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Research Article

Taxonomic revision of the land snail genus *Perpolita* (Gastrodontidae: Gastropoda)

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Using an integrative approach considering nuclear and mitochondrial molecular phylogeny, shell morphology, expressed ecological niches and biogeography, we revise the taxonomy and nomenclature within the Holarctic land snail genus *Perpolita* (Gastrodontidae; Gastropoda). All supported taxa were found to be not only genetically distinct but also to possess diagnostic conchology, especially in terms of colour and the strength of microsculptural spiral grooves ('sillons') cut into the bottom shell surface. Our revision resulted in: (i) synonymization of *Perpolita suzannae* into *P. dalliana*; (ii) erection of *Lapa* gen. nov. to encompass species limited to tropical/subtropical habitats in the Caribbean basin; (iii) elevation of *Perpolita radiatella* to a full species, ranging from Continental Europe to the Yukon. It had previously been confused with both *P. electrina* and *P. hammonis*; (iv) erection of *Perpolita radiatella hesperia* subsp. nov. to designate a distinct genetic race ranging from the Altai Mountains to central Europe.

http://zoobank.org/urn:lsid:zoobank.org:pub:3FFD4B50-1CD2-4C1C-A27C-F20C9EA7534C

Key words: geometric morphometrics, Holarctic, identification key, new genus, new subspecies, nomenclature

Introduction

Advances in quantitative multivariate methods using data ranging from DNA-sequence patterns to physical morphology and expressed ecological niche space have allowed for development of empirical, consensus-based taxonomic decision-making (e.g., Bickford et al., 2007; Köhler & Johnson, 2012; Tan et al., 2010). By seeing traditional taxonomic units as testable hypotheses – and by only accepting those which ultimately survive empirical confrontation across a consensus of information channels (Dayrat, 2005) – it is possible to root out spurious concepts which only exist within the minds of individual taxonomists (Nekola et al., 2022). In land snails this process has generally identified a 50% error rate in traditional concepts either through over-splitting, over-lumping, or the use of incorrect diagnostic features (Nekola & Horsák, 2022). However, unless such studies are accompanied by formal taxonomic revision, accepted nomenclature will not reflect these biological realities (Fišer et al., 2018; Jörger & Schrödl, 2013; Schlick-Steiner et al., 2010). Not formally conducting taxonomic acts thus introduces significant error into biodiversity research and limits the effectiveness of conservation planning (Mace, 2004; Raczkowski & Wenzel, 2007).

Here we revise nomenclature within the land snail genus *Perpolita* which represents a common constituent of assemblages across the Holarctic. This is necessary given that traditional, empirically unvetted concepts within the genus possess an 80% error rate compared with consensus mtDNA and nDNA sequence (Saito et al., 2024). In the following we use an integrative approach that empirically challenges all currently accepted traditional taxonomic concepts in this genus, considering not only mtDNA and nDNA phylogenetics, but also conchometrics as well as climatic and environmental niches. We use these data to not only refine species-scale taxonomy, but also genus and subspecies-

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level concepts. From this we formally revise the nomenclature so that it reflects biological reality.

Material and methods

Specimens

We focus on the six nominal species and one subspecies traditionally recognized to exist within *Perpolita* prior to Saito et al. (2024): *P. binneyana* (Morse, 1864) and *P. electrina* (Gould, 1841) are from temperate/boreal North America (Hubricht, 1985; Pilsbry, 1946); *P. petronella* (Pfeiffer, 1853) and *P. hammonis* (Strøm, 1765) are limited to temperate/boreal Eurasia (Sysoev & Schileyko, 2009; Welter-Schultes, 2012); while *P. dalliana* (Pilsbry, 1889) and *P. suzannae* (Pratt, 1978) are restricted to subtropical areas adjacent to the Gulf of Mexico (Hubricht, 1985; Pilsbry, 1946). Additionally, two subspecies are recognized within *P. binneyana*, with the nominate form occurring east of 100°W and *P. b. occidentalis* Baker, 1930 to the west (Pilsbry, 1946).

The generic assignment of this group has been subjected to various approaches. Baker (1941) noted their anatomical similarity to *Nesovitrea* Cooke, 1921 of tropical Oceania. Moreover, it erected *Nesovitrea* as a subgenus within *Retinella* Fischer, 1877, while *Perpolita* was treated as a 'section' within *Retinella* to hold these species. Based on this some subsequent authors (e.g., Hubricht, 1985; Turgeon et al., 1998; Welter-Schultes, 2012) lumped *Perpolita* into *Nesovitrea*. While this on the surface may appear biogeographically suspect, some boreal Alaska–Hawaiian disjunctions do exist in vascular plant species (e.g., Luer, 1975). However, based on consistent shell differences between the Oceania and Boreal species (in particular the bigger size and wider umbilicus of the former), and in deference to Schileyko (2003), Sysoev and Schileyko (2009) and MolluscaBase (2025), we have chosen in this work to use *Perpolita* to designate the genus for the boreal taxa.

The traditional species concepts within *Perpolita* were generally based on shell traits (especially size and colour) combined with geography (e.g., see Forcart, 1960; Taylor, 1908; Waldén, 1966, 1968 and synonymies in Systematics section below). Saito et al. (2024), however, revealed existence of significant taxonomic error rates among these empirically unvetted concepts, and with *P. dalliana* and *P. suzannae* being very genetically distinct from the remaining Perpolita. In spite of this no formal taxonomic acts were taken in that work. We aim to rectify this issue here.

Sample selection and DNA extraction

We used the 111 DNA extractions in Saito et al. (2024) to document gene pools across the entire geographic and ecological ranges of each *Perpolita* taxon. To these we have added additional samples for further exploration of optimum genus-level assignment. Information regarding these are provided in Supplemental Table S1. These new extractions are based on the methods of Saito et al. (2024) with total DNAs being isolated using the E.Z.N.A. Mollusc DNA Kit (Omega BioTek, GA, USA), following manufacturer protocols.

An individual of *Glyphyalinia wheatleyi* (Bland, 1883) collected at Natural Bridge, Rockbridge County, Virginia, USA represents perhaps the most important of these new extractions. This sample is from the site designated as the type location for *Glyphyalinia burringtoni* Pilsbry, 1928, a *nomen* subsequently synonymized into *G. wheatleyi* by Hubricht (1976). Because Baker (1928) used *G. burringtoni* as the type species for *Glyphyalinia* (*Glyphyalus*), subsequent elevation of this subgenus by de Winter et al. (2016) means that the genetics of the Natural Bridge *G. wheatleyi* population defines the putative genus *Glyphyalus*. This is of importance to the current work because the nearest known genetic neighbour of '*Glyphyalus*' *quillensis* is *Perpolita dalliana* (de Winter et al., 2016).

DNA sequence analyses

Species-level phylogeny within the group was previously reconstructed (Saito et al., 2024) separately for mtDNA (cytochrome b [CytB]) and nDNA (concatenated Internal Transcribed Spacer 1 of the rRNA gene cassette [ITS1] and Intron 8 of the Embryonic Lethality and Abnormal Visual System [ELAV8]; Nekola et al., 2023). We augment this here with POPART (Leigh & Bryant, 2015) haplotype network analysis using the TCS algorithm (Clement et al., 2000) to estimate population structure between the two geographically-constrained subclades within *P. radiatella.* Information regarding this is provided in Supplemental Table S2.

Because our prior work on *Perpolita* was focused on and limited to the species-scale (Saito et al., 2024), larger-scale taxonomic hypotheses were not considered. To investigate the number of genera present within the traditional concept of *Perpolita*, we constructed alignments containing representatives of all traditionally recognized *Perpolita* taxa plus other gastrodontid genera across four different genes: mitochondrial CytB and cytochrome c oxidase subunit 1 (CO1) plus nuclear ITS1 and ELAV8. While some of these sequences were generated *de novo* (especially for ELAV8) using the same protocols as in our previous studies (Horsáková et al., 2022; Saito et al., 2024), the remainder represent data retrieved from GenBank. We also note that new CytB, ITS1 and ELAV8 sequences for *Glyphyalus quillensis* were obtained from the same extractions used by de Winter et al. (2016) to generate CO1. All new sequences were deposited in GenBank (accession numbers PV123935–PV123946, PV154135–PV154140 and PV163298–PV163303). Full information regarding the provenance of all used sequences is found in Supplemental Table S1.

All regions were aligned using MUSCLE (Edgar, 2004) with default settings implemented on AliView (Larsson, 2014). Phylogenies were then independently reconstructed from each region using Bayesian inference (BI), maximum likelihood estimation (ML), and neighbour joining (NJ) via MrBayes 3.2.7a (Ronquist & Huelsenbeck, 2003), IQ-TREE 2.2.0 (Minh et al., 2020) or MEGA 10 (Stecher et al., 2020). For BI, appropriate evolutionary models (Supplemental Table S3) were selected using PartitionFinder 2 (Lanfear et al., 2017) under the Bayesian information criterion (BIC). BIs was performed with four simultaneous chains, sampling trees every 1000 generations for one million generations. The effective sample sizes (> 200) were confirmed for all parameters using Tracer v. 1.7 (Rambaut et al., 2018), and then we discarded the first 10% trees as burn-in. The remaining trees were summarized to reconstruct the maximum clade reliability tree, and the tree topology was evaluated by Bayesian posterior probability (BPP). For ML, appropriate evolutionary models (Supplemental Table S3) were selected using ModelFinder Plus including the free rate heterogeneity models implemented on IQ-TREE 2.2.0. Each model was evaluated using BIC and each ML tree topology was assessed using ultrafast bootstrapping (UFB; Hoang et al., 2018), each with 1000 replicates. NJ was conducted using maximum composite likelihood, and the tree topologies were assessed using bootstrapping (NJB).

Morphological examinations

Shell data were measured from 1–9 adult/sub-adult (≥ 2.75 whorls) individuals per genetically validated lot within collections housed at Masaryk University. We have supplemented these with type specimen shell images for *P. hammonis* (Neotype, Naturhistorisk museum, Oslo, Norway, NHMO-D27826), *P. viridula* (Menke, 1830) (Lectotype, Senckenberg Natural History Museum, Frankfurt am Main, Germany, SMF166599), and *P. radiatula* var. *radiata* (Lectotype, the Academy of Natural Sciences of Philadelphia, USA, AMS85788). In total, we examined 207 specimens (23 individuals from 5 populations for *P. binneyana*, 39/9 for *P. electrina*, 50/26 for *P. hammonis*, 30/10 for *P. petronella*, 24/6 for *P. radiatella radiatella*, 38/15 for the western *P. radiatella* subclade, plus the three museum specimens above; Supplemental Table S4).

All shell measurements were based on top, bottom and front images taken with an Olympus SZX10 microscope with Olympus C-7070 Wide Zoom camera and QuickPHOTO MICRO software at ca. 20×. Between 5–10 images were taken with focus from the bottom to top of the shell, and composited into a single, in-focus image using Combine ZM (https://combinezm.en.lo4d.com/windows).

From these seven shell measurements were determined using the methods of Cameron (2003): shell height (SH), width (SW), umbilicus width (UW), three different whorl widths (C1, C2 & C3), and the number of whorls (NW; Supplemental Fig. S1). Because these measurements are influenced by shell maturity/size, and not all potential standardized values are useful in shell characterization, we chose to only analyse four ratios which not only capture the major components of shell morphology but also collectively use all shell measurements: shell height vs. shell width; umbilicus width vs. number of whorls; expansion rate of early whorls (C2 vs. C1); and expansion rate of later whorls (C3 vs. C2). For each of these we estimated significance of differences between all pairwise combinations of the six genetically confirmed taxa using the Wilcoxon rank sum test. Because 15 total tests were performed within each, *P*-values were corrected using Holm's method.

Geometric morphometrics (GM; Rohlf & Marcus, 1993) was also used to investigate differences between taxa. These were based on 14 landmarks (Supplemental Fig. S1) visible in apertural view, which were digitized using tpsDig v.2.16 (Rohlf, 2010) with tps files being generated in tpsUtil v.1.53 (Rohlf, 2012). Generalized Procrustes Analysis in MorphoJ 1.07a (Klingenberg, 2011) was used to normalize rotation, translation, and size effects (Rohlf & Slice, 1990). Extracted Procrustes coordinates were then used to perform both Principal Components Analysis (PCA) and Canonical Discriminant Analysis (CDA). Results were visualized using the 'ggplot2' package in R (Wickham, 2016).

Two qualitative shell characters were also recorded. These included shell colour (dark red/brown to white) and distinctness of microsculptural radial grooves or striae (e.g., 'sillons' of Welter-Schultes, 2012: 208) on the shell bottom. This feature has been previously shown to be of species-scale diagnostic importance in the genus *Euconulus* (Horsáková et al., 2020; Welter-Schultes, 2012).

In addition to these conchological analyses, the genital anatomy of the two most genetically divergent members of *Perpolita* (*P. hammonis* and the western subclade of *P. radiatella*) were documented using standard tissue fixation and dissection methods.

Climatic niches and distribution

To obtain a general understanding of potential geographic ranges we used species-specific climate envelopes for each genetically validated taxon. These were generated using Maxent modelling of interpolated climate data from each of the 1781 verified *Perpolita* lots in the authors' collections based on genetically confirmed diagnostic criteria. The protocols, data and analyses used – as well as the climate envelopes generated from them – are presented in Saito et al. (2024). Here we plot these projected climate envelopes and known global occurrence data for each taxon based on not only the re-verified occurrence data in Saito et al. (2024), but also literature information (mainly Pilsbry, 1946; Hubricht, 1985; Sysoev & Schileyko, 2009; Welter-Schultes, 2012). From these, the ability of each species to saturate its potential global climate range can be determined. Additionally, given their importance in driving compositional turnover of land snail assemblages (Nekola, 2003), we qualitatively recorded water availability (wetland to upland) and tree cover (open to wooded) score from each collection site.

