

First records of *Arion intermedius* and *Arion transsylvanus* (Stylommatophora: Arionidae) in Hungary

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Abstract

Two *Arion* species are reported for the first time from Hungary. *Arion intermedius* Normand, 1852 is a widely introduced species native to Western Europe and some adjacent regions. Reliable records from Slovakia and Austria are sparse and scattered, and our finding is located near the Austrian border, so it should be considered as a probable introduction to Hungary. *Arion transsylvanus* Simroth, 1885 is a near-cryptic species in the *Arion subfuscus* species complex with a restricted distribution mostly in the Carpathian Mountains of Romania. The Hungarian locality of this species is in the Bükk Mountains, which is the southernmost part of the Western Carpathian Mountains. Hence, we propose that this is possibly part of the species' native range or perhaps a natural range expansion rather than a human-mediated introduction. With these new species, the Hungarian slug fauna consists of 33 species. Nine of these have been discovered or their presence confirmed only in the last six years.

Key words terrestrial slugs, morphology, introductions, distribution, barcoding.

Introduction

Non-indigenous species are continuously spreading across the world (Pyšek *et al.* 2020), most likely as a consequence of the increasing pace and extent of trade (Hulme 2009; Peltanová *et al.* 2012). This has had a crucial effect on the composition of the Hungarian mollusc fauna. We have been investigating the Hungarian slug fauna for six years, summarising our knowledge in an identification guide (Turóci & Páll-Gergely in press). Of the seven species that we have so far added to the Hungarian species list, all are quite likely human-mediated introductions (Turóci *et al.* 2020, 2023).

Arion Férussac, 1819 is a genus of terrestrial slugs with a centre of diversity in Southwest Europe (Quinteiro *et al.* 2005), although several species have been introduced widely to other continents (Herbert 2010) and some are serious pests (Barker 2002). Adult size varies considerably between species (Hutchinson *et al.* 2017). Species identification and taxonomy within the genus presents various challenges, including near-cryptic species (e.g. Davies 1977; Pinceel *et al.* 2004), interspecific hybridisation (Zemanova *et al.* 2017; Reise *et al.* 2020), and considerable intraspecific variation in colouration, largely genetic but also influenced by diet (Jordaens *et al.* 2000).

Based on our studies of museum specimens and fresh collections, we knew of seven *Arion* species that live or have lived in Hungary (Turóci & Páll-Gergely in press). Now we also report *A. intermedius* and *A. transsylvanus* for the first time from Hungary. *Arion intermedius* was identified on the basis of external appearance, genital anatomy and mitochondrial DNA, while the latter was the main basis for identifying *A. transsylvanus*.

Arion intermedius is the smallest representative of the genus, reaching 15–25 mm when mature. Colouration ranges from yellowish white to brown and dark grey. Characteristically, its tubercles stand up, forming a point or serrated ridge and producing a prickly appearance even to the naked eye (Frömming 1954; Wiktor 1973; Kerney & Cameron 1979; Falkner 1990; Rowson *et al.* 2014). This is especially marked when the animal is contracted. Another diagnostic external character is a row of tiny dark dots above the anterior foot fringe (Quick 1949; Cameron *et al.* 1983).

It is found from southern Scandinavia to Italy and from the northern parts of Portugal and Spain to western Poland (Welter-Schultes 2012). Reports from the edge of its European range, which thus might represent introductions, include southern Italy (Bacheljau 1985), Bulgaria (Dedov *et al.* 2017), Austria (Duda *et al.* 2019), Finland (Koivunen *et al.* 2014), and Iceland (Kerney & Cameron 1979). It has been introduced also to North and South America, South Africa, Sri Lanka, Australasia and multiple oceanic islands (Herbert 2010; Gutiérrez Gregoric *et al.* 2013; Araiza-Gómez *et al.* 2021).

Arion intermedius has a wide ecological tolerance. It inhabits damp deciduous forests and the margins of streams and lakes, and is often amongst wet leaf litter, but it can also be one of the commonest slugs in pasture and arable fields (Barker 1991; Bohan *et al.* 2008). It can appear in acidic soil, in coniferous forests or even sandy areas (Welter-Schultes 2012; Rowson *et al.* 2014). In Switzerland it occurs up to 1000 m above sea level (Rüetschi *et al.* 2012).

Arion transsylvanus is a medium-sized slug 40–70 mm long when crawling. Jordaens *et al.* (2010) listed different colour morphs of the species ranging from bright pale orange to deep- and dark-brown variations, each varying in the visibility of the faint lateral bands. It belongs to the *Arion subfuscus* species complex, together with *Arion subfuscus* (Draparnaud, 1805) and *Arion fuscus* (O. F. Müller, 1774). Jordaens *et al.* (2010) established that *A. transsylvanus* was a distinct species based on allozymes, mtDNA sequences, and genital anatomy.

It is a Carpathian species and widely distributed in Transylvania (part of Romania), where it is the only known representative of the *A. subfuscus* species complex (Jordaens *et al.* 2010). There is one record in eastern-Poland but in no other Carpathian regions has it been reported (including southwestern Poland and the High Tatras along the Polish–Slovak border). In these regions, it is substituted by its congener *A. fuscus*. *Arion transsylvanus* lives mostly in deciduous and coniferous forests but also in semi-disturbed habitats, including roadsides, riverbanks and meadows. Most records are from below 1300 m altitude but it has been reported from 2300–2500 m (Simroth 1885; Grossu 1970).

Material and methods

Sample collection

Sampling localities are given in Table 1. In the case of *A. intermedius*, one of us (RV) photographed and collected mollusc specimens in Kámoni Arborétum, Szombathely (Alpokalja Mountains, 18.X.2023) during a region-wide collecting trip. After a photograph suggested that a specimen that was not collected was *A. intermedius*, ÁT & RV revisited the same location (22.X.2023) and RV visited again on 12.XII.2024.

With *A. transsylvanus*, two of us (BPG & RF) collected slug specimens in the Bükk Mountains (6.XI.2020), of which some belonged to the *A. subfuscus* species complex. Many were juveniles, so we returned to the original locality (28.V.2024) to seek further, more mature specimens.

Sample collection involved sifting through leaf litter and lifting decayed logs and other material, and picking up any slugs found.

Table 1. Collection data with inventory numbers and GenBank accession numbers (when applicable). Numbers in the brackets after the HNHN inventory numbers indicate the number of collected specimens.

