our tree are too weak to draw a definitive conclusion. Moreover, our results are based solely on CO1 divergence. The same CO1 sequences of *V. breve* (MT181520–21) and *Hessemilimax kotulae* (Westerlund, 1883) (MT181515–16) have been used to construct a comprehensive phylogenetic tree of vitrinids incorporating CO1, 16S, H3, and ITS2 gene sequences (Pfarrer *et al.* 2021). In this broader analysis, *H. kotulae* and *V. breve* formed a well-supported cluster (90% bootstrap support). Our findings highlight the need to include specimens from different *Semilimax* species or even multiple populations in similar studies to clarify the true relationships among these genera.

Citizen science

Knowledge of the Belgian Vitrinidae owes much to citizen science. While *Vitrina pellucida* (O.F. Müller, 1774), *Phenacolimax major*, and *Eucobresia diaphana* (Draparnaud, 1805) have been added to the Belgian malacofauna in the 19th and early 20th (Adam 1947; Delcourt & Bronne 2024), the discoveries of *Vitrinobrachium breve* (Bronne *et al.* 2022) and *Semilimax pyrenaicus* occurred after the launch of Waarnemingen.be / Observations.be in 2008. The first sightings

of both species were reported by field naturalists who did not specialize in gastropods. In the case of *V. breve*, it was later suggested that the species had been long overlooked by confusion with *E. diaphana* (Delcourt & Bronne 2024).

International platforms like Observation.org, with its local adaptations, and iNaturalist offer easy uploads of photographs, which enables efficient verification. Nevertheless, the identification of Vitrinidae can be arduous, or impossible with only photographs (Forcart 1944; Hausser 2005; Wiese 2014). Taxonomic uncertainties make documentation even more important. International platforms naturally open data to foreign researchers and naturalists, reducing identification errors by limiting local biases and encouraging the exchange of ideas.

A Lusitanian species

A Lusitanian species is typically characterized by a disjunct distribution, occurring in the Iberian Peninsula and southwestern Ireland, with either no or highly fragmented populations in the regions between these areas (i.e. England and France) (Vialatte *et al.* 2008). Only two terrestrial gastropods currently show such a distribution. *Geomalacus maculosus* Allman, 1843 is one of them, and *Semilimax pyrenaicus* is the other. They are mostly to be found in the northern Iberian Peninsula and south-western Ireland. Although *Arion flagellus* Collinge, 1893 is now widely distributed across much of the British Isles (Rowson *et al.* 2014b), it was originally described from south-western Ireland and later found in northern Spain (Quinteiro *et al.* 2005).

Other terrestrial gastropods are also considered to have a Lusitanian distribution but occupy broader areas in the United Kingdom and/or localized regions in France, such as *Ashfordia granulata* (Alder, 1830). *Elona quimperiana* (Blainville, 1821) is a particular case, as its distribution is restricted to Brittany and the northern Iberian Peninsula, extending to the French Basque Country (Vialatte *et al.* 2008). *Pyramidula umbilicata* (Montagu, 1803), cited as another example of a species with a Lusitanian distribution (Gómez *et al.* 2007), is now considered as a junior subjective synonym of *P. pusilla* (Vallot, 1801), which has a wide distribution across Europe (Gittenberger & Bank 1996; Horsáková *et al.* 2022). Approximately 15 species of plants are also known to exhibit a Lusitanian distribution (Seawright 2024). The disjunct range of these species has led to several hypotheses, including the survival of the species during the Last Glacial Maximum in an ice-free pocket located notably in southwestern Ireland (*in situ* glacial refugia hypothesis) (Forbes 1846) or a post-glacial colonization of Ireland from more southern glacial refugia via

land bridges from Britain (Charlesworth 1930). However, recent research on plants (Beatty & Provan 2013; Skeffington & Scott 2021, 2023), *A. flagellus* (Quinteiro *et al.* 2005) and *G. maculosus* (Reich *et al.* 2015) strongly suggest that their presence instead results from human-aided post-glacial dispersal. It has further been suggested that Irish *Cepaea nemoralis* (Linnaeus, 1758) originated in the Pyrenees and reached Ireland by anthropochory from northern Spain (Grindon & Davison 2013). This plausible hypothesis of anthropogenic dispersal in *S. pyrenaicus* warrants further investigation through an in-depth study of the genetic diversity within its populations. Kerney (1999) suggested that *S. pyrenaicus* may have been introduced in Ireland in the 18th or 19th century when exotic ornamental trees and shrubs were massively imported.