Results

DNA sequence analysis 1: genus-scale

For all mtDNA and nDNA amplicons (Fig. 1) most *Perpolita* species existed as a strongly supported monophyly (CytB: 0.94/-/96; CO1: 0.97/100/80; ITS1: 1.00/85/97; ELAV8: 1.00/100/100). However, *Glyphyalus quillensis*, *Perpolita dalliana* and *P. suzannae* represented a monophyly (CytB: BPP = 1.00/UFB = 90/NJB = 99; CO1: 1.00/100/100; ITS1: 1.00/97/100; ELAV8: 1.00/100/100) sister to but separated by a long branch from the remaining *Perpolita.* Both of these clades are members of deeper grouping containing *Aegopinella*, *Glyphyalinia*, *Pilsbryna*, *Retinella*, and *Striatura* – genera which have generally been assigned to the Gastrodontidae (Bouchet et al., 2017). Additionally, in all trees other limacoid genera such as *Deroceras*, *Euconulus*, and *Oxychilus* fall outside this grouping. Of particular importance is the relative position of *Glyphyalinia wheatleyi*, which represents a separate distant branch within the Gastrodontidae. Given that our sequence was obtained from a type location *G. burringtoni* individual, its topological position demonstrates that

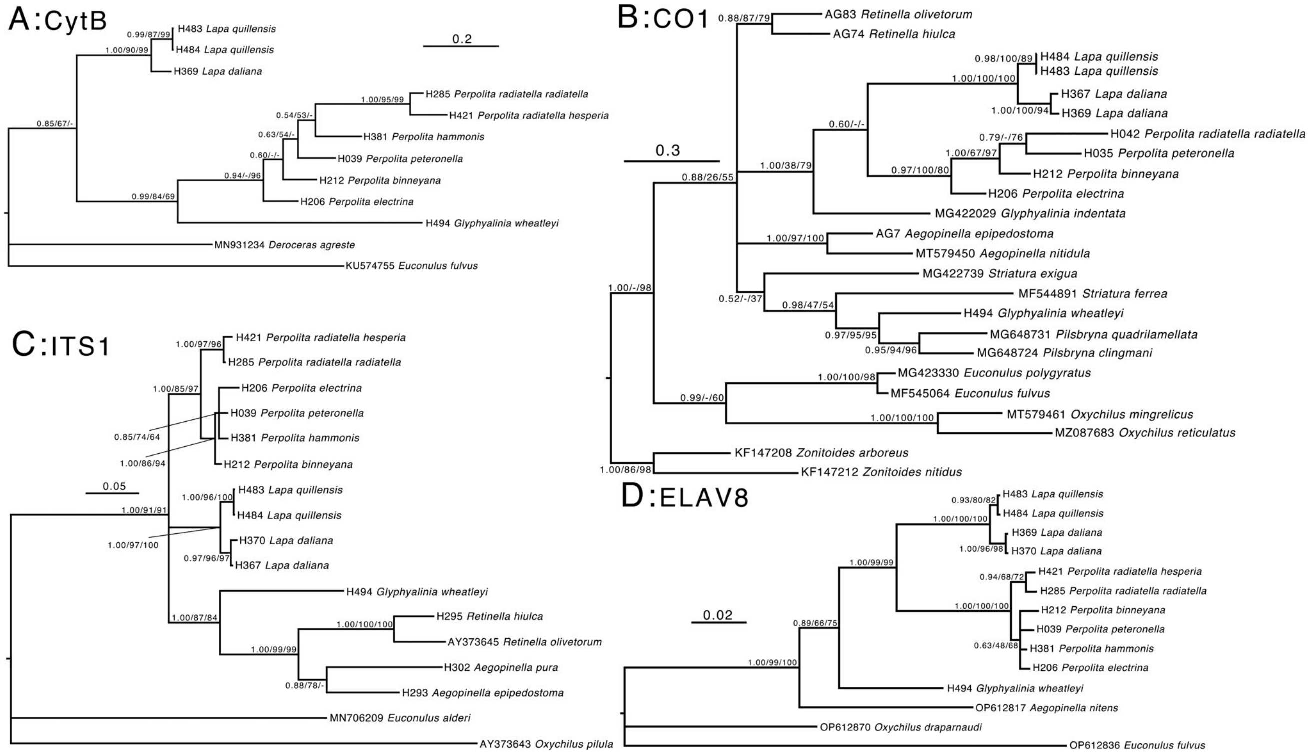

Fig. 1. Bayesian phylogenies of the genus *Perpolita*, *Lapa* gen. nov. and related genera. Labels indicate specimen codes and species names (Supplemental Table S1). Three different support values (Bayesian Posterior Probability/Ultrafast bootstrapping in maximum likelihood tree/Bootstrapping in neighbour joining tree) are displayed along the branches, except for the terminal nodes for visibility.

Glyphyalus is not available for the *dalliana*/*quillensis*/*suzannae* clade. Rather, a new *nomina* must be erected, which we will call *Lapa* gen. nov. Please see Systematics section below for full details.

DNA sequence analysis 2: species/subspecies scale

As shown by Saito et al. (2024), *Lapa dalliana* and *L. suzannae* share almost identical nDNA sequence, with ELAV8 possessing the same haplotype and only a single 4 bp insert differentiating samples in ITS1 (Fig. 1C–D). As a result, they should be considered a single species-level entity, for which *L. dalliana* has priority. In all trees the remaining *Perpolita* represent five reciprocally-monophyletic species: *P. binneyana*, *P. electrina*, *P. hammonis*, *P. petronella* and *P. radiatella* (Fig. 1).

As documented by both tree topologies and haplotype network analysis (Fig. 2), *P. radiatella* is segregated into two distinct gene pools, one ranging from Alaska to the Urals, and the other from the Altai to central Europe. These two clades are largely inseparable in the nDNA ITS1 + ELAV8 network (Fig. 2A), being demarcated by only 1–2 out of 19 total variable base pairs. As a result, we interpret *P. radiatella* to represent a single species. However, 26 bp substitutions – or approximately 38% of variable base pairs – distinguish the two geographically-structured subclades in mtDNA CytB (Fig. 2B). This suggests the existence of two subspecies. As there is no available *nomen* for the western race, we describe it here as *P. radiatella hesperia* subsp. nov. Please see Systematics section below for full nomenclatural details.

Morphological examinations

While all four standardized shell measurements (height vs. width; umbilicus width vs. number of whorls; early and late whorl expansion rate) documented significant variation between at least some pairwise comparisons, no taxon demonstrated statistically unique values (Table 1, Supplemental Table S5, Figs 3, 4 & Supplemental Dataset S1). Rather, considerable overlap was noted, with 2–4 taxa possessing statistically similar standardized scores. For shell height vs. width, *P. hammonis* possessed the lowest spire, ranging upward from

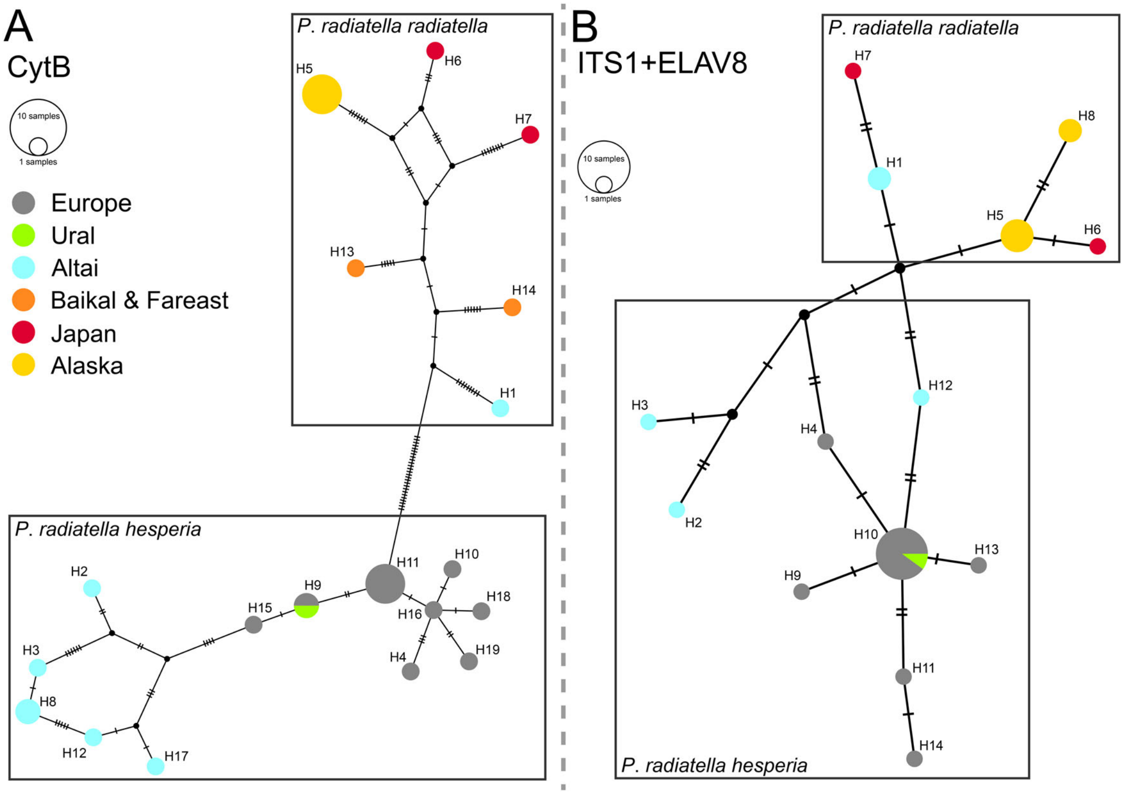

Fig. 2. Haplotype networks based on TCS algorithm (Clement et al., 2000) of mitochondrial cytochrome *b*, and Internal Transcribed Spacer 1 of the rRNA gene cassette plus Intron 8 of the Embryonic Lethality and Abnormal Visual System. The size of each circle represents the number of sequences with the respective haplotype and number. Letters adjacent to the haplotypes indicate haplotype numbers, and the colour of each circle indicates the geographic region of the sample (Supplemental Table S2). The bar on the branch denotes a mutation.

Table 1. Summary of morphological values of *Perpolita* species. Mean values and ranges (in brackets) are provided.

	P. binneyana	***P. electrina***	***P. hammonis***	***P. petronella***	***P. radiatella radiatella***	***P. radiatella hesperia* subsp. nov.**
SH (mm)	1.71 (1.44–2.00)	1.95 (1.66–2.23)	1.69 (1.44–2.09)	2.08 (1.73–2.69)	1.79 (1.52–2.12)	1.60 (1.40–1.94)
SW (mm)	3.35 (2.82–3.92)	3.68 (3.19–4.23)	3.39 (2.89–4.38)	3.89 (3.24–4.66)	3.45 (2.92–4.14)	3.11 (2.71–3.73)
SH/SW	0.51 (0.47–0.56)	0.53 (0.49–0.58)	0.50 (0.46–0.54)	0.54 (0.50–0.58)	0.52 (0.48–0.55)	0.51 (0.46–0.55)
UW/NW	207 (148–269)	210 (159–287)	192 (134–278)	213 (134–300)	220 (159–287)	210 (129–244)
Expansion Rate: Early	2.03 (1.58–2.58)	1.93 (1.58–2.35)	2.15 (1.65–2.70)	1.83 (1.40–2.25)	2.07 (1.54–2.52)	2.15 (1.60–2.71)
Expansion Rate: Late	1.91 (1.45–2.44)	1.81 (1.37–2.32)	1.75 (1.30–2.59)	1.91 (1.47–2.48)	1.69 (1.26–2.28)	1.70 (1.25–2.26)

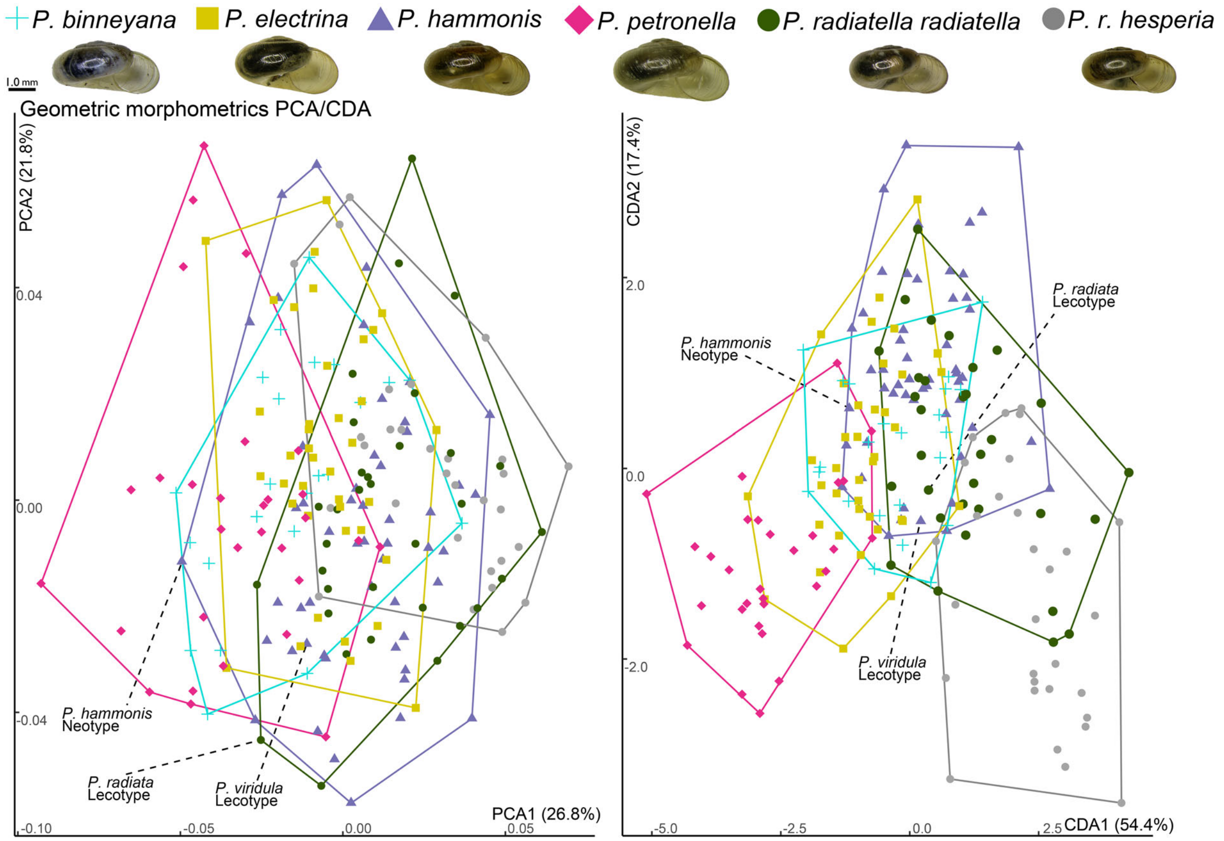

Fig. 3. Position of landmarked *Perpolita* shells along the first two axes of principal component analysis (PCA) and canonical discriminant analysis (CDA) based on geometric morphometrics of Holarctic *Perpolita* species. Colours and shapes of each plot indicate species/subspecies and type specimens used in these analyses were labelled individually. See Supplemental Table S4 for information of specimens used in the analyses, Supplemental Dataset S1 for full results of PCA and CDA, and Supplemental Table S5 for the eigen values and the proportion of variances for PCA.