Species	Location	Latitude, Longitude	Date	Inventory numbers	Gen Bank acc. no.
<i>A. intermedius</i>	Kámoni Arborétum, Szombathely, Alpokalja mts. 220 m a.s.l.	47.2548° N, 16.6070° E	22.X.2023	105715 (1)	PQ428078
				105714 (1)	PQ428079
				105734 (1)	
				105735 (1)	
				105632 (4)	
<i>A. transsylvanus</i>	Beech forest, Nagyvisnyó, Bükk Mts. 810 m a.s.l.	48.0714° N, 20.4887° E	6.XI.2020	105716 (1)	PP574416
<i>A. fuscus</i>	Beech forest, Nagyvisnyó, Bükk Mts. 810 m a.s.l.	48.0714° N, 20.4887° E	28.V.2024	105634 (1)	PV151526

Storing, handling, and photographing of specimens

Living slugs were placed in plastic containers with holes in their lids along with a damp paper towel to prevent desiccation. We kept them in a refrigerator until processing. Living individuals were photographed, killed, and preserved following the methods detailed by Turóci *et al.* (2023).

We used the following equipment for photographing the slugs: Canon EOS 2000d camera, Tamron SP AF 90 mm F/2.8 Di MACRO 1:1 macro objective, one camera-mounted flash, two studio flash units (BlitzBirne Mikrosat), and two white umbrellas.

Dissection was carried out under a Zeiss Stemi 305 stereomicroscope. The genital organs were photographed with the same camera as above, but with a Canon MP-E 65 mm F/2.8 1–5× macro objective.

Ethanol-preserved voucher specimens currently in the Plant Protection Institute, HUN-REN Centre for Agricultural Research, Martonvásár will be deposited in the Hungarian Natural History Museum, Budapest (HNHN) (Table 1 lists inventory numbers).

Identification

Identification of all specimens was based on external and anatomical traits. Concerning *A. transsylvanus*, we found only one specimen, which was too immature to be identified anatomically; in this case we relied on DNA analysis.

DNA analysis

We sequenced two fragments of mitochondrial DNA, either of which is sufficient to confirm species identities: the standard barcoding parts of the COI gene (for two individuals of *A. intermedius* and one of *A. fuscus*) and of the 16S ribosomal gene (for one individual of *A. transsylvanus*).

For *A. intermedius*, DNA was extracted with the EZNA Mollusc & Insect DNA Kit (Omega Bio-tek, USA). PCR amplifications were performed with Phusion Hot Start II High-Fidelity PCR Master Mix in a final volume of 20 µl using 2 µl DNA extract as a target. Primers were LCO1490 and HCO2198 (Folmer *et al.* 1994). PCR protocol: 98 °C 30 s; 40 cycles of 95 °C 10 s, 45 °C 30 s, 72 °C 30 s; finally 72 °C 5 min. Products were sent to LGC Genomics GmbH (Germany) for purification and Sanger sequencing in both directions using the same primers. Electropherograms were individually examined using CodonCode Aligner (Richterich 2004) version 8.0.2 (CodonCode Corporation, USA).

For *A. fuscus*, DNA was extracted using the method of Winnepenninckx *et al.* (1993). PCR was performed using dNTP Mix, key buffer and Taq-DNA-Polymerase (VWR, Germany) in a final volume of 10 µl using 1 µl DNA as a target. Primers were as for *A. intermedius*. PCR protocol: 94 °C 3 min; 5 cycles of 94 °C 30 s, 45 °C 30 s, 72 °C 1 min; 35 cycles of 94 °C 30 s, 51 °C 1 min, 72 °C 1 min; finally 72 °C 10 min. The resulting fragments were purified using QiaQuick Gel Extraction Kit (Qiagen, Hilden, Germany) and sent to Laborzentrum BiK-F (Frankfurt am Main, Germany) for direct sequencing in both directions. Electropherograms were examined and sequences aligned by eye using BioEdit (Hall 1999).

For *A. transsylvanus*, DNA was extracted using Mag-Bind Blood & Tissue DNA HDQ 96 Kit (Omega Bio-Tek, USA). The rest of the procedure was the same as for *A. fuscus* except that we used the 16Sar and 16Sbr8 primers (Simon *et al.* 1994) with a protocol of: 94 °C 4 min; 36 cycles of 94 °C 45 s, 49 °C 45 s, 72 °C 90 s; finally 72 °C 10 min.

Sequences have been deposited in GenBank (Table 1).

Results

Arion intermedius

We collected eight specimens. They were adult and about 20 mm long, up to 23 mm when fully extended. The general appearance when alive was of a pale-yellowish or light-greyish body with faint lateral bands and dark head and tentacles (Figs 1, 2). All specimens exhibited the diagnostic prickly appearance generated by the pointed tubercles, although some individuals more so than others. Most also showed one or more tiny black dots above the foot fringe near the head (another character known only in this species), but these were not apparent in two of the living specimens. The mucus was yellow and dense.

Preserved specimens were light-yellowish or cream with smooth (i.e. not prickly) skin (Fig. 3A). Lateral bands were generally more visible on preserved individuals than on living specimens. Dark dots above the anterior foot fringe were also apparent in most preserved specimens, although they could be faint or even absent (Fig. 3B). For anatomical confirmation of identity, it was already informative that fully developed genitalia were found in animals of this size, ruling out most other *Arion* species, which mature at a larger size. Other distinctive anatomical characters were the large and round bursa copulatrix with a short, thick peduncle, and the short and tubular oviductus (Fig. 3C–E).

In Hungary we collected *A. intermedius* specimens in October and they laid eggs at the beginning of November. The eggs were 2–3 mm in diameter, white, and were laid in clutches typically of about 10 eggs (Fig. 4A). Freshly hatched specimens were about 3 mm long. Hatchlings and juveniles were similar in external appearance to adults, and the prickly appearance was visible from hatching (Fig. 4B).

The only known locality of *A. intermedius* in Hungary remains the Kámoni Arborétum, Szombathely (Fig. 5A), outside but close to the part open to the public. We found the slugs at three locations within 50 m of each other on both sides of the Gyöngyös stream, which originates over the border in Austria. The slugs were found under the bark of decaying logs amongst deep leaf litter in woodland of mainly *Alnus glutinosa* and *Acer platanoides* (Fig. 6A).

The partial-COI sequences of two individuals from this locality were identical. The most similar haplotype in GenBank differs by just one nucleotide and had been found in *A. intermedius* from two distant sites in the eastern USA (GenBank EU382743.1 and MG813885.1).