The Belgian population represents, to our knowledge, the north-easternmost population of a Lusitanian gastropod in continental Europe. It is separated by more than 620 km from the closest reliable mention of the same species, in Rennes, France (Fig. 7).

Possible origins of the Belgian population

Semilimax pyrenaicus is known to inhabit humid and shady environments and as such is often found among rocks or within moist ground litter in woodlands, predominantly on

Figure 7. Administrative districts where presence of *Semilimax pyrenaicus* is long known or supported by recent convincing documentation (dark grey), directly observed by a presumably reliable observer (orange), or considered doubtful (orange cross-hatching) (see text). Green star: Schoten. Yellow stars: origin of the other CO1 sequences of the *Semilimax pyrenaicus* cluster (Fig. 6).

non-calcareous soils. In Ireland, it has been recorded in these habitats and occasionally in more open settings, typically in areas altered or disturbed by human activity. However, the species appears to require the absence of grazing animals (Welter-Schultes 2012). In Brittany, the species is confined to oak–beech forests aged 60–120 years (Bénéat 1999), a pattern also observed in Schoten. Similarly, Kerney (1999) reported that nearly all recorded habitats of *S. pyrenaicus* in Ireland have undergone anthropogenic modifications.

Woodlands have been present in Schoten since at least the end of the 18th century (Agentschap voor Natuur en Bos 2021; Bibliothèque royale de Belgique & Digitaal Vlaanderen 2023a, b). The woodland from which we describe *S. pyrenaicus* was very young in 1948 (Cartesius 2008). Over the past 14 years, the second author has documented 337 observations of gastropods in the whole of Schoten, though very few within the woodlands, as most are privately owned. It cannot be ruled out that *S. pyrenaicus* has been present for a long time. The observed local dispersal of the population in Schoten (Fig. 2) suggests that *S. pyrenaicus* is present for at least several years. The Atlantic climate, along with the habitat's close resemblance to the environmental conditions described for the species, further supports the likelihood of a persistent population. Moreover, reproduction can be inferred from the observation of individuals of different age classes, ranging from early juveniles to adults.

Long-distance dispersal is long known for *V. pellucida*. The literature provides multiple accounts of ornithochory (bird-mediated dispersal) for this species, either directly observed in various bird species (including *Alauda* Linnaeus, 1758 sp., *Anthus pratensis* (Linnaeus, 1758), *Corvus cornix* Linnaeus, 1758, *Erithacus rubecula* (Linnaeus, 1758), *Fringilla coelebs* Linnaeus, 1758, *Oenanthe oenanthe* (Linnaeus, 1758), *Parkesia noveboracensis* (Gmelin, 1789), and *Sylvia communis* (Latham, 1787)) (Brandes 1951; Williamson *et al.* 1959; Harris *et al.* 1960; Butot 1977; Atkinson 1987; Horsák *et al.* 2013) or strongly inferred from its arrival on a recently emerged island (Butot 1977). The recent find of a live population of this Holarctic semi-slug in Tierra de Fuego (Argentina) adds a very probable example of anthropochory (human-mediated dispersal). Nuclear ribosomal genes analysis revealed a close genetic match with British populations, strongly supporting the hypothesis of human-mediated introduction (Cuezzo & Dellagnola 2024).