P. binneyana, *P. radiatella hesperia*, *P. r. radiatella*, to *P. electrina* to *P. petronella* having the highest. For umbilicus width vs. number of whorls, *P. radiatella hesperia* possessed the narrowest relative umbilicus width, followed by *P. hammonis*, *P. binneyana*, *P. electrina*, and *P. petronella*, with *P. r. radiatella* having the largest. For early whorl expansion rates *P. petronella* grew the most slowly, followed by *P. electrina*, *P. binneyana*, *P. hammonis*, and *P. r. radiatella*, with *P. r. hesperia* having the most rapid growth. For later whorl expansion

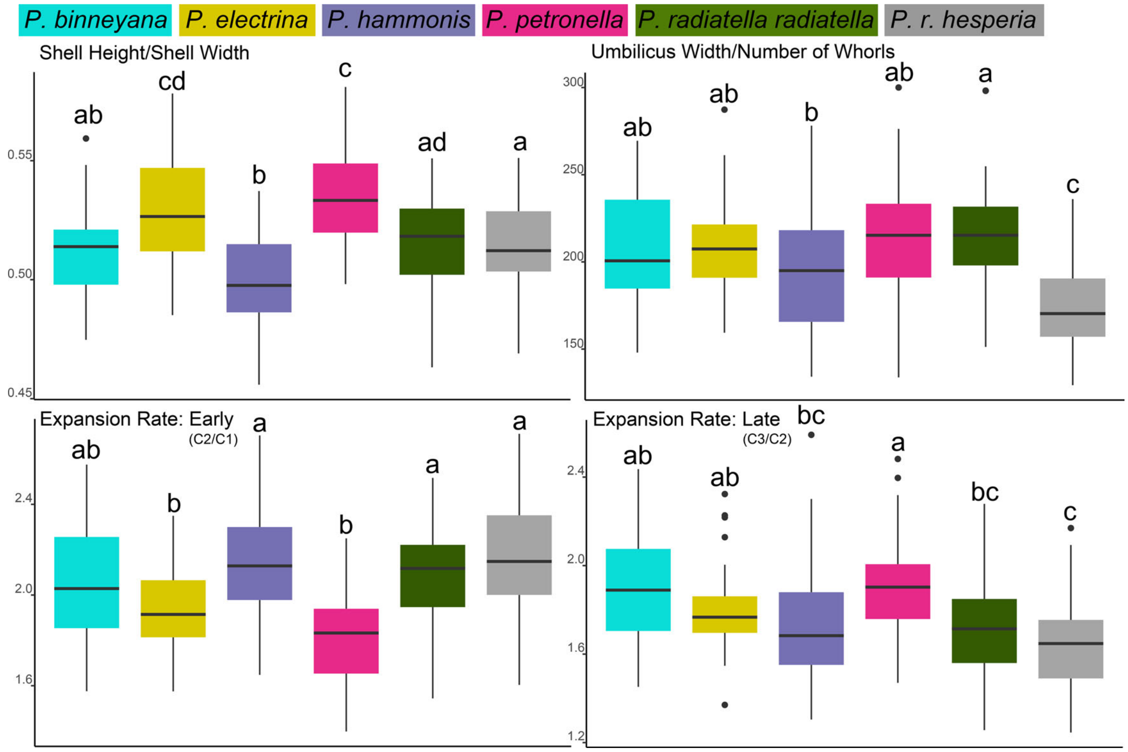

Fig. 4. Variation in shell characters of *Perpolita* species. Colours indicate species/subspecies. Letters above each bar indicate statistical significance of Wilcoxon rank sum test with Holm's correction for p values, meaning that there is a significant difference between the different letters at adjusted p level of 0.05. See Supplemental Table S6 for specific p values.

rates *P. r. hesperia* possessed the slowest growth, followed by *P. r. radiatella*, *P. hammonis*, *P. electrina*, and *P. binneyana*, with *P. petronella* having the fastest.

While geographic morphometric analyses of the 14 measured landmarks also demonstrated trends, profound overlap was again observed between taxa (Fig. 3). In PCA, almost complete overlap was noted along Axis 2. However, a gradient was present along Axis 1, with *P. petronella* possessing the lowest scores, trending higher through *P. electrina*/*P. binneyana*, *P. hammonis*, and *P. r. radiatella* to *P. r. hesperia*. While less overlap was observed in CDA between endpoint taxa (*P. petronella* vs. *P. r. hesperia*), gradual transitions again prevailed with none possessing unique scores. Because CDA does not detrend Axis 2 scores, the horseshoe shape of the scatterplot likely represents a simple mathematical artefact (Hill & Gauch, 1980) which does not inform regarding landmark arrangements. We note that the *P. hammonis* neotype exists on the margin of – and the *P. viridula* lectotype within – the characteristic polygon demarcating *P. hammonis* in both PCA and CDA space. Additionally, the *P. radiata* lectotype exists on or within the polygon characterizing *P. radiatella radiatella* in both PCA and CDA space.

In terms of qualitative shell characters, we noted consistent variation between taxa in shell colour with *P. petronella* having the lightest shells and *P. hammonis* having the darkest (Fig. 5). Of even more utility was the distinctness of sillons on the bottom shell surface, ranging from strong (*P. hammonis*) to absent in *P. binneyana* and *P. electrina* (Fig. 5).

Genitalic anatomy comparisons (Fig. 6) documented no diagnostic differences between *P. radiatella* and *P. hammonis*, the two most genetically divergent taxa.

Climatic and environmental niche difference

Potential vs. actual range maps for all species (Fig. 7) document that *P. hammonis* has the most restricted climate niche of all *Perpolita* species, being limited to maritime climates west of the Urals to Iceland, Madeira and the Azores. *Perpolita petronella* had a more extensive range extending from the eastern Atlantic coast of Scandinavia and central Europe east to the mountains of central Siberia. *Perpolita binneyana* and *P. electrina* had largely sympatric geographic ranges, extending from the Atlantic coast across north temperate and boreal North America to the Rocky Mountains/Alaska, with disjunct populations occurring south along the Rockies to the USA/Mexican border. Lastly, *P. radiatella* s.lat. possessed the largest potential and actual range, extending across Eurasia from Scandinavia and central Europe

Identification key for the Holarctic *Perpolita*

1(2) Fresh shell always translucent pale-yellowish to white (i.a, ii.a), bottom sillons weak (i.b) or absent (ii.b)……..........….......go to 3

2(1) Fresh shell dark brown-reddish (iii.a) /excluding rare albinos/, bottom sillons absent (iii.b) to strong (v.b)………..….........go to 5

3(4) Samples from Europe to Central Siberia, larger, higher spire (i.a), sillons weak (i.b), narrow umbilicus (i.c), wetlands…..***P. petronella***

4(3) Samples from N America, smaller, lower spire (ii.a), sillons absent (ii.b), widely open umbilicus (ii.c), mesic sites……….***P. binneyana***

5(6) Samples from N America, larger, aperture widely open (iii.a), very narrow umbilicus (iii.c), wetlands…………………….........***P. electrina***

6(5) Samples from Europe to Alaska and Yukon, smaller, aperture less open (iv.a, v.a)…..go to 7

7(8) Samples from the Urals to Alaska and Yukon, sillons very weak (iv.b) or absent ……………………………………........***P. radiatella***

8(7) Samples west of Urals..go to 9

9(10) Sillons mostly absent,(iv.b) narrower umbilicus (iv.c), mostly in wetlands…………….………………………..............***P. radiatella***

10(9) Sillons always strong (v.b), wider umbilicus (v.c), various habitats including mesic and acidic……………………….........***P. hammonis***

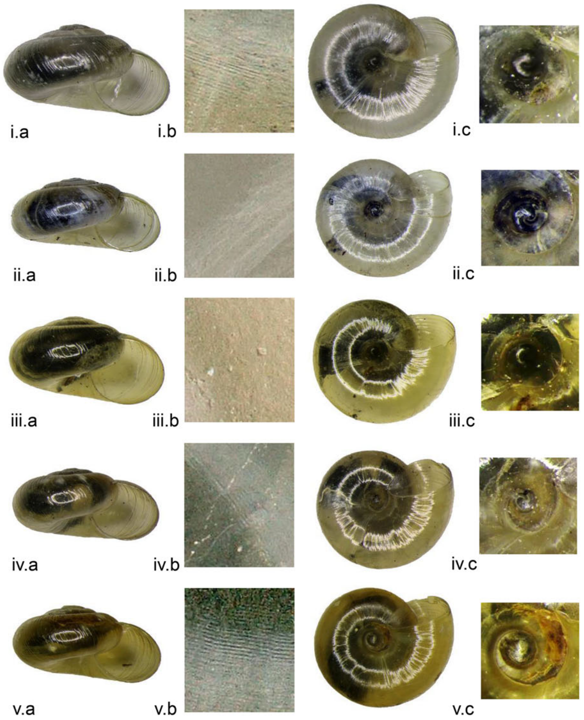

Fig. 5. Identification key for Holarctic *Perpolita* based on shell features and geographic information. Note that *P. hammonis* rarely develops a white-greenish form (see von Proschwitz, 1985), which is easy to confuse with *P. petronella* if only shell colour is considered.

to the Yukon in North America. While the nominate subspecies ranges from Western Siberia east to the Yukon, subsp. *hesperia* ranges from the mountains of central Asia west to the Northern Atlantic and the Alps, with an extensive zone of overlap occurring in Western Siberia (Fig. 7C).

Our cursory consideration of environmental range also suggest important distinguishing responses between taxa, with *P. binneyana*, *P. hammonis*, and *P. r. radiatella* occurring in upland, typically forested, habitats. However, *P. petronella*, *P. electrina*, and *P. r. hesperia* are typically lowland species, often being found in open graminoid-dominated sites.

Systematic account

Abbreviations for museum specimens: **ANSP**: Academy of Natural Sciences of Philadelphia (Philadelphia, Pennsylvania, USA); **BSNH**: Boston Society of Natural History (Boston, Massachusetts, USA); **NHMO**: Naturhistorisk Museum Oslo (Oslo, Norway); **NHMUK**: Natural History Museum (London, UK); **P**: Národní muzeum (Prague, Czech Republic); **RMNH**: Naturalis Biodiversity Center (Leiden, the Netherlands); **SMF**: Senckenberg Naturmuseum Frankfurt (Frankfurt, Germany); **USNM**: Smithsonian National Museum of Natural History (Washington, DC, USA).

Family **Gastrodontidae** Tryon, 1866

Genus ***Lapa*** **Saito & Nekola, gen. nov.**

Diagnosis. Shell dextral, flat, adult shell width up to approximately 6.0 mm (e.g., *L. quillensis*: 4.5–5.9 mm, $n = 11$ in de Winter et al., [2016]; *L. dalliana*: 2.25–2.50 mm, $n = 8$ in Pratt, [1978]); shell colour ivory or brownish ivory. Last whorl descending, slightly inflated toward aperture. At least weakly shouldered on periphery. Aperture oval in lateral view. Upper shell surface smooth with fine, distinct and slightly irregular radial striae. Umbilicus widely open.

Type species. *Glyphyalus quillensis* de Winter et al., 2016.

Etymology. *Lapa* means “snail” in the Muscogee/Creek language group, which includes Seminole of south Florida.

Differential diagnosis. Based on mitochondrial CO1/CytB, and nuclear ITS1/ELAV8 sequences, *Lapa* is distinct from all other genera in the Gastrodontidae while being sister to *Perpolita.* It can be conchologically distinguished from *Perpolita* by its widely open umbilicus,

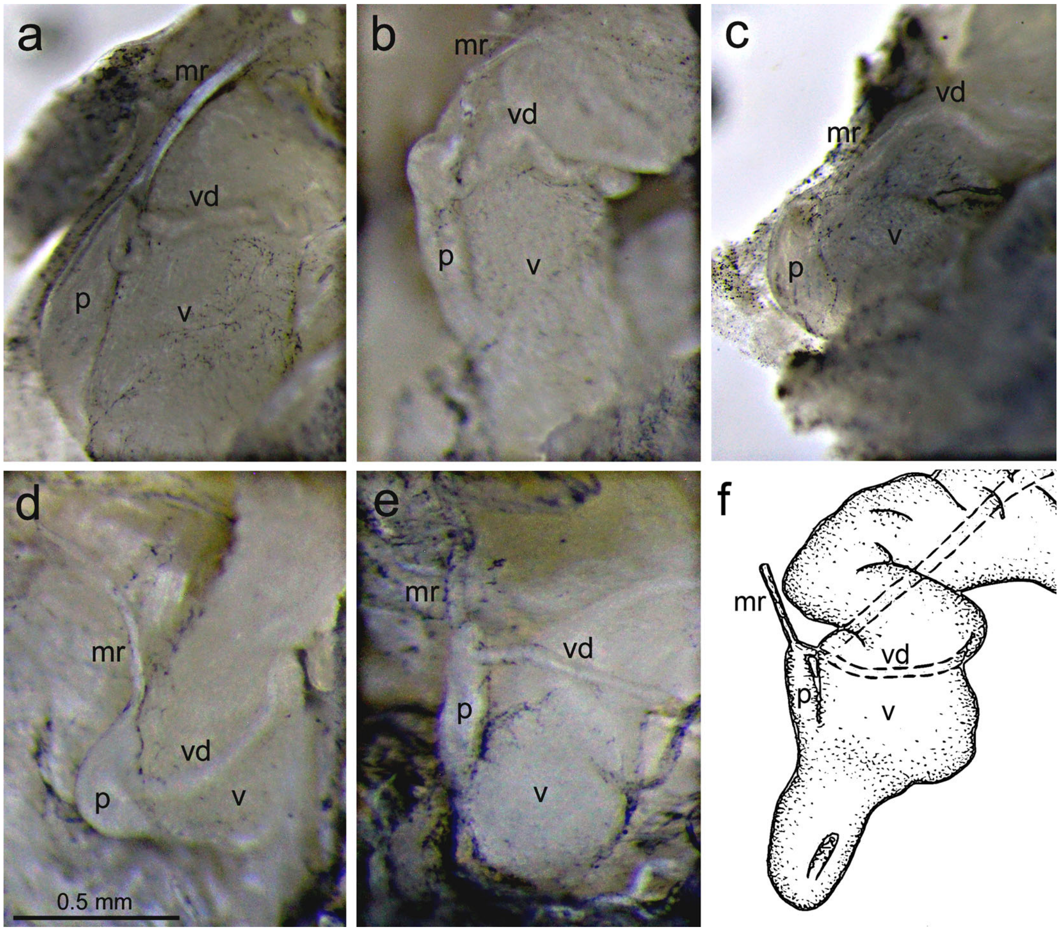

Fig. 6. Images of *Perpolita* genitalia: a–c, *P. radiatella hesperia* subsp. nov., Slovakia, Šúr NNR; d–e, *P. hammonis* (Strøm, 1765), Czechia, Řeka NR; f, *P. hammonis*/*radiatella*, adopted from Riedel (1980). Photos (a–e): M. Horsák. Abbreviations: mr, penial retractor muscle; p, penis; v, vagina; vd, vas deferens.

shouldered periphery and flatter shell shape. Fine, distinct and irregular striae on the top of the shell separates it from *Glyphyalinia* (*Glyphyaloides*) *roemeri* (Pilsbry & Ferriss, 1906) – the type species of *Glyphyaloides* Baker, 1930 (as *Vitrea dalliana roemeri*) – which has more fine, weak and regular striae/growth lines on the shell top (Pilsbry, 1946; Welter-Schultes, 2012). Others – such as *Glyphyalinia indentata*, the type species of *Glyphyalinia*, *Glyphyalinia* (*Glyphognomon*) *sculptilis* (Bland, 1858), the type species of *Glyphognomon* Baker, 1930, and *Glyphyalinia* (*Glyphyalops*) *rhoadsi* (Pilsbry, 1899), the type species of *Glyphyalops* Baker, 1928 – have more spaced, almost regular striae, which extend to the shell bottom. Genitalic morphology is only known for *L. dalliana* (as *Perpolita suzannae*): as shown by Pratt (1978), genitalic morphology of *Lapa* was also very simple and similar to *Perpolita* although a difference may exist in the inserted position of penial retractor (Baker, 1941; Hayase et al., 2016). Radula morphology is only known from *L. quillensis*: the central tooth exhibits tricuspid with an elongate cone and the marginal tooth exhibits an elongate and sharp unicuspid (de Winter et al., 2016). This pattern is also similar to *Perpolita*/*Nesovitrea* (e.g., Baker, 1941; Hayase et al., 2016; Pilsbry, 1946).

Distribution. North American Gulf Coast south to at least Saint Eustatius Island in the Caribbean.

Remarks. We note that based on shell similarity with *L. dalliana*, *Helix subhyalina* L. Pfeiffer, 1867 may belong in *Lapa*. Sadly this issue remains empirically unresolved due to lack of representative DNA sequence (see Discussion). In addition, *Zonitoides socorroensis* Dall, 1926 was treated as the subspecies of *Retinella subhyalina* by Baker (1930); however, based on the shell image from the original description, *Z. socorroensis* has regular striae, taller shell shape and lower expansion rate of shell coiling. Thus, it should not be a subspecies of *H. subhyalina*, or be included in *Lapa* or *Perpolita*.