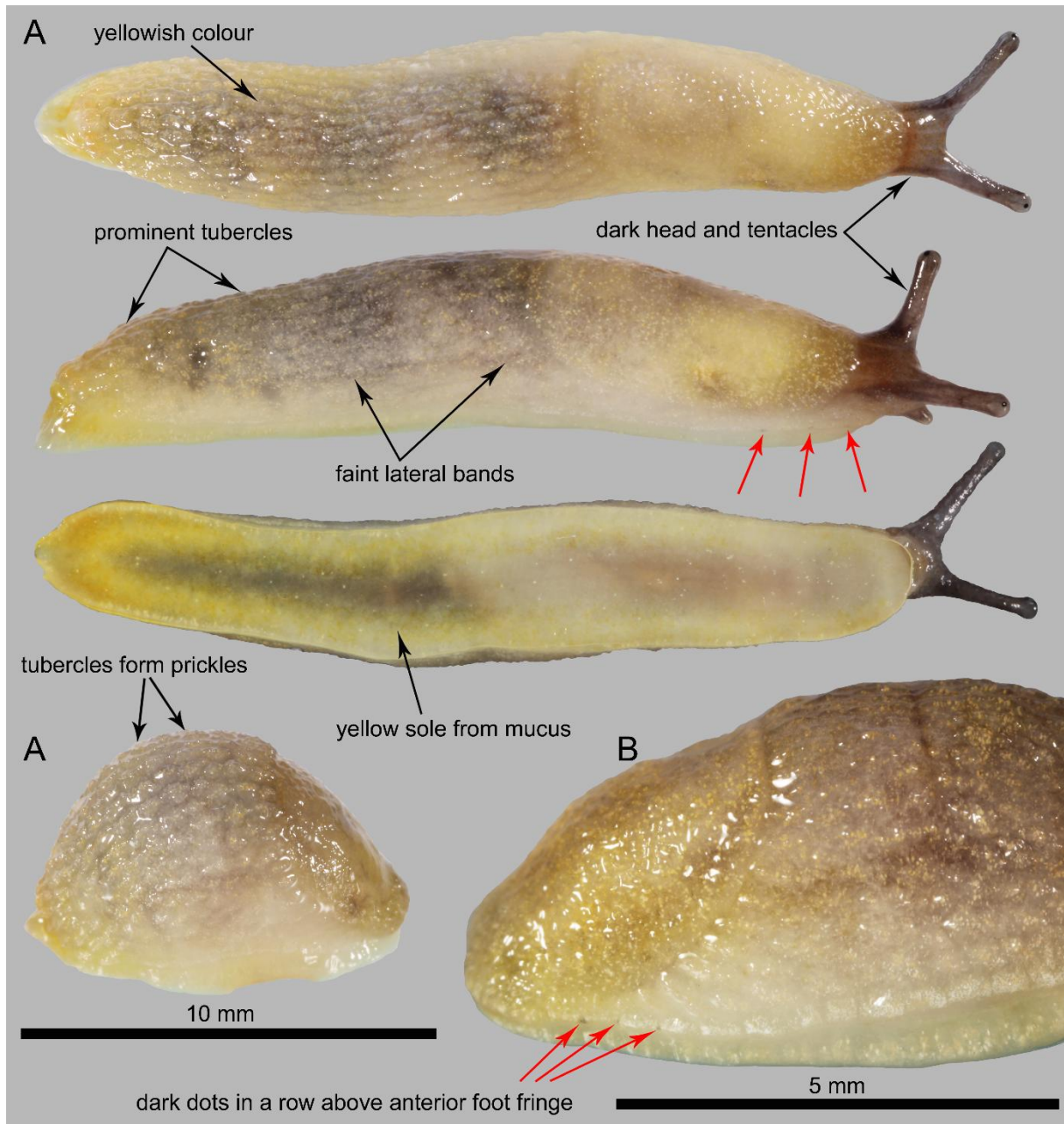


Figure 1. Two living specimens of *Arion intermedius* from Hungary (**A**: HNHM 105715, **B**: HNHM 105633). Red arrows indicate the dark dots above the anterior foot fringe.



Figure 2. Two more living specimens of *Arion intermedius* from Hungary (**A:** HNHN 105735, **B:** HNHN 105714). Some specimens displayed stronger lateral bands (**A**) or their skin was smoother than others (**B**). Comparisons in the labels are with Fig. 1A (HNHN 105715).