Although no confirmed cases of long-distance dispersal facilitated by avian transport have been reported for other species within the Vitrinidae, such events have occasionally been speculated, based on analogies with *V. pellucida*. Exam-
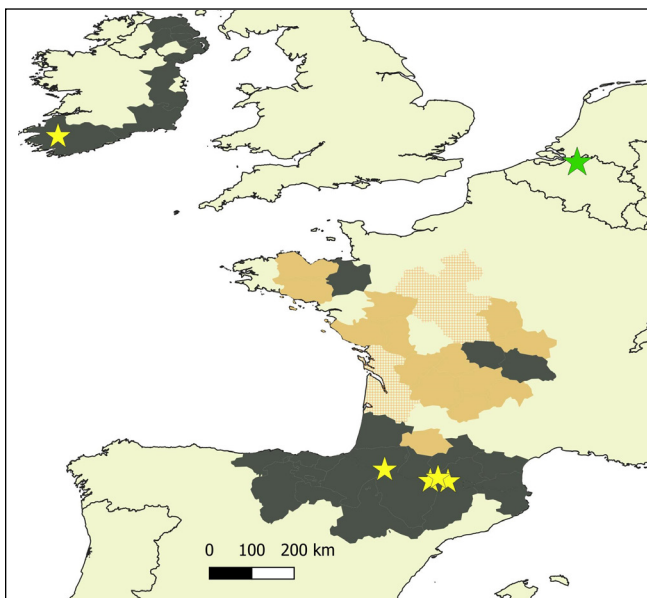
ples include the isolated individual of *Vitrinobrachium breve* discovered in the Rýzmburk castle in Czechia (Horsák *et al.* 2013). The extension of the long-distance dispersal ability of *V. pellucida* to other members of the Vitrinidae may be inappropriate because of an important morphological difference, the capacity of *V. pellucida* to fully retract into its shell, which may be necessary for the protection against desiccation during a long journey.

The immediate vicinity of two garden centers strongly suggests a likelier potential pathway for a recent introduction of the species into the woodland. The trade of life plants is known as an important pathway for gastropods (Dörge *et al.* 1999; Cowie *et al.* 2008; Bergey *et al.* 2014; Krumpalova 2018; Gutiérrez Gregoric *et al.* 2020; Stanley & Dymond 2020). The find of individuals from two exotic plathyhelminth species associated with the plant trade— *Marionfyfea adventor* Jones & Sluys, 2016 and *Parakontikia ventrolineata* (Dendy, 1892), discovered in Belgium in 2021 and 2016, respectively (Van den Neucker *et al.* 2020; Soors *et al.* 2022)—in the studied area highlights the role of these garden centers in the introduction of non-native species in the area, including in the woodland (Fig. 2).

The likelihood that the Irish population of *S. pyrenaicus* originates from the continent suggests that the haplotype(s) found in Ireland may also persist there. Therefore, the close similarity of the CO1 sequences of the Belgian population to that from Ireland may not necessarily be indicative of an Irish origin. Moreover, the export volume of potted plants from Ireland is significantly lower than that of France and Spain. For instance, in 2022, the Republic of Ireland exported only 2,127 tons of potted plants, compared to 64,208 tons from France, and 267,963 tons from Spain (WITS 2024a). In Spain, the value of live plants exported from the four autonomous communities where *S. pyrenaicus* occurs accounts for 17% of the country total, with the largest portion (83.90%) corresponding to Catalonia (FEPEX 2024). In France, the Nouvelle-Aquitaine region accounted for 9.13% of the national continental area dedicated to horticulture and 11.14% of the national continental production value during 2019–2020 (Avelin 2021). Nurseries are notably present in the Landes, a non-montane department of the Nouvelle-Aquitaine where *S. pyrenaicus* has been recorded. Open-air plants comprised an average of 55% of French horticultural export between 2014 and 2019 (Avelin 2020). This could suggest that the population in Schoten is more likely to have originated from Spain or France. However, eggs or animals may have been transported along with commercial peat. Before the enactment of the Peat Protection Act in the Republic of Ireland and the Peat Trade Ban in the

UK in 2021, large quantities of peat were exported from Ireland for horticultural use. In 2019, the Republic of Ireland, for instance, exported 791,370 tons of peat (WITS 2024b).

The installation of *S. pyrenaicus* north of its main continental range is unlikely to pose risks to other species or the human economy. To our knowledge, no species in the Vitrinidae has ever been suspected to pose environmental risks. In Ireland, *S. pyrenaicus* is not considered a horticultural or agricultural pest (Rowson *et al.* 2014b). Regardless of the pathway, its introduction in the northern areas could provide an opportunity for the species' survival, especially given the uncertain climate future of the Pyrenees, its core range (Amblar-Francés *et al.* 2020).

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