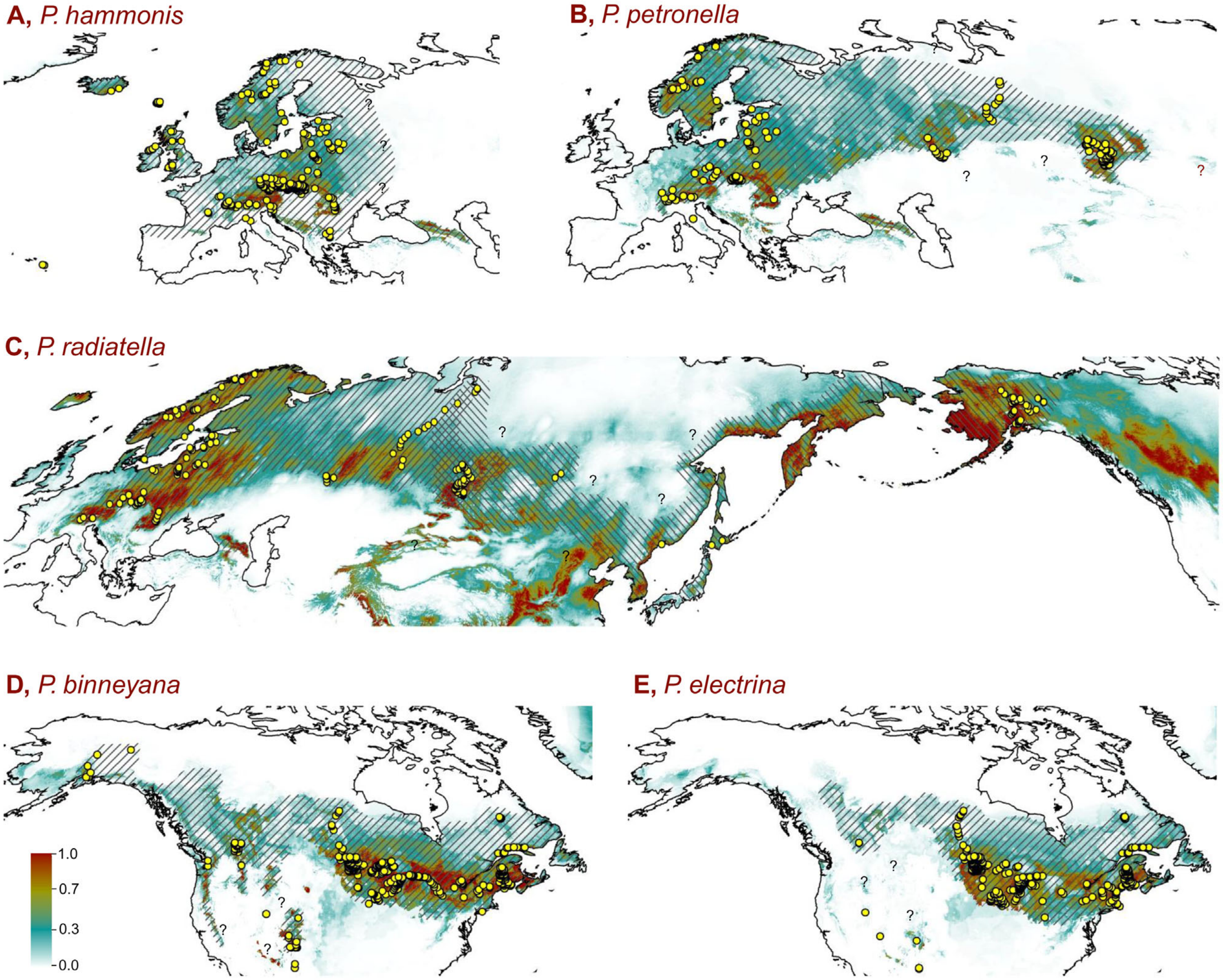

Fig. 7. A map of validated and potential distributions of each *Perpolita* species. Yellow points represent validated occurrences by this study and the colour spectrum indicates climatic suitability for each species based on climatic niche modelling adopted from Saito et al. (2024). The diagonal lines indicate assumed distribution based on literature data, climatic model prediction and our field experience.

***Lapa dalliana* (Pilsbry, 1889)** comb. nov

Zonites dallianus Simpson, 1888, p. 96, [*nomen nudum*].

Zonites dallianus Pilsbry, 1889, p. 83, pl. 3, figs 9–11, (original description).

Vitrea dalliana – Pilsbry & Ferriss, 1906, p. 152, fig. 9.

Retinella dalliana – Baker, 1928, p. 16.

Retinella (*Perpolita*?) *dalliana* – Baker, 1930, p. 199; Baker, 1933, p. 5.

Retinella (*Perpolita*) *dalliana* – Pilsbry, 1946, pp. 262–264, fig. 129.

Nesovitrea suzannae Pratt, 1978, pp. 19–20, figs 1–4. Type locality: Goose Island State Park, 1 mile east of Lamar, Aransas Co., Texas. Type material: Holotype (USNM711140; Pratt, 1978) [junior synonym].

Nesovitrea (*Perpolita*) *suzannae* Pratt, 1978, p. 19.

Nesovitrea? *dalliana* – Riedel, 1980, p. 85.

Nesovitrea dalliana – Hubricht, 1985, p. 23; Nekola, 2014, p. 12.

Nesovitrea suzannae – Hubricht, 1985, p. 23; Nekola, 2014, p. 12.

Perpolita dalliana – Saito et al., 2024, pp. 1–3, 5–6, 10, figs 1–4.

Perpolita suzannae – Saito et al., 2024, pp. 1, 3, 56, 10, figs 1–2.

Type locality. Shaw's Point, Manatee Co., Florida (Pilsbry, 1946).

Type material. Lectotype: ANSP60056 (Baker, 1962).

Differential Diagnosis. *Lapa quillensis* has a bigger and flatter shell than *L. dalliana* (Fig. 8).

Distribution. Central Texas Gulf Coast east to SE Georgia and the entirety of the Florida peninsula.

Ecology. Occurs in leaf litter across a range of habitats ranging from open sandy roadsides and wooded wetlands to upland oak and subtropical hardwood hammocks.

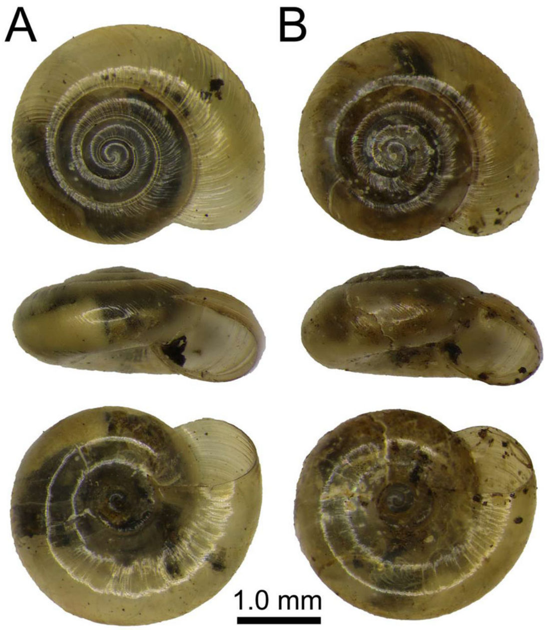

Fig. 8. Shell images of *Lapa dalliana* (Pilsbry, 1889): **A**. Lee County, Florida, USA; H367; **B**. Madison County, Florida, USA; H368.

Lapa quillensis (de Winter et al., 2016) comb. nov.
Nesovitrea sp. – Van der Valk, 1987, p. 283.
Glyphyalus quillensis de Winter et al., 2016, pp. 39–45, figs 1–5 (original description).

Type locality. 17.4780 N, 62.9634 W, The Quill, crater bottom, alt. 300 m, Saint Eustatius Island (de Winter et al., 2016).

Type material. Holotype: RMNH.5004017[shell] – RMNH.5004018 [soft parts, radula, jaw, DNA] (de Winter et al., 2016).

Differential Diagnosis. This species has larger shell width and flatter shell shape than any other *Lapa* and *Perpolita* considered here (de Winter et al., 2016).

Distribution. Saint Eustatius Island.

Ecology. Occurs in humid lowland tropical forest with rock outcrops (de Winter et al., 2016).

Genus ***Perpolita*** Baker, 1928

Type species. *Helix hammonis* Strøm, 1765 (by original designation in Baker, 1928; however, the designation was based on a misidentification of *Perpolita electrina*, and fixed here under Art. 70.3.1 of the ICZN).

Perpolita binneyana **(Morse, 1864)**

Hyalina binneyana Morse, 1864, p. 13, pl. 2, fig. 9, text-figs 25–26 & pl. 6, fig. 27 (original description).
Helix binneyana – Tryon, 1865, p. 188. [not L. Pfeiffer, 1847]

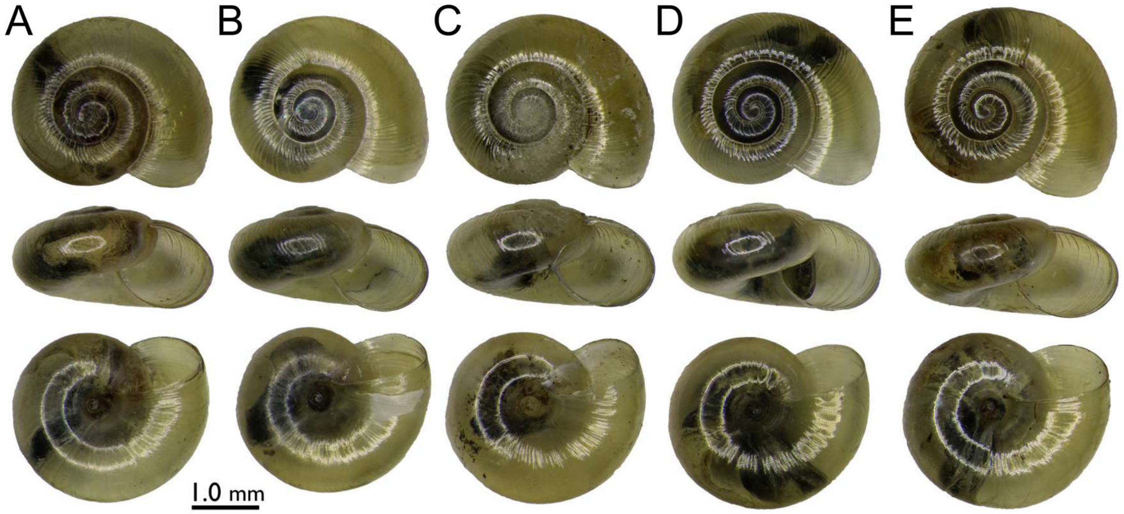

Fig. 9. Shell images of type specimens of *Perpolita radiatella hesperia* subsp. nov.: **A**. Holotype (Galvydiškes, Lithuania; NHMUK 20250026); **B**. Paratype (Galvydiškes, Lithuania; NHMUK 20250027); **C**. Paratype (Springs of Drava River, Italy; RMNH.MOL.452058); **D**. Paratype (Scuol, Lac Noir, Switzerland; NHMUK 20250030); **E**. Paratype (Domzhericy, Čistik, Belarus; NHMUK20250029).

Helix morsei Tryon, 1865, p. 188 [as a new replacement name for *Helix binneyana*; junior synonym].

Hyalina binneyana – Tryon, 1866, p. 252, pl. 4, fig. 31; Binney & Bland, 1869, pp. 39–40, figs 56–58; Jeffreys, 1872, p. 245.

Zonites binneyanus – Binney, 1878, pp. 120–121, fig. 36; Binney, 1885, pp. 180–181, fig. 174.

Vitrea binneyana – Dall, 1905, pp. 8, 39, fig. 27.

Hyalina binneyi Baker, 1930, p. 198 [*nomen nudum*].

Retinella (*Perpolita*) *binneyana* – Baker, 1928, p. 18, pl. 3, fig. 5; Baker, 1941, pp. 329–330; Pilsbry, 1946, pp. 259–262, figs 127–125, 127a.

Retinella (*Perpolita*) *binneyana binneyana* – Baker, 1930, p. 198; 1933, p. 5.

Retinella (*Perpolita*) *binneyana occidentalis* Baker, 1930, pp. 198–199, pl. 9, figs 1–3. Type locality: along McAleer Creek, near border of King Co., Washington. Type material: Holotype (ANSP150605; Baker, 1930) [junior synonym]; Baker, 1933, p. 5; Baker, 1941, pp. 329–330; Pilsbry, 1946, p. 262, figs 128–1, 128–3.

Retinella binneyana – Baker, 1939, p. 100.

Nesovitrea (*Perpolita*) *binneyana* – Forcart, 1957, p. 110; Roth & Sadeghian, 2003, p. 48.

Nesovitrea binneyana binneyana – Riedel, 1980, p. 85.

Nesovitrea binneyana occidentalis – Riedel, 1980, p. 85.

Nesovitrea binneyana – Hubricht, 1985, p. 23; Nekola, 2014, p. 12.

Nesovitrea (*Perpolita*) *binneyana occidentalis* – Roth & Sadeghian, 2003, p. 48.

Perpolita binneyana – Forsyth et al., 2022, pp. 1005, 1011; Saito et al., 2024, pp. 1–3, 5–12, figs 1–7, tables 3–4.

Type locality. Maine, USA (Morse, 1864).

Type material. Not located and perhaps lost.

Differential Diagnosis. In addition to genetic differences, the paler whitish shell colour and preference for upland habitats are important in differentiating *Perpolita binneyana* from *P. electrina*. While *P. petronella* also has white shells, it is larger in diameter, has a taller spire, and is largely limited to wetlands (Fig. 5).

Distribution. Temperate/boreal USA and Canada from Alaska to Labrador, south to Long Island, New York, southern Ontario, northern Michigan, northeastern Iowa and south along the Rocky Mountains to New Mexico and Texas; Fig. 7).

Ecology. Occurs across a wide range of forested upland habitats ranging from xeric pinelands to temperate forest and taiga. It is micro-sympatric with *P. electrina* in the drier parts of wooded wetlands.

Remarks. No evidence for gene pool partitioning or subspecies demarcation exists between eastern and western North American *P. binneyana* populations. As a result, we feel that subspecific classification within *P. binneyana* is inadvisable (Saito et al., 2024).

Perpolita electrina (Gould, 1841)

Helix electrina Gould, 1841, pp. 183–184, fig. 111, (original description); A. Binney, 1841, p. 423, pl. 22, fig. 2; Adams, 1841, pp. 273–274; De Kay, 1843, p. 30, pl. 3, fig. 26; A. Binney, 1851, pp. 236–238; Adams, 1853, p. 161; Morse, 1864, p. 13, text-fig. 23, pl. 6, fig. 24.

Helix janus Adams, 1841, p. 274. Type locality: Middlebury, Vermont, USA [junior synonym].

Hyalina viridula – Binney & Bland, 1869, pp. 34–35, figs 41–43 [part].

Hyalina electrina – Tryon, 1866, p. 251, pl. 4, fig. 25; Jeffreys, 1872, p. 245.