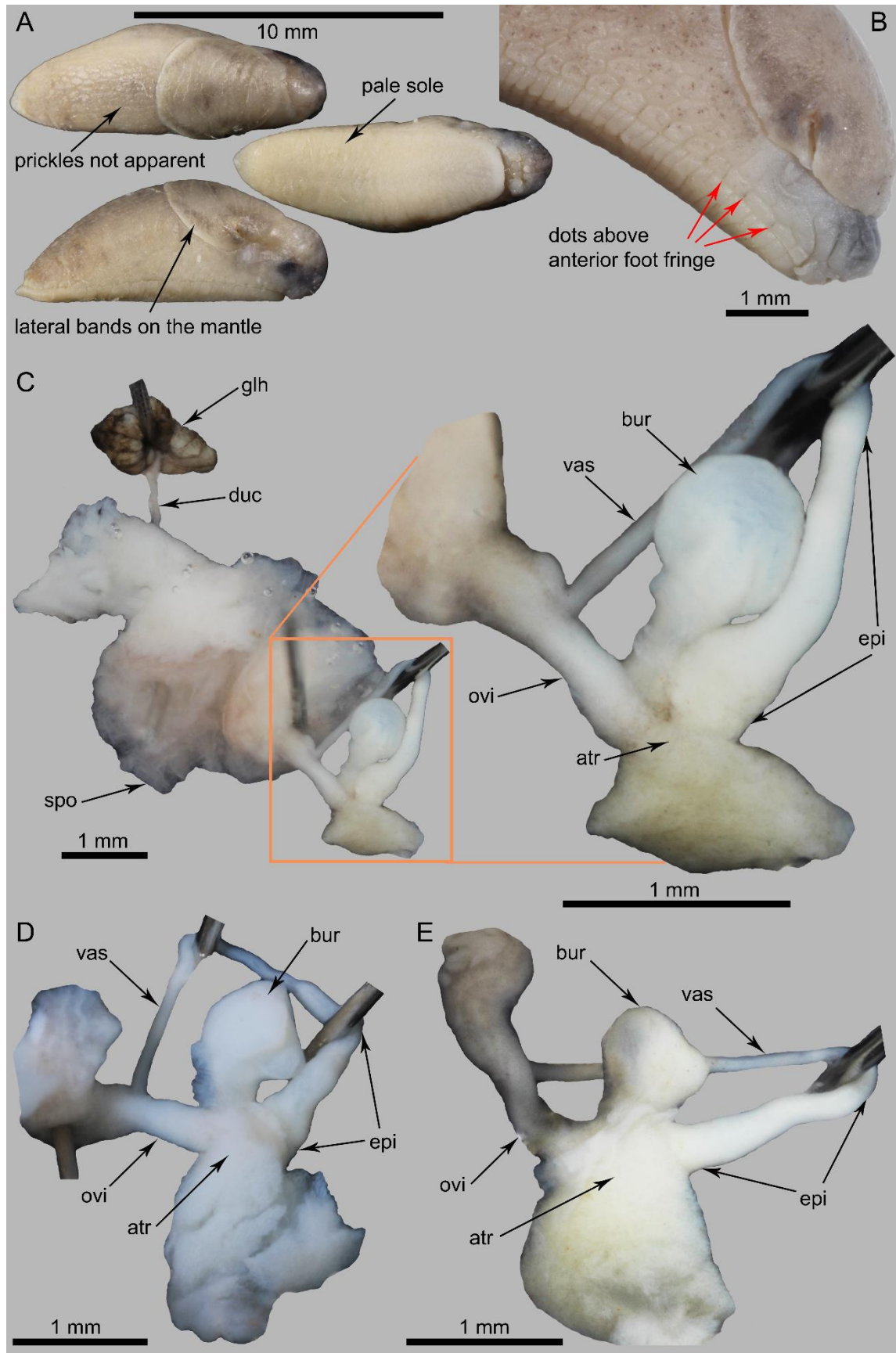


Figure 3. Two preserved specimens (**A:** HN105715, **B:** HN105633) and the genitalia of *Arion intermedius* specimens from Hungary (**C:** HN105714, **D:** HN105715, **E:** HN105734). Abbreviations: atr = atrium, bur = bursa copulatrix, duc = ductus hermaphroditicus, epi = epiphallus, glh = glandula hermaphrodita, ovi = oviductus, spo = spermooviductus, vas = vas deferens.

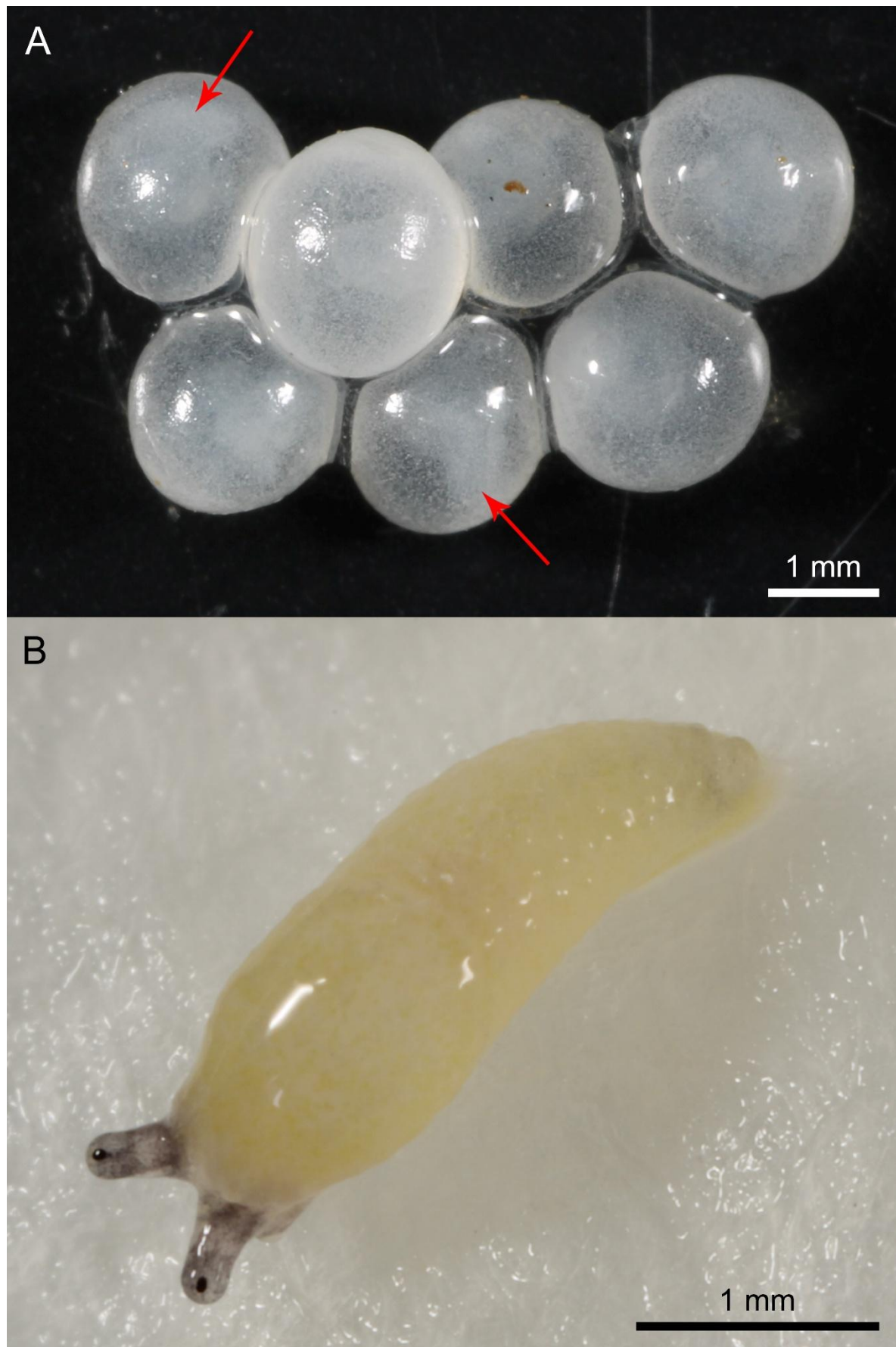


Figure 4. **A:** Egg clutch of *Arion intermedius*. The red arrows indicate embryos inside the eggs. **B:** A freshly hatched *A. intermedius*.