Zonites viridulus – Binney, 1878, pp. 115–116, pl. 29, fig. 1 [part]; Binney, 1885, pp. 64–65, figs 21–22 [part].

Vitrea hammonis – Walker & Pilsbry, 1902, p. 431, pl. 24, figs 10–12; Pilsbry & Ferriss, 1906, p. 151 [part].

Vitrea radiatula – Dall, 1905, pp. 8, 38–39 [part].

Hyalinia radiatula electrina – Taylor, 1908, pp. 97–100, figs 139–145 [part].

Retinella (*Perpolita*) *hammonis* – Baker, 1928, pp. 16–17, pl. 3, figs 1–4 [part].

Retinella (*Perpolita*) *electrina* – Baker, 1930, p. 196 [part]; Baker, 1933, p. 5 [part]; Baker, 1941, pp. 328–330; Pilsbry, 1946, pp. 256–259, figs 126 & 127-1–127-4 [part].

Glyphyalinia (*Perpolita*) *electrina* – Riedel, 1957, p. 407.

Nesovitrea (*Perpolita*) *hammonis* – Forcart, 1957, pp. 109–110, 115, fig. 4 [part].

Nesovitrea electrina – Riedel, 1980, p. 85 [part]; Hubricht, 1985, p. 23; Nekola, 2014, p. 12.

Nesovitrea (*Perpolita) electrina* – Zilch, 1959, p. 246, fig. 871; Roth & Sadeghian, 2003, p. 48.

Perpolita electrina – Forsyth et al., 2022, p. 1011; Saito et al., 2024, pp. 1–3, 5–13, figs 1–7, tables 3–4.

The following is sometimes treated as a synonym of *P. electrina* (MolluscaBase, 2025), but it is distinct from *Perpolita* based on the original description (Hombron & Jacquinot, 1847). To clarify the genus and species for this entry, further taxonomic consideration is required:

Helix janus var. *bifrons* Hombron & Jacquinot, 1847, pl. 5, figs 1–3.

The following is also sometimes treated as a synonym of *P. electrina* (MolluscaBase, 2025), but based on Pilsbry (1946) and Hubricht (1985) it represents a different entity:

Hyalinia radiatula electrina var. *circumstriata* Taylor, 1908, pp. 97–99, fig. 140, pl. 10 [= *Glyphyalinia wheatleyi* (Bland, 1883)].

Type locality. Fresh Pond, Cambridge, Massachusetts, USA; Missouri, USA (Gould, 1841).

Type material. Syntype: Massachusetts State Cabinet 107 & BSNH2392; possibly lost (Johnson, 1964).

Differential Diagnosis. In addition to genetic differences, the dark brown-red shell colour, slightly smaller size, and preference for wetland habitats differentiate it from *P. binneyana*. It is distinguished from *P. hammonis* and *P. radiatella* by its taller shell with comparatively more open umbilicus (Fig. 5).

Distribution. Temperate/boreal USA and Canada from British Columbia east to Newfoundland/Labrador, south to New York, Ohio, Iowa and along the Rocky Mountains to southern New Mexico; Fig. 7).

Ecology. Occurs across a variety of wetland habitats ranging from sedge meadows and fens to wooded wetlands. It also may be occasionally found in mesic to xeric grasslands.

Perpolita hammonis (Strøm, 1765)

Helix hammonis Strøm, 1765, p. 435, pl. 6, fig. 16 (original description); Kennard & Woodward, 1920, p. 84; Waldén, 1968, pp. 41–42, 44–48.

Helix (*Helicella*) *vitrina* Férussac, 1821, p. 45 [*nomen nudum*; see Alder, 1838].

Helix radiatula Alder, 1830, p. 38. Type locality: the vicinity of Newcastle upon Tyne [junior synonym]; Alder, 1838, p. 340; Dumont & Mortillet, 1857, pp. 339–340 [part].

Helix viridula Menke, 1830, p. 127. Type locality: Pyrmont [Germany]. Type material: Lectotype (SMF166599/1; Supplemental Fig. S2B); note that Waldén (1966, 1968) gave SMF166600/1, which is the number of paratype that also represent *P. hammonis* s.str.) [junior synonym]; Dumont & Mortillet, 1857, p. 340; Westerlund, 1865, p. 40 [part].

Zonites radiatulus – Gray, 1840, pp. 173–174 [part; pl. 5, fig. 50 is not *Perpolita hammonis*]; Jeffreys, 1862, p. 166; Bourguignat, 1864a, p. 2627; Bourguignat, 1864b, pp. 44–45, pl. 3, figs 15–17; Fagot, 1879, p. 287.

Zonites radiatulus var. *vitrina* Gray, 1840, p. 174. Type locality: the British Islands [junior synonym].

Helix (*Hyalina*) *radiatula* – Brown, 1844, p. 53, pl. 18*, figs 5–6.

Zonites (*Aplostoma*) *striatulus* – Moquin-Tandon, 1855, pp. 86–87 [part; not pl. 9, figs 19–21].

Zonites (*Aplostoma*) *purus viridulus* – Moquin-Tandon, 1855, pp. 87–89.

Helix radiatula var. *concolor* Dumont & Mortillet, 1855, p. 234. Type locality: Savoie et du basin du Léman [junior synonym].

Helix petronella – Dumont & Mortillet, 1857, pp. 338–339 [part].

Zonites radiatulus var. *viridescentialba* Jeffreys, 1862, p. 166. Type locality: the British Isles [junior synonym].

Hyalina (*Euhyalina*) *petronellae* – Stabile, 1864, p. 52 [part].

Hyalina hammonis – Mörch, 1864, pp. 11–12; Esmark, 1882, p. 95.

Helix (*Helicella*) *hammonis* – Westerlund, 1865, pp. 39–40 [part].

Hyalina viridula – Binney & Bland, 1869, pp. 34–35, figs 41–43 [part].

Zonites (*Hyalina*) *hammonis* – Westerlund, 1871, pp. 25–26 [part].

Zonites (*Hyalina*) *hammonis viridula* – Westerlund, 1871, p. 25.

Zonites radiatulus var. *alba* Jeffreys, 1872, p. 245. Type locality: Europe [invalid name due to publication as a synonym, ICZN art. 11.6].

Hyalina (*Euhyalina*) *viridula* – Clessin, 1876, pp. 74–75.

Hyalina (*Euhyalina*) *radiatula* – Clessin, 1876, p. 75, fig. 31 [part].

Oxychilus radiatulus – Jousseaume, 1877, pp. 419–421 [part; not pl. 2. figs 1–2].

Zonites viridulus – Binney, 1878, pp. 115–116, pl. 29, fig. 1 [part].; Binney, 1885, pp. 64–65, figs 21–22 [part].

Hyalinia hammonis – Esmark, 1882, pp. 98, 103; Westerlund, 1897, pp. 34–35.

Hyalinia (*Polita*) *radiatula* – Pollonera, 1885, p. 525.

Hyalinia (*Hyalinia*) *hammonis* – Esmark, 1886, p. 103.

Hyalinia (*Hyalinia*) *hammonis* var. *virescens* Esmark, 1886, p. 103 [*nomen nudum*].

Hyalinia (*Euhyalina*) *hammonis* – Esmark, 1886, p. 126.

Hyalinia (*Polita*) *hammonis* – Westerlund, 1886, pp. 44–45 [part]; Babor & Novák, 1909, p. 122 [part].

Vitrea (*Polita*) *radiatula* – Smith, 1891, p. 339.

Hyalinia hammonis f. *viridula* – Westerlund, 1897, p. 35.

Hyalinia hammonis t. *virescens* – Westerlund, 1897, p. 35.

Vitrea radiatula – Dall, 1905, pp. 8, 38–39 [part].

Vitrea hammonis – Pilsbry & Ferriss, 1906, p. 151 [part].

Hyalinia radiatula radiatula – Taylor, 1908, pp. 87–107, figs 128–130, 132–134, 145, pl. 10 [part].

Hyalinia (*Polita*) *hammonis* var. *viridula* – Babor & Novák, 1909, p. 122.

Helicella (*Retinella*) *radiatula* – Kennard & Woodward, 1926, pp. 181–183 [part].

Retinella (*Perpolita*) *hammonis* – Baker, 1928, pp. 16–17, pl. 3, figs 1–4 [part]; Baker, 1941, pp. 328–330; Likharev & Rammelmeier, 1952, p. 270, fig. 195 [part].

Retinella hammonis – Germain, 1930, p. 157, fig. 133, pl. 1, figs 23, 25–26 [part].

Glyphyalinia (*Perpolita*) *radiatula* – Riedel, 1957, pp. 406–407, fig. 18, pl. 46, fig. 6.

Nesovitrea hammonis – Waldén, 1966, pp. 161–194, figs 2–6, 10–14, 18; Welter-Schultes, 2012, p. 401, text-figs [part]; Waldén, 1968, pp. 41–42, 44–46, 48; Riedel, 1980, p. 85 [part].

Nesovitrea (*Perpolita*) *hammonis* – Forcart, 1957, pp. 109–110, 115 [part; not fig. 4]; Forcart, 1960, pp. 219–220; Riedel, 1966, pp. 72–73, figs 47–49.

Perpolita hammonis – Sysoev & Schileyko, 2009, p. 122 [part];

Saito et al., 2024, pp. 1–3, 5–13, figs 1–7, tables 3–4.

The following are sometimes treated as synonyms of *P. hammonis*; however, their actual identities remain uncertain:

Helix nitidula ver. β Draparnaud, 1805, pp. 117–118, pl. 8, figs 21–22 [invalid name].

Helix (*Helicella*) *nitidosa* Férussac, 1821, p. 41.

Helix (*Zonites*) *striatula* Gray, 1821, p. 239.

While the following are sometimes treated as synonyms of *P. hammonis* (Taylor, 1908; Kennard & Woodward, 1926), based on the illustrations and descriptions of type or possible type specimens in the original descriptions (Bourguignat, 1864a; Fagot, 1879; Moquin-Tandon, 1855; Turton, 1831) and subsequent studies (Bourguignat, 1864b) they appear to be distinct from *Perpolita*. To clarify the genus and species for each, further taxonomic considerations are required:

Helix brevipes Turton, 1831, p. 65, fig. 50 [not Draparnaud, 1805].

Zonites (*Aplostoma*) *striatulus* var. *albinos* Moquin-Tandon, 1855, pp. 86–87.

Zonites dumontianus Bourguignat, 1864a, p. 26.

Zonites subradiatulus Fagot, 1879, pp. 287–288 [from clay layer].

Type locality. Molde, Moere, Norway (Waldén, 1968).
Type material (Supplemental Fig. S2A). Neotype: NHMO-D27826 (Waldén, 1968).

Differential Diagnosis. In addition to genetic differences, the darker brown shell distinguishes it from *P. petronella* and *P. binneyana.* The distinct sillons on the bottom shell surface and preference for upland habitats differentiates it from both *P. electrina* and *P. radiatella* (Fig. 5). It is dimorphic in shell colour, with rare white-greenish individuals occurring within populations of typical brown form. This colour morph – termed 'f./var. *viridula/viridescentialba/concolor*' – appears most frequent in Scandinavia (von Proschwitz, 1985). Such shells may be confused with *P. petronella* by casual observers.
Distribution. Europe from Belarus and Ukraine west though Scandinavia and the British Isles to Madeira, Azores, and Iceland; Fig. 7.
Ecology. Occurs in a wide range of habitats from open to forest, humid to mesic, and acidic to alkaline. It is less common only in very dry and calcareous places (Horsák et al., 2013).

Perpolita petronella (L. Pfeiffer, 1853)

Helix petronella de Charpentier, 1852, p. 3 [*nomen nudum*]

Helix petronella Pfeiffer, 1853, p. 95 (original description); Dumont & Mortillet, 1857, pp. 338–339 [part]; Waldén, 1968, pp. 43, 46–47.

Hyalina (*Euhyalina*) *petronellae* – Stabile, 1864, p. 52 [part].

Zonites (*Hyalina*) *petronella* – Westerlund, 1871, pp. 26–27 [part].

Hyalina (*Euhyalina*) *radiatula* var. *petronella* – Clessin, 1876, p. 76.

Hyalina petronella – Esmark, 1882, pp. 95–96.

Hyalinia petronella – Esmark, 1882, pp. 98, 103.

Hyalinia (*Polita*) *petronella* – Pollonera, 1885, p. 525.

Hyalinia (*Polita*) *petronella* var. *cenisia* Pollonera, 1885, p. 525. Type locality: Piemonte, Italy [junior synonym].

Hyalinia (*Hyalinia*) *petronella* – Esmark, 1886, p. 103.

Hyalinia (*Euhyalina*) *petronella* – Esmark, 1886, p. 126.

Hyalinia (*Polita*) *petronella* – Westerlund, 1886, p. 45 [part].

Hyalinia petronella – Westerlund, 1897, p. 35.

Hyalinia radiatula petronella – Taylor, 1908, pp. 95–96, figs 136–137, 145 [part].

Zonitoides petronellus – Babor & Novák, 1909, p. 123 [part].

Helicella (*Retinella*) *petronella* – Kennard & Woodward, 1926, p. 183.

Retinella petronella – Germain, 1930, pp. 157–158.

Retinella (*Perpolita*) *petronella* – Likharev & Rammelmeier, 1952, p. 271, fig. 196 [part].

Glyphyalinia (*Perpolita*) *petronella* – Riedel, 1957, p. 407.

Nesovitrea (*Perpolita*) *hammonis* – Forcart, 1957, pp. 109–110, 115 [part].

Nesovitrea (*Perpolita*) *petronella* – Forcart, 1960, pp. 219–221, figs 1–2; Riedel, 1966, pp. 68–71, figs 42–46 [part].

Nesovitrea petronella – Waldén, 1966, pp. 161–174, 176–194, figs 2–3, 7–9, 15–17, 19; Welter-Schultes, 2012, p. 401, textfigs; Waldén, 1968, p. 48; Riedel, 1980, p. 85.

[?]*Perpolita petronella* – Schileyko, 2003: figs 1842B–C.

Perpolita petronella – Sysoev & Schileyko, 2009, p. 122, fig. 60B; Saito et al., 2024, pp. 1–3, 5–13, figs 1–7, tables 3–4.

The following is sometimes treated as a synonym of *P. petronella* (Likharev & Rammelmeier, 1952; Riedel, 1966); however, its actual identity remains uncertain.

Hyalinia petronellae var. *subnitidosa* Mousson, 1873, pp. 195–196.

The following is sometimes treated as a synonym of *P. petronella* (Taylor, 1908), but is assigned to a different genus by Welter-Schultes (2012).

Zonites jaccetanicus Bourguignat, 1870, pp. 41–42 [= *Zonitoides jaccetanicus*].

Type locality. Summae Alpes Helvetiae [Summit of Swiss Alps] (Pfeiffer, 1853).

Type material. Lectotype: BMNH1966231 (Forcart, 1960; Waldén, 1968).

Differential Diagnosis. In addition to genetic differences, shell size is usually bigger than other *Perpolita* species, with the expansion rate of early coiling being distinctively lower, with the shell colour being whitish (Fig. 5).

Distribution. Interior Scandinavia, east Germany and French/Italian Alps east at least to the Altai in southern Siberia (Fig. 7). We note that empty shells occur within a sample collected at a single site in Primorsky Krai in far-eastern Siberia (Frank Walther lgt.; M. Horsák det.), well outside of its documented native distribution. Additional investigation will be required to determine the status of this record.