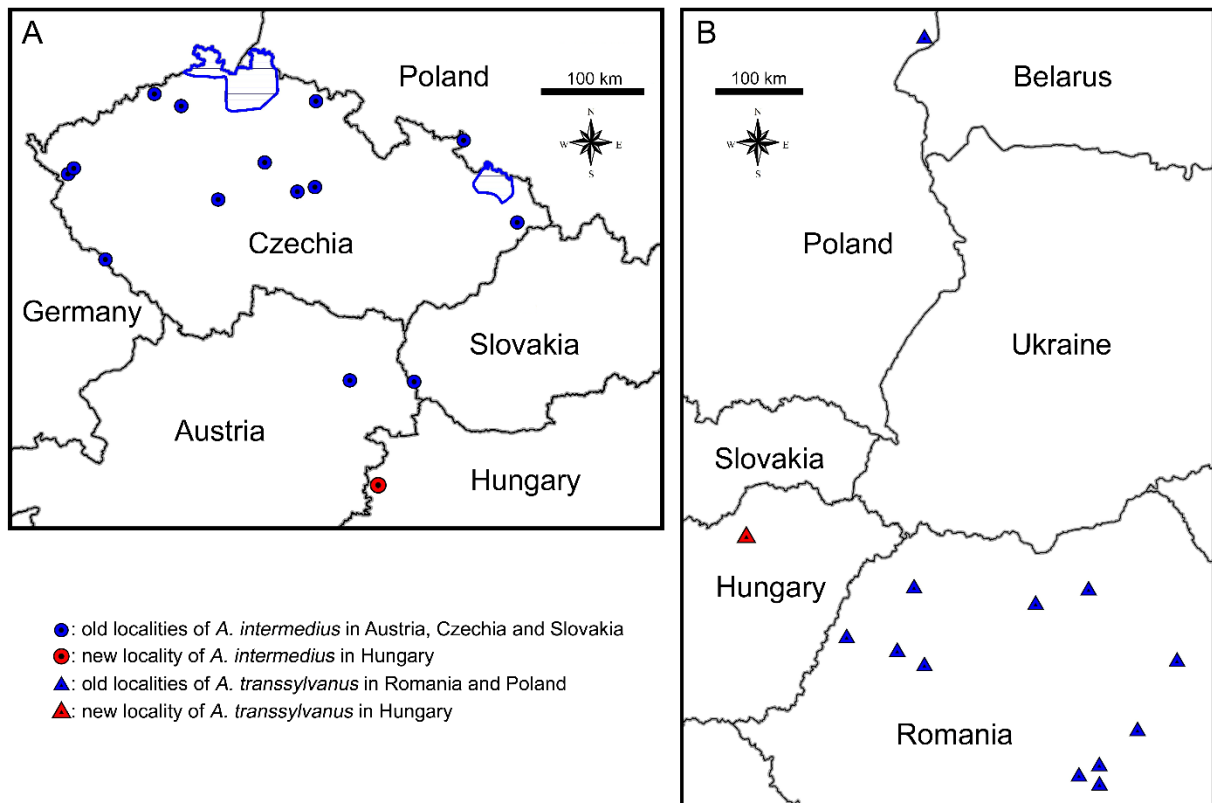


Figure 5. Localities of *Arion intermedius* (A) and *A. transsylvanus* (B) in Hungary and nearby countries. A is based on data from Duda *et al.* (2019), Čejka *et al.* (2021) and Horsák *et al.* (2025); localities in Poland and Germany are not mapped. B is based on data from Jordaens *et al.* (2010).

Arion transsylvanus

On the first collecting trip in November, we collected a single individual, a juvenile, which only later was identified as *A. transsylvanus* on the basis of its 16S mtDNA sequence.

The 455-bp sequence was a close match (0.2–1.7%) to the 14 *A. transsylvanus* 16S haplotypes generated by Jordaens *et al.* (2010). In particular the Hungarian sequence differed by a substitution of just 1 bp from the 402-bp haplotype AY860806.1, from an animal collected in eastern Poland. In comparison, Jordaens *et al.* (2010) reported a difference of 15% to the other species in the *A. subfuscus* species complex.

The juvenile Hungarian specimen was 45 mm when fully extended. The colouration was a particularly vivid orange, especially on the back (Fig. 7). This is not diagnostic since Jordaens *et al.* (2010) documented wide and overlapping ranges of colouration in this species and its close relatives. One difference from their description of *A. transsylvanus* is that the foot fringe of our slug was light without dark stripes; this might reflect its juvenile state. The mucus was sticky, but not so much as that of *Arion vulgaris*, for instance. After preservation our specimen was approximately half as long as when living (25 mm after preservation). The body had become light brown with a pinkish tinge, and the dark markings showed up more conspicuously (Fig. 8).

The single specimen proved to be too juvenile to conclude anything about species identity from the genital anatomy.

The site at which we found *A. transsylvanus* in Hungary is on the plateau of the Bükk Mountains (Fig. 5B, Table 1) at a relatively high altitude (above 800 m a.s.l. compared to the highest point of the country: 1014 m, Kékestető). It was found in a natural habitat in a beech forest. Although forestry activity takes place in the area, the locality is fairly undisturbed. The specimen was found under deep leaf litter in the stump of a beech tree (Fig. 6B).