Ecology. It is a wetland species, typically of high elevation forest spring areas and in areas of colder climate such as Scandinavia. Rare lowland populations in Central Europe represent relicts from Early Holocene (Horsák et al., 2013). In Siberia is also common in mesic hemiboreal forests (M. Horsák, unpubl. data).

Perpolita radiatella radiatella (Reinhardt, 1877)

Hyalina (*Euhyalina*) *radiatella* Reinhardt, 1877a, p. 90 (original description); Reinhardt, 1877b, pp. 313–314, pl. 9, fig. 5.

Hyalina pellucida Lehnert, 1884, p. 172. Type locality: Point Barrow, Alaska [junior synonym; not O. F. Müller, 1774; not A. Gould, 1843; not C. B. Adams, 1845].

Vitrea radiatula var. *radiata* Pilsbry & Hirase, 1904, p. 117. Type locality: Tōya, Kuziro, Yesso (Hokkaido) [Toya, Kushiro Town, Hokkaido Pref.]. Type material. Holotype (ANSP85788a; Supplemental Fig. S2C) [junior synonym].

Vitrea radiatula – Dall, 1905, p. 8, 3839 [part].

Retinella (*Perpolita*) *electrina* – Baker, 1930, p. 196 [part]; Baker, 1933, p. 5 [part]; Pilsbry, 1946, pp. 256–259, figs 126 & 127-1–127-4 [part].

Retinella radiatula – Kuroda & Miyanaga, 1939, pp. 68, 70.

Retinella (*Perpolita*) *hammonis* – Likharev & Rammelmeier, 1952, p. 270 [part].

Nesovitrea (*Perpolita*) *hammonis* – Forcart, 1957, pp. 109–110, 115 [part].

Nesovitrea (*Perpolita*) *hammonis* – Riedel, 1967, pp. 365–366.

Radiatell[sic] *raduatula*[sic] *radiata* – Kwon & Habe, 1979, p. 29.

Nesovitrea electrina – Riedel, 1980, p. 85 [part].

Nesovitrea hammonis – Riedel, 1980, p. 85 [part]; Welter-Schultes, 2012, p. 401, textfig [part]; Hayase et al., 2016, pp. 23–24, figs 7-3, 8-1a-1c.

Retinella radiatula radiata – Minato, 1988, p. 130.

Retinella radiatella – Minato, 1988, p. 131.

Perpolita electrina – Schileyko, 2003: figs. 1842 A.

Perpolita hammonis – Sysoev & Schileyko, 2009, p. 122, fig. 60 A [part].

Perpolita radiatella – Saito et al., 2024, pp. 1–3, 5–12, figs 1–7, tables 3–4 [part].

The following is described as a subspecies of *P. radiatella*; however, based on the original description (Kwon & Lee, 1991) it is distinct from *Perpolita*. Further taxonomic consideration is required to assign its correct generic status.

Retinella radiatula coreana Kwon & Lee, 1991, pp. 7–8, text fig.

Type locality. Mohedsi, Hakotade, Yesso [Hakodate, Hokkaido Pref., Japan].

Type material. Not located. Types do not reside in the Museum für Naturkunde Berlin (T. Saito, per. obs.) or Senckenberg Naturmuseum Frankfurt (Sigrid Hof, pers. comm.).

Differential Diagnosis. In addition to genetic differences, the shell colour is usually brown, distinguishing it from *P. binneyana* and *P. petronella*. It is distinguished from *P. hammonis* by its missing or very weak bottom sillons (Saito et al., 2024). While it also tends to possess a flatter spire and wider umbilicus than *P. electrina* considerable overlap exists (Fig. 5).

Distribution. Western Siberia east to Alaska and the Yukon (Fig. 7). Based on nDNA and mtDNA signal, northern Western Siberia represents a co-occurrence/hybrid zone with *P. radiatella hesperia* subsp. nov.

Ecology. Although it ranges across a wide variety of habitats from wetlands, sedge meadows and subalpine meadows to riparian and mesic forests to xeric grasslands, it appears to be most frequent in upland sites (Hayase et al., 2016; Riedel, 1967).

Remarks. The original description of *P. radiatella radiatella* lists two type localities: Kino-O-Sima [Kii Oshima Island, Wakayama Prefecture] and Hakodate, Hokkaido Prefecture. The former is based on a report of *Hyalina electrina* by Adams (1868), which is highly doubtful (Kuroda, 1941) given that Kii Oshima is one of the warmest places on Honshu Island, Japan.

***Perpolita radiatella hesperia* Saito & Nekola, subsp. nov**

Perpolita hammonis – Sysoev & Schileyko, 2009, p. 122 [part].

Nesovitrea hammonis – Riedel, 1980, p. 85 [part]; Welter-Schultes, 2012, p. 401, textfig [part].

Perpolita radiatella – Saito et al., 2024, pp. 1–3, 5–12, figs 1–7, tables 3–4 [part].

Type locality. 55.7835 N, 22.9722E, Galvydiškes, Lithuania.

Type material. Holotype: NHMUK 20250026 (Fig. 9A); Paratypes: NHMUK 20250027–20250030, RMNH.MOL.452056–452058, P6M044040–044042 (Fig. 9B–E).

Etymology. 'Hesperia' means "western" in Greek, reflecting the western distribution of this subspecies.

Description. Shell dextral, discoidal, small, up to 3.73 mm in shell width (2.71–3.73; $n = 30$ in our measurement), 1.94 mm in shell height (1.40–1.94); shell spire low; shell colour glossy light brown. Last whorl descending, slightly inflated toward aperture, without angle or keel. Aperture oval in lateral view. Upper shell surface having irregular striae extending to lateral side. Bottom shell surface having no or very weak sillons. Umbilicus small.

Differential Diagnosis. This subspecies can only be identified using genetic markers. Potential shell differences with *P. r. radiatella*, such as its narrower umbilicus, appear to be under ecophenotypic control and should not be used to demarcate this race (Fig. 5).

Distribution. Interior Scandinavia, central Europe, and Italian Alps east to the Altai Mountains in Siberia. Northern Western Siberia represents a co-occurrence/hybrid zone with *P. radiatella radiatella.*

Ecology. Compared with *Perpolita hammonis*, *P. radiatella hesperia* tends to occur more often in wetlands, especially minerotrophic fens (Horsák et al., 2013; M. Horsák unpubl. data).

Remarks. Based on our literature survey all prior European *Perpolita* nomina appear to be synonymies with *P. hammonis* and *P. petronella* based on the original descriptions, type specimens and geographic location of the type locality and are thus not available for this subspecies.

Discussion

The integrative revision conducted here documents that the traditional understanding of *Perpolita* was flawed, in fact representing two distinct genera, one (*Lapa*) confined to tropical/semitropical areas adjacent to the Gulf of Mexico/Caribbean, and the other (*Perpolita*) being confined to the boreal areas across the Holarctic. *Lapa* represents at least two species, with *L. quillensis* having been previously assigned to *Glyphyalus*, and *L. dalliana* having been incorrectly split into two species. We note that the nomenclature of this genus remains unresolved because we were unable to secure amplifiable DNA for *Helix subhyalina* Pfeiffer, 1867, which has typically been assigned to *Perpolita* (Pilsbry, 1946). This Mexican Gulf Coast taxon has shells which fall within the normal variability of *L. dalliana*. If DNA sequence shows it to be a member of the same species-level clade, then the rules of priority would require the use of *L. subhyalina* for the entire Gulf Coast entity.

Perpolita represents five species (*P. binneyana*, *P. electrina*, *P. hammonis*, *P. petronella*, *P. radiatella*) which are distinct not only in their mtDNA and nDNA sequences but also their conchology, geographic, and ecological ranges. These differences have been summarized via a dichotomous key which allows for accurate specimen identification without the need for DNA sequence barcodes (Fig. 5). Because no diagnostic conchometric differences exist between taxa – as has been often seen in land snails genera such as *Euconulus* (Horsáková et al., 2020), *Paralaoma* (Nekola et al., 2024), and *Pyramidula* (Horsáková et al., 2022) – the primary features used for identification are qualitative features of shell colour and sillon strength on the bottom shell surface in addition to population location in both geographic and ecological space.

We found no diagnostic differences in the genitalic anatomy of the two most genetically distant species. Previous studies have alluded to a high degree of anatomical similarity within *Perpolita* (Baker, 1928), with Waldén (1966) documenting the high degree of overlap between *P. hammonis* (possibly including *P. radiatella*), *P. petronella*, and *P. electrina* individuals. We thus conclude that genitalic anatomy is of little use in distinguishing *Perpolita* species. We note that this lack of species-scale signal in genital morphology is a general issue in land snails: Roth et al. (2013) for instance documented that genital differences traditionally assumed to correlate with subgenus-level distinctions in *Deroceras* Rafinesque, 1820 actually represent between-individual variation within *D. laeve* (Müller, 1774). In general, the use of genital anatomy for species-scale diagnoses is complicated by intraspecific polymorphism (Baur, 2007), anatomical plasticity (Baur et al., 1993), ontogenetic changes (Emberton, 1985), and technical issues related to tissue fixation, dissection, and/or observation (Emberton, 1989). We have found these issues to be so profound that genitalic and radular anatomy, on average, provide much less useful information streams in distinguishing genetically defined species than shell features (Nekola, 2014).

An unresolved issue, however, is the correct generic assignment for the *binneyana*/*electrina*/*hammonis*/*petronella*/*radiatella* clade. Unfortunately, our attempts at locating mummified tissue with extant long-stranded DNA within Hawaiian *Nesovitrea* lots at ANSP and UMMZ universally failed. We were also unable to secure mummified tissue samples and/or DNA sequence from the Bishop Museum (Norine Yeung, pers. comm.). Thus, final resolution of this issue will require additional work, likely involving newly obtained field samples.

We also note in passing some interesting incongruencies between projected and observed ranges. For instance, the estimated climate range for *P. binneyana* appears considerably overestimated on its southeastern margin, with no occurrences being known south of the Great Lakes east from Iowa even though climate niche models suggest it should extend south to the Ohio River. This discrepancy appears due to the fact that the southernmost sites in Iowa are all associated with unique microclimates associated with cold, moist air emanating from ice caves. Since this habitat type does not extend east of the upper Mississippi River Valley (Nekola, 1999), the actual range of this species terminates 500–700 km north of projected envelope southern limit. While a similar issue is present in *P. electrina*, whose southernmost sites tend to be spring fens associated with cool groundwater upwellings, the fact that these habitats do occur across north-central and northeastern North America allows for congruence in its projected and actual ranges.

However, not all apparent cases of undersaturated potential ranges are due to such microclimatically driven biases. For instance, *P. radiatella* appears to be absent from appropriate climatic zone regions in China, the Himalayas, and the North American taiga east of the Yukon. While we are rather certain – based on our field work – that it is truly absent from British Columbia east to Hudson's Bay and the Great Lakes, we are less certain of its absence from temperate east Asia. There are some reliable records of *Perpolita* from the Honshu Island and South Korea (Hayase et al., 2016; Riedel, 1967), and we would not be surprised if future investigators document populations from other temperate Asian regions, perhaps hidden away in other gastrodontid/zonitid genera. And in Europe, both *P. petronella* and *P. radiatella hesperia* have actual ranges that terminate in interior Scandinavia and central Europe well before the end of appropriate regional climates closer to the Atlantic coast. We suspect, but cannot prove, that this is due to factors other than climate and dispersal limitation – such as soil and water chemistry – defining their western range limits.

We lastly note that of the seven traditionally recognized taxa (eight if '*Glyphyalus*' *quillensis* is included), only *P. petronella* remained unchanged in its nomenclature and confirmed diagnostic traits following integrative revision. All the remaining demonstrated errors including: assignment to the wrong genus (e.g., *G. quillensis*, *P. dalliana*), over-splitting (e.g., *L. suzannae*, *P. binneyana occidentalis*), and overlumping (with *P. radiatella* being placed into both *P. electrina* and *P. hammonis*). Also, the critical diagnostic trait of sillon strength on the shell bottom had never been previously noted. This 80% error rate is a reminder that traditional taxonomic hypotheses should be considered suspect and likely not reflective of actual biological divisions – even for seemingly well-known groups. Empirical testing of traditional taxonomic hypotheses is thus essential for improving our understanding of land snail biodiversity and the conservation actions required to protect it.

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Supplemental material

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Data accessibility statement

All data generated during this study are included in this published article, its supplementary materials, Zenodo (10.5281/zenodo.14300346) and deposited in GenBank (PV123935–PV123946, PV154135–PV154140 and PV163298–PV163303). Holotype and paratypes are deposited in NHMUK20250026–20250030, RMNH.MOL. 452056–452058 and P6M044040–044042.

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Table S1 in Saito et al. 2025. Samples used for genus level phylogenies.

Species	Code	Locality	GenBank Acce. Nos.	Reference
Cytb dataset				
Deroceras agreste	–	Sweden, Västergötland	MN931234	Zając & Stec, 2020
Euconulus fulvus	DLR211 (MTH10-41)	USA, Oregon	KU574755	GenBank
Glyphyalinia wheatleyi	H494	USA, Virginia	*	This study
Lapa quillensis	H483	Lesser Antilles, St. Eustatius Isl.	*	This study
	H484	Lesser Antilles, St. Eustatius Isl.	*	This study
Lapa dalliana	H369	USA, Florida	PP573463	Saito et al., 2024
Perpolita binneyana	H212	USA, Maine	PP573433	Saito et al., 2024
Pe. electrina	H206	USA, Maine	PP573420	Saito et al., 2024
Pe. hammonis	H381	Norway, Kveriksuoset	PP573471	Saito et al., 2024
Pe. petronella	H039	Switzerland, Grindjisee	PP573400	Saito et al., 2024
Pe. radiatella radiatella	H285	Russia, Tyumenskaya Oblast	PP573425	Saito et al., 2024
Pe. radiatella hesperia subsp. nov.	H421	Lithuania, Galvydiškes	PP573489	Saito et al., 2024
CO1 dataset				
Aegopinella nitens	AG07	France, Jura	*	This study
A. nitidula	ZMH100975-2841	Germany, Elgersburg	MT579450	Neiber et al., 2020
Euconulus fulvus	BIOUG24635-C07	Canada, Yukon Territory	MF545064	deWaard et al., 2019
E. polygyratus	BIOUG24635-F09	Canada, Ontario, Ottawa Region	MG423330	GenBank
Glyphyalinia indentata	BIOUG15235-C06	Canada, Ontario, Pelee Island	MG422029	GenBank
G. wheatleyi	H494	USA, Virginia	*	This study
Lapa quillensis	H483	Lesser Antilles, St. Eustatius Isl.	*	This study
	H484	Lesser Antilles, St. Eustatius Isl.	*	This study
Lapa dalliana	H367	USA, Florida	*	This study
	H369	USA, Florida	*	This study
Oxychilus mingrelicus	ZMH86999-1754	Russia, Bolshoy Sochi	MT579461	Neiber et al., 2020
O. reticulatus	ZMH86479-3528	Georgia, Jikha	MZ087683	Neiber et al., 2022
Perpolita binneyana	H212	USA, Maine	*	This study
Pe. electrina	H206	USA, Maine	*	This study
Pe. peteronella	H035	Sweden, Viken	*	This study
Pe. radiatella radiatella	H042	Russia, Tyumenskaya Oblast	*	This study
Pilsbryna clingmani	UF341346A	USA, North Carolina	MG648724	GenBank
Pi. quadrilamellata	UF434354c	USA, Tennessee	MG648731	GenBank
Retinella hiulca	AG83	Italy, Lombardia	*	This study
R. olivetorum	AG74	France, Bouches-du-Rhône	*	This study
Striatura exigua	BIOUG14969-G05	Canada, New Brunswick	MG422739	GenBank
S. ferrea	BIOUG12145-H01	Canada, Nova Scotia	MF544891	deWaard et al., 2019
Zonitoides arboreus	E003	Malaysia, Sabah	KF147208	Capinha et al., 2014
Z. nitidus	HK0002	Netherlands, Leiden	KF147212	Capinha et al., 2014