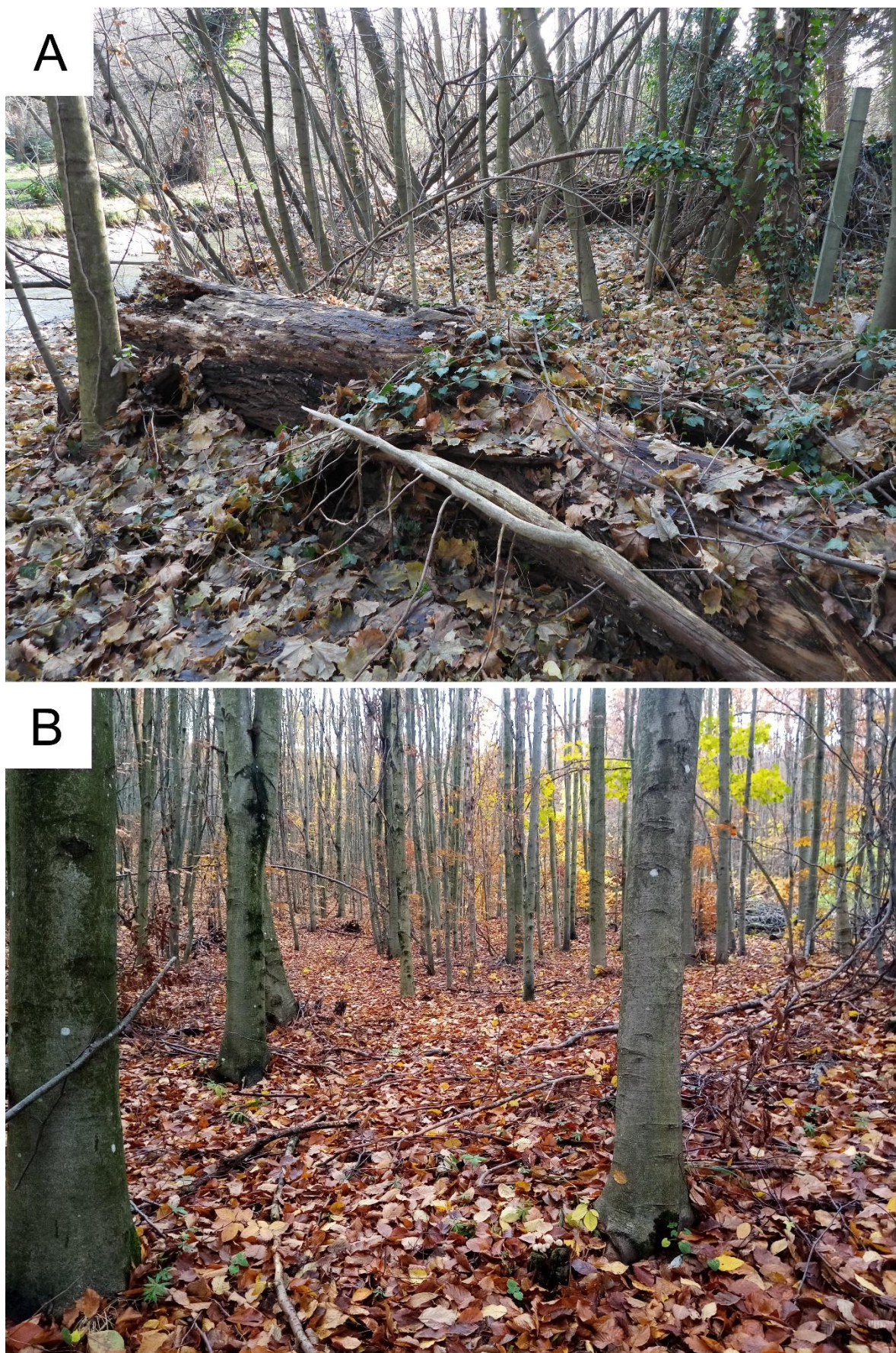


Figure 6. Habitats of the two newly discovered species in Hungary. **A:** *Arion intermedius*, photographer = BPG, **B:** *Arion transsylvanus*, photographer = RV.

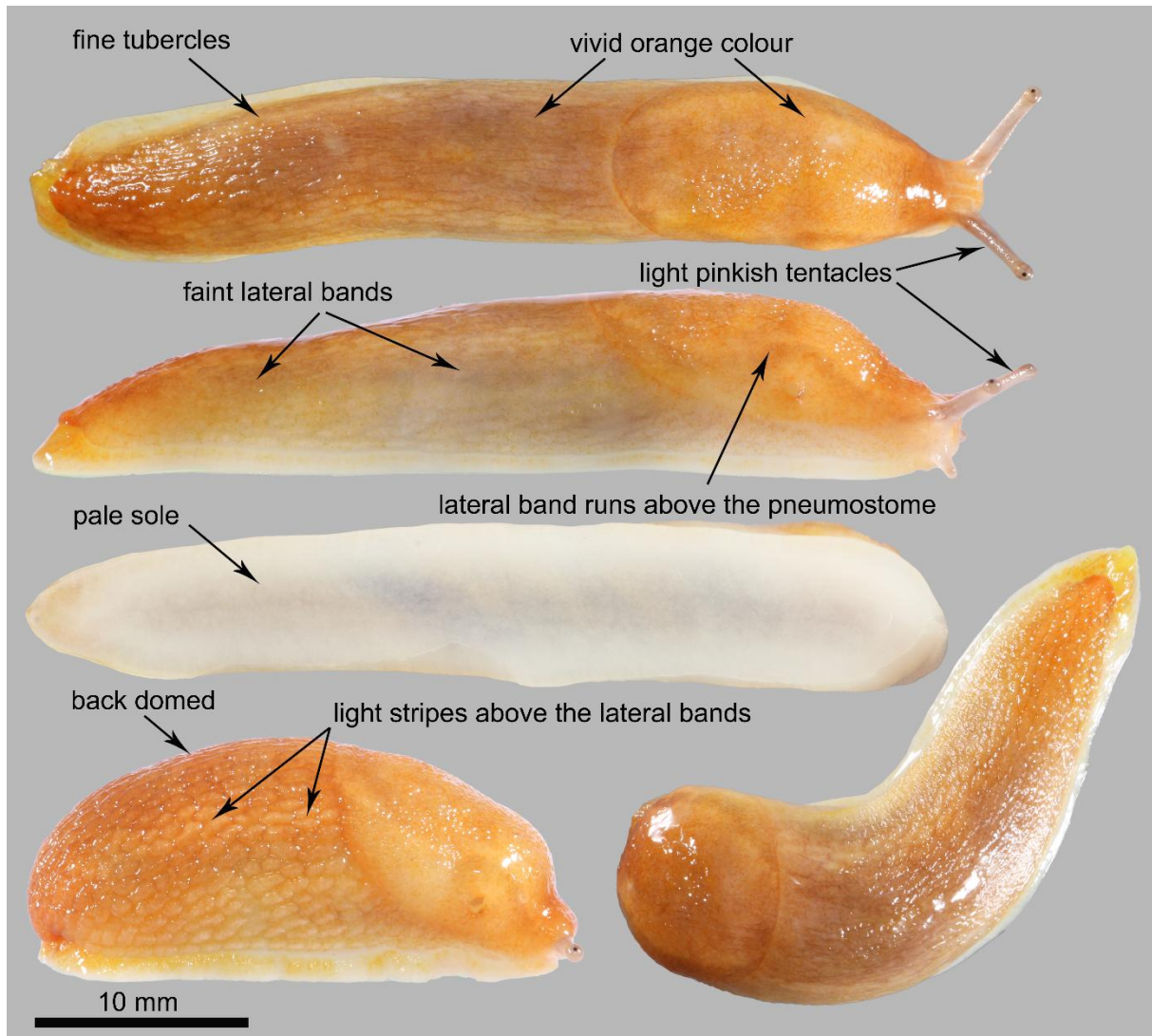


Figure 7. The living juvenile specimen of *Arion transsylvanus* from Hungary (HNHM 105716). The two bottom two photographs show the animal partially contracted.