ITS1 dataset				
Aegopinella epipedostoma	H293	Czech Republic, Moravia, Vápenky	*	This study
A. pura	H302	Czech Republic, Moravia, Štramberk	*	This study
Euconulus alderi	E188	France, Massif Central	MN706209	Horsáková et al., 2019
Glyphyalinia wheatleyi	H494	USA, Virginia	*	This study
Lapa quillensis	H483	Lesser Antilles, St. Eustatius Isl.	*	This study
	H484	Lesser Antilles, St. Eustatius Isl.	*	This study
Lapa dalliana	H367	USA, Florida	PP565334	Saito et al., 2024
	H370	USA, Florida	PP565333	Saito et al., 2024
Oxychilus pilula	–	Italy, Capraia Isl.	AY373643	Manganelli et al., 2004
Perpolita binneyana	H212	USA, Maine	PP565305	Saito et al., 2024
Pe. electrina	H206	USA, Maine	PP565245	Saito et al., 2024
Pe. hammonis	H381	Norway, Kveriksuoset	PP565294	Saito et al., 2024
Pe. peteronella	H039	Switzerland, Grindjisee	PP565270	Saito et al., 2024
Pe. radiatella radiatella	H285	Russia, Tyumenskaya Oblast	PP565308	Saito et al., 2024
Pe. radiatella hesperia subsp. nov.	H421	Lithuania, Galvydiškes	PP565324	Saito et al., 2024
Retinella hiulca	H295	Italy, Lombardia	*	This study
R. olivetorum	–	Italy, Siena	AY373645	Manganelli et al., 2004
EVAL8 dataset				
Aegopinella nitens	AG09	France, Doubs, Jougne	OP612817	Nekola et al., 2022
Euconulus fulvus	E163	Iceland, Skaftafell National Park	OP612836	Nekola et al., 2022
Glyphyalinia wheatleyi	H494	USA, Virginia	*	This study
Lapa quillensis	H483	Lesser Antilles, St. Eustatius Isl.	*	This study
	H484	Lesser Antilles, St. Eustatius Isl.	*	This study
Lapa dalliana	H369	USA, Florida	PP573355	Saito et al., 2024
	H370	USA, Florida	PP573356	Saito et al., 2024
Oxychilus draparnaudi	–	USA, Colorado	OP612870	Nekola et al., 2022
Perpolita binneyana	H212	USA, Maine	PP573314	Saito et al., 2024
Pe. electrina	H206	USA, Maine	PP573321	Saito et al., 2024
Pe. hammonis	H381	Norway, Kveriksuoset	PP573358	Saito et al., 2024
Pe. Petronella	H039	Switzerland, Grindjisee	PP573336	Saito et al., 2024
Pe. radiatella radiatella	H285	Russia, Tyumenskaya Oblast	PP573370	Saito et al., 2024
Pe. radiatella hesperia subsp. nov.	H421	Lithuania, Galvydiškes	PP573386	Saito et al., 2024

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Table S2. Saito et al., 2025. Evolutionary models used in phylogenetic analyses.

Regions	**Cytb (codon position_1/2/3)**		**CO1 (codon position_1/2/3)**	
Methods	ML	BI	ML	BI
Models	1: K3Pu+F+R2/2+3: HKY+F+G4	1: HKY+G/2: K80+G/3: F81+I	1: K3Pu+F+R2/2: TN+F+G4/3: F81+F+I+G4	1: HKY+G/2: GTR+G/3: F81+I

ITS1		**ELAV8**	
ML	BI	ML	BI
TPM3+G4	K80+G	HKY+F+G4	HKY+G

Table S4. Saito et al., 2025. Samples used for morphometrics analyses.

Species	ID	Specimens nos. used for morhpological examination	Latitude °N	Longitude °E	Locality	Habitat	Date	Collector
Perpolita binneyana	H208	1	47.89440	-95.62500	USA, Minnesota, Polk County	Disturbed aspen, balsam poplar forest	08/2001	J. Nekola
P. binneyana	H209	1	35.73400	-106.44340	USA, New Mexico, Sandoval County	Cool base of open talus slope	06/2007	J. Nekola
P. binneyana	H213	5	55.03470	-98.53920	Canada, Manitoba, S. of Thompson	Spruce-Larix-Alder-Cloudberry wetland	08/2003	J. Nekola
P. binneyana	H215	4	50.20250	-63.40170	Canada, Quebec, Duplessis County	Spruce-balsam forest and bodering fen	08/2006	J. Nekola
P. binneyana	H216	6	64.56980	-149.09790	USA, Alaska, North Nenana	Aspen forest on S-facing rocky slope	08/2007	J. Nekola
P. binneyana	H255	6	47.89440	-95.62500	USA, Minnesota, Polk County	Disturbed aspen, balsam poplar forest	08/2001	J. Nekola
P. electrina	H200	3	45.89330	-84.74900	USA, Michigan, Mackinac County	Thuja swamp forest and rich fen	09/2009	J. Nekola
P. electrina	H201	7	54.79550	-98.77530	Canada, Manitoba, Pipun	Alder-Willow-Dogwood thicket	08/2003	J. Nekola
P. electrina	H202	6	42.68770	-91.57780	USA, Iowa, Clayton County	Xeric, N-facing limestone glade	08/2002	J. Nekola
P. electrina	H205	1	50.22580	-63.44240	Canada, Quebec, Duplessis County	Mesic Abies-Picea-Acer forest	08/2006	J. Nekola
P. electrina	H206	7	44.81880	-68.72260	USA, Maine, Penobscot County	Alnus scrub on disturbed river bank	10/2002	J. Nekola
P. electrina	H207	1	44.82670	-75.62200	Canada, Ontario, Leeds and Grenvil County	Black Ash-alder swamp forest	10/2008	J. Nekola
P. electrina	H243	5	50.92130	-116.42291	Canada, British Colombia, Incommapleux Kelly creek	Extremely rich fen in the river aluvium	11/2008	M. Horsák
P. electrina	H341	6	42.28150	-91.83230	USA, Iowa, Benton County	Rich hillside fen	09/2012	J. Nekola
P. electrina	H353	3	46.71810	-96.29280	USA, Minnesota, Clay County	Xeric prairie with aspen scrub	07/2000	J. Nekola
P. hammonis	H046	4	46.65397	7.00603	Switzerland, Le Bugnon, Maules	Rich Sphagnum-fen	08/2012	M. Horsák, V. Horsáková
P. hammonis	H047	1	64.02667	-16.97650	Iceland, NP Skaftafell	Shruby tundra	08/2016	M. Horsák
P. hammonis	H050	2	62.56839	12.24583	Sweden, Hamratjäller, Röstavallen	Alkaline fen	08/2006	M. Horsák
P. hammonis	H051	4	49.60694	16.16508	Czech Republic, Rožanecké paseky	Slope fen	08/2012	M. Horsák, V. Horsáková
P. hammonis	H344	1	46.80047	10.26419	Switzerland, Ftan	Calcareous fen	08/2012	M. Horsák, V. Horsáková
P. hammonis	H345	1	42.33949	23.53116	Bulgaria, Prodanov, Prodanovci	Alkaline meadow fen	07/2005	M. Horsák
P. hammonis	H347	1	49.66653	15.85269	Czech Republic, PR Řeka, Hluboká	Alkaline fen	04/2012	M. Horsák, V. Horsáková
P. hammonis	H351	4	46.55125	11.60172	Italy, Christel Alm	Rich Sphagnum-fen by Doser Schweige and Mont de Bulacia	07/2013	M. Horsák, V. Horsáková
P. hammonis	H354	1	46.54353	8.35950	Switzerland, Prameny Rhony	Rich Sphagnum-fen	08/2012	M. Horsák, V. Horsáková
P. hammonis	H355	1	46.54353	8.35950	Switzerland, Prameny Rhony	Rich Sphagnum-fen	08/2012	M. Horsák, V. Horsáková
P. hammonis	H358	2	37.76856	-25.47800	Portugal, Azores Isl., Lagoa da Fogo Lake	N wall shrubs	09/2008	M. Horsák
P. hammonis	H361	1	46.77806	10.28164	Switzerland, Scuol, Lac Noir 2	Highly alkaline fen	08/2012	M. Horsák, V. Horsáková

P. hammonis	H365	5	57.63917	-4.19833	UK, Scotland, Jemimaville	Damp mossy open birch forest	07/2018	M. Horsák
P. hammonis	H366	5	56.15667	-3.88222	UK, Scotland, Aviemore, Loch Baeg	Sphagnum-rich fen in the littoral of the lake	07/2018	M. Horsák
P. hammonis	H371	4	47.23342	13.50667	Austria, Obertauren, Glőcknerin hill	Alpine vegetation with Salix reticulata, under shrubs	09/2013	M. Horsák
P. hammonis	H372	1	54.76114	26.78186	Belarus, Stakhoucy, Stakhouci	Alkaline meadow fen (Sphagno-Tomentypnion)	07/2017	M. Horsák, V. Horsáková
P. hammonis	H377	1	46.60708	6.00786	France, Les Thévenins, Lac des Rouges-Truites	Highly alkaline fen	08/2016	M. Horsák, V. Horsáková
P. hammonis	H379	1	46.21667	25.88981	Romania, Vrabia	Nutrient-rich alkaline fen with Primula farinosa a Carex lasiocarpa	08/2014	M. Horsák, V. Horsáková
P. hammonis	H381	1	69.06778	20.56772	Norway, Kveriksuoset	Water logged Sphagnum-fen	07/2019	M. Horsák, V. Horsáková
P. hammonis	H383	1	46.52578	11.62700	Italy, Paluch din Ladins	Alkaline meadow fen (Sphagno-Tomentypnion)	07/2013	M. Horsák, V. Horsáková
P. hammonis	H391	1	54.73136	28.26172	Belarus, Čistik, Domzhericy	Highly alkaline fen with Saxifraga hirculus	07/2017	M. Horsák, V. Horsáková
P. hammonis	H416	1	50.18343	16.83399	Czech Republic, Velká Morava	Upper Morava river valley	07/2002	M. Horsák
P. hammonis	H418	1	49.51927	18.63024	Czech Republic, Horní Lomná	Rich Sphagnum-fen	09/2000	M. Horsák
P. hammonis	H419	1	49.51927	18.63024	Czech Republic, Horní Lomná	Rich Sphagnum-fen	09/2000	M. Horsák
P. hammonis	H420	1	55.78350	22.97219	Lithuania, Galvydiškes	Highly alkaline fen with Saxifraga hirculus	08/2015	M. Horsák, V. Horsáková
P. hammonis	H422	1	55.76292	26.36167	Latvia, Matīša	Poor Sphagnum-fen	08/2015	M. Horsák, V. Horsáková
P. hammonis	H423	1	57.60203	26.19442	Latvia, Bednes	Alkaline meadow fen (Sphagno-Tomentypnion)	08/2015	M. Horsák, V. Horsáková
P. hammonis	H426	1	59.30333	25.11939	Estonia, Paraspõllu	Water logged calcareous fen	08/2015	M. Horsák, V. Horsáková
P. petronella	H035	1	63.49822	15.39256	Sweden, Viken, Hagamarken	Alkaline fen	08/2006	M. Horsák
P. petronella	H036	2	62.30053	9.60631	Norway, Dovre Fiell	Dovre Fiell NP, sloping spring fen	08/2006	M. Horsák
P. petronella	H037	1	46.48569	8.47172	Switzerland, All´Acqua	Alkaline fen	07/2013	M. Horsák, V. Horsáková
P. petronella	H038	1	62.23814	10.66461	Norway, Størmyra NR	Rich Sphagnum-fen	08/2006	M. Horsák
P. petronella	H039	1	46.01067	7.79614	Switzerland, Grindjisee	Alkaline fen	08/2012	M. Horsák, V. Horsáková
P. petronella	H040	6	51.73389	85.72333	Russia, Altai Republic, Altai Mts., distr. Maima	Hemiboreal forest with Pinus sylvestris on a river terrace	07/2011	M. Horsák
P. petronella	H041	5	51.62333	85.69500	Russia, Altai Republic, Altai Mts., Shebalino distr.	Hemiboreal Pinus sylvestris forest on a steep NE facing slope	08/2005	M. Horsák
P. petronella	H357	4	52.80639	58.29833	Russia, Bashkortostan Republic, Irendyk range, Baimak distr.	Wet hemiboreal forest	07/2007	M. Horsák
P. petronella	H359	5	48.85008	19.87703	Slovakia, Polomka pod tratí	Moderately rich fen with Sphagnum, Aulacomnium, and Tomenthypnum	06/2012	M. Horsák, V. Horsáková
P. petronella	H387	4	59.00583	69.04833	Russia, Tyumenskaya Oblast', distr. Uvat, Turtas	Boreal forest	08/2013	M. Horsák
P. radiatella hesperia	H043	4	50.54694	87.78472	Russia, Altai Republic, Altai Mts., Ulagan distr., Ulagan: near the road to Aktash 16 km SW of the village	Species-rich grassland	07/2006	M. Horsák
P. radiatella hesperia	H044	1	51.73444	85.73167	Russia, Altai Republic, Altai Mts., distr. Maima, Ust'-Muny: slope above the road ca 2.5 km NNW of the village	Hemiboreal forest in a shallow ravine	07/2011	M. Horsák
P. radiatella hesperia	H048	1	51.57167	86.09944	Russia, Altai Republic, Altai Mts., Nizhnii Kuyum: Kuyum river valley, 0,3 km NNE of the settlemet	Species-rich steppic meadow on a stepp S facing slope	08/2005	M. Horsák