After the molecular data revealed the presence of *A. transsylvanus*, we (RF & BPG) returned to the original site in May 2024 to collect more specimens. All four found were juveniles and the single example sequenced had the COI mtDNA sequence of *A. fuscus*.

Discussion

The small size of *Arion intermedius* makes it is easy to overlook or to casually dismiss as a juvenile of another species. Nevertheless it is a species that can often be reliably identified on the basis of external characters, particularly the prickly appearance and the tiny dots along the foot fringe. However, these characters are not always apparent, and in particular preserved slugs often look smooth; in those cases, dissection or sequencing is needed for reliable identification.

Within Hungary, the possibility of misidentification is perhaps greatest with *Arion obesoductus* Reischütz, 1973 formerly referred to as *Arion alpinus* Pollonera, 1887. Many populations from Central Europe and the Eastern Alps turned out to be *A. obesoductus*, and *A. alpinus* was synonymised with *A. intermedius* (Manganelli *et al.* 2010). Although *A. obesoductus* has not been recorded from Hungary, it is not improbable that it does or will occur. *Arion obesoductus* is known from Czechia (Dvořák *et al.*

2006), eastern Germany (Schniebs & Reise 1997) and Austria (Duda *et al.* 2019). More brownish colour morphs of *A. intermedius* resemble *A. obesoductus*, although the latter lacks the prickly appearance and dots along the foot sole. Internally, *A. intermedius* has a short, thin and tubular oviduct, whilst that of *A. obesoductus* is longer and wider. Also the bursa copulatrix differs: large and spherical with a short and wide peduncle in *A. intermedius* and elongated and thin without a prominent transition into its peduncle in *A. obesoductus*.

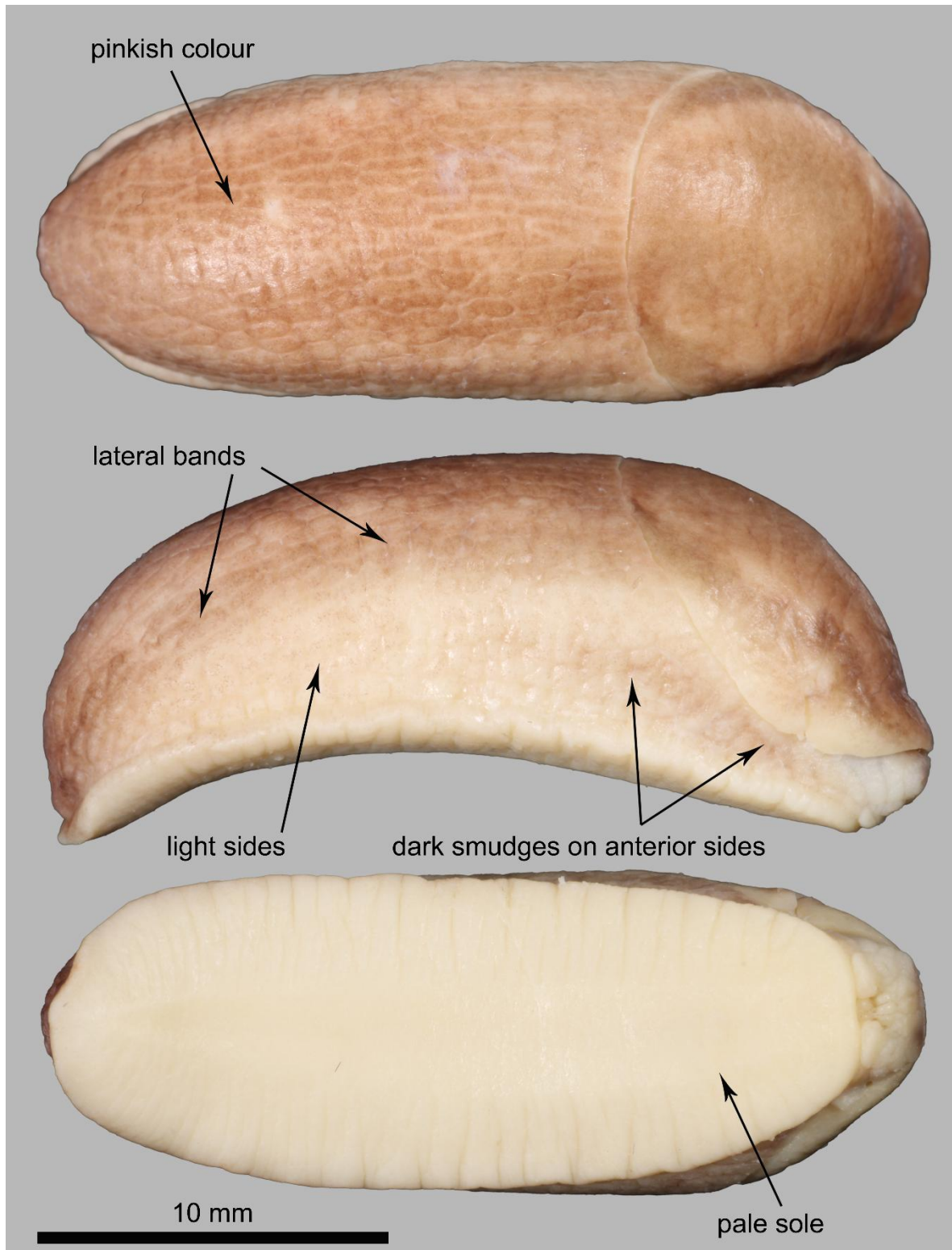


Figure 8. External morphology of the juvenile *Arion transsylvanus* specimen from Hungary after preservation (HNHM 105716).

Certain species of the subgenus *Kobeltia* (*Arion hortensis* and *Arion distinctus*) might also be confused with a dark-grey *A. intermedius*. If such slugs lack the diagnostic external characters of *A. intermedius*, *Kobeltia* species can be ruled out by their longer and thicker oviduct, which consists of more parts (*A. distinctus* 2 or 3 parts; *A. hortensis* always 3 parts) (Backeljau & De Bruyn 1990).

Surprisingly, one of the biggest species of *Arion*, *Arion ater* can also superficially resemble *A. intermedius* in external appearance. Hatchlings of *A. ater* overlap *A. intermedius* in size and may also have straw-coloured bodies with dark tentacles. The proportions and, later in development, the prominence of the foot fringe give a different general impression, but those without experience of both species should not identify an *A. intermedius* lacking the prickly tubercles or the small dots without checking for maturing genitalia. However, *A. ater* is rare or extinct in Hungary (Turóci & Páll-Gergely in press).

In other genera, juveniles of *Krynockia melanocephalus* and certain colour morphs of some *Deroceras* species might look superficially similar to *A. intermedius* but these can be immediately ruled out by the position of the pneumostome relative to the mantle (posterior in Agriolimacidae, anterior in Arionidae) and the shape of the tail (pointed in Agriolimacidae, rounded in Arionidae).

The life cycle of *A. intermedius* in the wild is one year. In southern England, individuals are highly synchronised in when they mature, in September (Hutchinson *et al.* 2017). The species was believed to reproduce only by selfing, based on genetic analyses (Foltz *et al.* 1982) and because of the lack of observations of spermatophores and mating (Davies 1977; Backeljau & De Bruyn 1990). Garrido *et al.* (1995) reported the presence of spermatophores for the first time, and the later discovery of some heterozygosity of allozymes implies that occasional outcrossing does occur (Reise *et al.* 2001; Jordaens *et al.* 2013).

A revisit to the collecting site of *A. intermedius* (by RV) in December 2024 resulted in the rediscovery of one living specimen (not collected). The occurrence in winter corresponds with studies elsewhere in its range (Hutchinson *et al.* 2017), but also December 2024 was mild even though the area lies in the vicinity of the eastern slopes of the Alps. That month in Szombathely, on 20 days the minimum temperature fell below freezing but none were colder than -5°C (AccuWeather). So possibly a population could persist over winter in that area.

Arion intermedius is presumed native to Western Europe, over much of which it occurs frequently (Rowson *et al.* 2014). Although it has recently appeared in Austria, which neighbours Hungary (Duda *et al.* 2019), whether the species is native to Central Europe is questionable. The closest location where the species shows a continuous distribution is in Czechia (Fig. 5A), more than 400 km from the Hungarian locality (Hlaváč & Horsák 2000). The absolute closest localities to Hungary are in Slovakia and Austria but these spots seem to be part of a sporadic rather than a continuous distribution. That suggests that *A. intermedius* is most likely an introduction to Hungary. In Kámoni Arborétum more than 3000 plant taxa are found, implying extensive exchange of horticultural specimens. *Arion intermedius* has several characteristics that enable it to exploit such interchange so as to colonise new sites. These include a broad ecological tolerance even of disturbed habitats, a tendency to ride on horticultural and agricultural products together with an ability to survive such journeys, and uniparental reproduction.

The situation with *A. transsylvanus* is rather different. In Hungary *A. transsylvanus* occurs in close proximity to *A. fuscus*, from which it is not distinguishable on external characters. Jordaens *et al.* (2010) provide anatomical characters to distinguish *A. transsylvanus* from *A. subfuscus* and *A. fuscus*. We cannot add to this since our specimen was juvenile.

Arion transsylvanus might also be confused with species besides those in the same complex. Certain colour morphs of *Arion vulgaris* juveniles can be similar to this species. Generally, *A. vulgaris* juveniles are more reddish than *A. transsylvanus*, which is usually yellowish with some orange tinge. The lineolation on the foot fringe is more prominent in *A. vulgaris* juveniles. It can be useful to consider the size of the tubercles; they are larger and the grooves between them are deeper in *A. vulgaris*, which results in a coarser skin surface compared with *A. transsylvanus*. The lateral bands are typically also stronger and wider in *A. vulgaris*.

According to current knowledge, *A. transsylvanus* is predominantly a Carpathian species, mostly restricted to the Transylvanian region in Romania (eastern and southern Carpathian Mountains and the Apuseni Mountains). The species is the only known representative of the *Arion subfuscus* species complex in Transylvania (Jordaens *et al.* 2010).

Besides the Romanian records, Jordaens *et al.* (2010) reported this species only from one site in eastern Poland. We are not aware of published records of the species since then, which may partly reflect a lack of confidence amongst malacologists in determining it anatomically and a lack of resources for DNA sequencing. However, Gural-Sverlova & Gural (2015) found no *A. transsylvanus*, only *A. fuscus*, in Ukraine, even though Ukraine bridges the gap between the Romanian and Polish records. Nevertheless, the absence of records between our finding in northern Hungary and the nearest locality in Romania (c. 200 km away) does not dissuade us from proposing that the species might be native in Hungary. One reason is that the Bükk Mountains are geographically part of the Western Carpathians. Furthermore, we found this species at a relatively high altitude (c. 800 m) in little-disturbed beech forest, which is consistent with occurrence data in Romania (Grossu 1970; Jordaens *et al.* 2010). Our collecting site was remote from settlements (along a hiking track c. 3 km from the village Répáshuta), which would be the most likely point of introduction. If it is indeed native in Hungary, *A. transsylvanus* would be the only such one of the nine slug species that we have either discovered as new to Hungary in the last six years or that were considered doubtful records until we confirmed them; the other eight species are very likely introductions. Besides *A. intermedius* and *A. transsylvanus*, these “new” species are: *Ambigolimax parvipenis* Hutchinson, Reise & Schlitt, 2022; *Ambigolimax valentianus* (A. Férussac, 1821); *Deroceras invadens* Reise, Hutchinson, Schunack & Schlitt, 2011; *Krynckillus melanocephalus* Kaleniczenko, 1851; *Limacus maculatus* (Kaleniczenko, 1851); *Milax nigricans* (Philippi, 1836); and *Tandonia kusceri* (H. Wagner, 1931). On the other hand, in Romania *A. transsylvanus* occurs also in synanthropic and other degraded habitats (Jordaens *et al.* 2010), so there is the potential that it has or will spread to such environments in countries adjacent to Romania, including Hungary.

The discovery of these two species of *Arion* may provide a guide to predicting what sort of further slug species might turn up new to the Hungarian fauna. Most likely are synanthropic species that spread as a result of trade and usually turn up in habitats like gardens, perhaps facilitated by the milder winters. A prediction for such a species is *Deroceras panormitanum* (Lessona & Pollonera, 1882) s.s., which has recently been reported in France (Ventura *et al.* in press). But additionally perhaps further native species have been overlooked in natural habitats in Hungary; these species may already be known from neighbouring countries. For instance, the genus *Lehmannia* has a centre of diversity in Romania, but the species are particularly hard to find during daylight and their identification requires dissection.

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Authors' Contribution

ÁT & BPG initiated the concept. RV, ÁT, RF and BPG collected the specimens. BS, MZN & KB were responsible for the sequencing. RV constructed the maps. ÁT wrote the manuscript, and all authors contributed to the final version, especially JMCH who corrected and edited the drafts.

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