P. radiatella hesperia	H049	3 including a paratype	46.72281	12.25303	Italy, Springs of Drava River	Alkaline fen	07/2013	M. Horsák, V. Horsáková
P. radiatella hesperia	H321	3 including a paratype	46.77719	10.28214	Switzerland, Scuol, Lac Noir	Alkaline fen	08/2012	M. Horsák, V. Horsáková
P. radiatella hesperia	H346	4	49.66653	15.85269	Czech Republic, PR Řeka, Hluboká	Alkaline fen	04/2012	M. Horsák, V. Horsáková
P. radiatella hesperia	H356	1	52.08639	57.33028	Russia, Bashkortostan Republic, Novoaleksandrovka	Hemiboreal forest with Larix sibirica	07/2007	M. Horsák
P. radiatella hesperia	H373	1	54.00506	23.21189	Poland, Sarnetki	Rich Sphagnum-fen	06/2011	M. Horsák, V. Horsáková
P. radiatella hesperia	H380	1	46.70008	12.22086	Italy, Toblacher See	Alkaline meadow fen	07/2013	M. Horsák, V. Horsáková
P. radiatella hesperia	H389	1	59.98750	71.28861	Russia, Tyumenskaya Oblast', Salym	Boreal forest	08/2013	M. Horsák
P. radiatella hesperia	H390	4 including a paratype	54.73136	28.26172	Belarus, Čistik, Domzhericy	Nutrient-rich alkaline fen with Saxifraga hirculus	07/2017	M. Horsák, V. Horsáková
P. radiatella hesperia	H421	9 including the holotype and paratypes	55.78350	22.97219	Lithuania, Galvydiškes	Highly alkaline fen with Saxifraga hirculus	08/2015	M. Horsák, V. Horsáková
P. radiatella hesperia	H427	2	59.30333	25.11939	Estonia, Paraspõllu	Calcareous fen	08/2015	M. Horsák, V. Horsáková
P. radiatella hesperia	H431	2	57.04431	22.78072	Latvia, Puzuru Grava	Calcareous fen overgrown by reed	08/2015	M. Horsák, V. Horsáková
P. radiatella hesperia	H433	1	57.37956	21.85511	Latvia, Zingeri	Small alkaline fen in a forest	08/2015	M. Horsák, V. Horsáková
P. radiatella radiatella	H203	6	65.46620	-148.33390	USA, Alaska, Livengood East	Rich riparian spruce/birch forest	08/2018	J. Nekola
P. radiatella radiatella	H285	1	43.36298	143.80370	Japan, Hokkaido Pref., Kamiashoro Motomachi		07/2012	J. Nekola
P. radiatella radiatella	H340	4	62.89070	-149.75010	USA, Alaska, Little Coal Creek trail	Acid spruce/alder/birch forest	08/2018	J. Nekola
P. radiatella radiatella	H342	4	61.20060	-149.96100	USA, Alaska, Earthquake Park	Open aspen beach ridge	08/2007	J. Nekola
P. radiatella radiatella	H343	3	61.77880	-148.47520	USA, Alaska, Chickaloon	Xeric, S-facing aspen-spruce slope	08/2007	J. Nekola
P. radiatella radiatella	H350	6	63.50080	-145.86000	USA, Alaska, Black Rapids	Rich riparian willow/alder	08/2018	J. Nekola
Museum specimens								
P. hammonis	HMO_D2782	Neotype: *P. hammonis*	NA	NA	Norway, Moere, Molde	NA	07/1915	F. Oekland
P. hammonis	SMF166599	Lectotype: *P. viridula*	NA	NA	Germany, Lower Saxony, Bad Pyrmont	NA	07/1827	K.T. Menke
P. radiatella radiatella	AMS85788	Lectotype: *P. radiatula* var. *radiata*	NA	NA	Japan, Hokkaido Pref., Kushiro, Toya	NA	10/1903	NA

Table S5. Saito et al., 2025. Eigen values and the proportion of variances of principal component analyses.

Proportion of variance

	0.26825	0.21773	0.10066	0.09031	0.07284	0.04259	0.03543	0.03526	0.03135	0.02147	0.01489	0.01290	0.01142	0.01056	0.00825	0.00728	0.00529
	GM_PCA1	GM_PCA2	GM_PCA3	GM_PCA4	GM_PCA5	GM_PCA6	GM_PCA7	GM_PCA8	GM_PCA9	GM_PCA10	GM_PCA11	GM_PCA12	GM_PCA13	GM_PCA14	GM_PCA15	GM_PCA16	GM_PCA17
x1	-0.09430	-0.01330	-0.04331	-0.09963	-0.16275	-0.03710	-0.06252	-0.22144	0.25835	-0.02845	-0.43063	0.46288	0.08342	-0.39495	0.00259	-0.04415	0.16186
y1	-0.17754	0.01902	0.14455	0.17345	-0.03017	-0.00405	0.00472	-0.10463	0.12565	-0.11744	-0.14140	0.29782	0.23685	-0.04513	0.15478	0.02109	-0.16414
x2	-0.32475	-0.16305	-0.06143	-0.10836	-0.10671	0.01320	0.26993	-0.23097	0.26146	0.15609	0.15831	-0.16751	-0.51851	0.04535	0.08817	-0.35416	-0.14793
y2	-0.20295	0.04207	0.12673	0.16955	0.00871	0.07730	0.02275	-0.07410	0.08229	-0.12696	0.09416	0.08200	0.07330	0.11704	0.07113	0.08726	-0.32649
x3	-0.26959	-0.07045	0.07773	-0.13998	-0.12460	-0.02287	0.27054	-0.12813	0.14958	0.00676	0.10900	-0.35275	0.43085	0.08654	-0.36754	0.36103	0.18526
y3	-0.16974	0.14762	0.09540	0.18438	0.01174	0.09169	-0.06858	0.00286	0.05382	-0.10226	0.13522	0.06553	-0.05779	0.11852	-0.22437	0.08557	-0.14062
x4	-0.35813	-0.16437	0.34945	-0.08280	-0.06094	0.09430	-0.21134	0.31058	-0.55130	0.28024	-0.08968	0.12798	-0.11184	0.03957	0.01711	-0.00687	0.09821
y4	-0.07727	0.31010	-0.14229	0.19365	-0.05645	0.20005	-0.15485	0.10469	0.16016	0.00764	0.08351	0.06479	-0.38838	-0.11107	-0.39102	0.04251	0.33601
x5	0.11462	0.17211	-0.35744	0.00245	0.13380	0.20581	-0.20445	0.06954	0.17683	0.40286	-0.13354	-0.26723	0.19133	-0.05845	0.25614	-0.03435	-0.12045
y5	0.00428	0.29554	0.04293	-0.48238	-0.53256	-0.01069	0.12672	0.02276	-0.12660	-0.02374	-0.11288	-0.10107	0.03399	0.02061	0.18577	-0.00770	-0.05318
x6	0.09605	-0.05087	-0.00437	-0.28912	0.42239	0.04998	-0.07370	-0.44763	-0.28618	-0.42467	0.04791	-0.00764	-0.07107	-0.04911	-0.04995	-0.02138	0.06149
y6	-0.08623	-0.29372	-0.21237	-0.03298	0.13013	-0.04214	0.04484	-0.16233	-0.14246	0.19831	0.05663	0.15881	0.03060	0.03670	-0.13705	-0.10876	-0.13975
x7	0.53470	-0.46945	0.20815	0.29198	-0.39543	0.11333	0.06220	-0.03856	0.08320	0.01978	0.09075	0.07452	-0.03898	0.07346	-0.04139	0.02349	0.02299
y7	-0.12188	-0.31222	-0.29249	0.00604	0.16590	-0.02026	-0.06829	-0.01557	0.02199	0.30302	0.08215	0.12595	0.16646	0.12936	0.10593	0.18369	0.26550
x8	-0.08647	-0.16492	-0.22748	-0.11532	0.11943	-0.13463	0.19257	0.66679	0.19471	-0.44598	0.02074	0.11856	-0.01390	0.08346	0.09937	-0.03043	0.07608
y8	-0.00868	-0.26930	0.07620	0.09439	0.10384	-0.21364	-0.12616	0.15612	0.01025	-0.07931	-0.38421	-0.44886	-0.07501	-0.38026	-0.19621	-0.01682	-0.32799
x9	0.12868	0.31389	0.34217	0.16466	0.37935	0.01035	0.53955	0.10510	-0.02598	0.27052	0.02215	0.09038	0.05135	-0.22925	0.01214	-0.04608	0.00334
y9	0.22757	-0.07511	0.40137	-0.44310	0.22111	0.35136	-0.27549	0.11809	0.36698	0.03521	0.08357	-0.02438	0.03378	0.09337	-0.02425	-0.10438	0.04630
x10	-0.13914	0.06811	0.07352	0.27621	-0.01747	0.05283	-0.23712	-0.11500	0.01466	-0.22089	0.09228	-0.17021	-0.01237	0.01874	0.42251	0.05071	0.19999
y10	0.13933	-0.06474	-0.23097	-0.03146	-0.08024	0.36583	0.21628	0.04746	-0.26657	-0.09820	0.22599	-0.03431	-0.11806	-0.43743	0.20642	0.35186	-0.06267
x11	-0.02902	0.11653	-0.10489	0.25374	-0.09860	0.27251	-0.09601	-0.00072	-0.16625	-0.16991	-0.08300	-0.18467	0.22132	0.13348	-0.06600	-0.36498	0.01954
y11	0.18765	0.04936	-0.21591	0.00471	-0.01854	0.12289	0.23574	0.02388	-0.22147	-0.04637	-0.20609	0.06827	0.15268	0.23597	-0.23351	-0.38052	0.04451
x12	0.14960	0.14456	-0.04562	0.02642	0.05783	-0.04084	-0.04826	-0.04144	-0.03279	0.02240	-0.36982	0.01535	-0.27044	0.40032	-0.05912	0.47595	-0.22395
y12	0.14635	0.04158	0.00516	-0.00605	0.09039	-0.24878	0.15746	-0.07479	0.01806	0.04137	-0.17495	-0.00946	-0.20542	0.29695	0.23691	0.07172	0.19768
x13	0.15594	0.12737	-0.11000	-0.08826	-0.09229	-0.29332	-0.21094	0.03870	-0.05353	0.05494	0.22918	0.07288	-0.00643	-0.12433	-0.18072	0.00828	-0.02178
y13	0.02903	0.06514	0.08789	0.07633	0.00061	-0.27488	-0.05839	0.01391	-0.01771	-0.01720	0.25865	-0.02099	0.14499	0.05138	0.22513	-0.13682	-0.08936
x14	0.12181	0.15383	-0.09648	-0.09201	-0.05400	-0.28352	-0.19046	0.03318	-0.02276	0.07631	0.33634	0.18745	0.06527	-0.02482	-0.13331	-0.01706	-0.31464
y14	0.11008	0.04466	0.11380	0.09347	-0.01447	-0.39467	-0.05674	-0.05837	-0.06439	0.02591	-0.00035	-0.22410	-0.02798	-0.12602	0.02035	-0.08870	0.41422

0.00388	0.00266	0.00217	0.00206	0.00130	0.00088	0.00056
GM_PCA18	GM_PCA19	GM_PCA20	GM_PCA21	GM_PCA22	GM_PCA23	GM_PCA24
0.03553	0.03950	-0.26046	-0.06229	-0.14483	0.19054	0.10241
-0.14799	-0.13076	0.36273	0.23208	0.21018	-0.49903	-0.20539
-0.05529	-0.15543	0.08682	-0.04322	-0.04833	-0.08361	-0.03971
-0.05190	0.06166	0.21550	-0.21785	0.18782	0.69244	0.11364
0.07097	0.11766	-0.00904	0.15045	0.00145	-0.01415	-0.00513
0.01740	-0.00615	-0.52330	-0.50606	-0.10758	-0.35036	0.00738
0.04512	0.03496	0.00710	0.04001	0.01160	0.01574	0.01578
0.11141	0.00535	0.15640	0.35151	-0.00668	0.09085	0.00463
-0.04325	0.14250	-0.01944	-0.05469	0.01020	-0.03991	-0.01175
0.02650	-0.06214	0.01650	-0.05645	0.00032	-0.01323	0.00253
0.04872	-0.14172	0.03250	0.02792	-0.00449	-0.00058	0.00383
-0.26342	0.57652	-0.12784	0.18254	0.02861	-0.01686	-0.07274
0.04182	-0.01672	-0.00017	-0.00191	-0.00613	0.00011	0.00810
0.13937	-0.52263	0.08132	-0.17898	-0.03876	0.03879	0.05095
-0.12770	0.06855	-0.00900	-0.01710	-0.00920	-0.00655	0.01279
0.25194	-0.09821	0.01199	0.02259	0.02300	-0.00539	0.00863
0.03590	-0.05512	0.00423	-0.03868	-0.01459	0.02308	-0.02187
-0.07418	0.04737	0.01476	0.01329	0.01335	-0.01033	-0.00699
0.30969	0.36226	0.17466	-0.12372	-0.15060	-0.10237	-0.04159
-0.09688	-0.00052	-0.06989	0.02602	0.01491	-0.04425	0.03499
-0.26603	-0.28601	-0.26382	0.17954	0.28355	0.07341	0.09155
0.29223	0.11593	0.29401	-0.20409	-0.26220	-0.03014	-0.05241
-0.27573	-0.07614	0.07869	0.07528	-0.27973	0.00939	-0.05251
0.29895	0.11076	-0.30754	0.14786	0.52101	-0.00575	0.07332
0.00394	-0.03347	0.04624	-0.22187	0.28363	0.10570	-0.66471
0.05206	-0.14398	-0.28993	0.42686	-0.52084	0.18038	-0.19758
0.17631	-0.00083	0.13168	0.09026	0.06746	-0.17080	0.60280
-0.55547	0.04679	0.16527	-0.23933	-0.06313	-0.02712	0.23905

	0.54391	0.17426	0.13572	0.09286	0.05324
GM_PCA1	GM_CDA1	GM_CDA2	GM_CDA3	GM_CDA4	GM_CDA5
GM_PCA2	0.80174	0.01699	-0.11710	-0.25779	-0.18004
GM_PCA3	0.02181	-0.16463	-0.24389	0.20585	-0.20997
GM_PCA4	-0.08657	-0.63244	-0.06808	-0.50656	0.17248
GM_PCA5	-0.23958	-0.05060	-0.37003	-0.22587	-0.05085
GM_PCA6	0.14010	0.24630	0.12231	-0.06919	0.42915
GM_PCA7	-0.09692	-0.30692	0.27406	-0.00925	-0.21724
GM_PCA8	-0.18997	0.28484	-0.09003	-0.35658	-0.08681
GM_PCA9	0.19905	0.00082	-0.34715	0.17619	-0.17361
GM_PCA10	0.20304	-0.11460	0.23094	0.05631	-0.08292
GM_PCA11	-0.08407	-0.17039	0.32146	0.23083	-0.23186
GM_PCA12	-0.16018	0.00985	-0.05114	-0.09176	-0.55394
GM_PCA13	-0.05304	0.31970	-0.14020	-0.19973	-0.31149
GM_PCA14	0.24589	-0.13250	0.09047	-0.05136	-0.02192
GM_PCA15	0.10609	0.11254	0.07264	0.13309	-0.09124
GM_PCA16	0.10783	-0.18566	-0.04643	-0.16498	0.01805
GM_PCA17	-0.06383	0.25787	-0.04880	-0.23540	0.07884
GM_PCA18	-0.00719	-0.00555	0.01320	0.15293	-0.21939
GM_PCA19	-0.00048	-0.06373	-0.00672	-0.18950	-0.23972
GM_PCA20	0.01705	0.06776	0.00455	-0.15000	-0.04803
GM_PCA21	0.00671	0.18759	0.58467	-0.29851	-0.16983
GM_PCA22	-0.08126	0.03269	0.06334	0.00789	0.01174
GM_PCA23	0.02057	-0.11138	-0.05760	0.09298	0.07222
GM_PCA24	0.08902	0.02210	-0.06716	0.11820	-0.00456
GM_PCA25	0.08711	-0.02421	0.12536	-0.13839	-0.01202

Table S6. Saito et al., 2025. Statistical significances of each measurement.

Shell Height/Shell Width	*P. binneyana*	*P. electrina*	*P. hammonis*	*P. petronella*	*P. radiatella radiatella*	*P. radiatella hesperia*
P. binneyana	–	–	–	–	–	–
P. electrina	**0.0488**	–	–	–	–	–
P. hammonis	0.1310	**<0.001**	–	–	–	–
P. petronella	**0.0056**	1.0000	**<0.001**	–	–	–
P. radiatella radiatella	1.0000	0.1019	**0.0062**	**0.0123**	–	–
P. radiatella hesperia	1.0000	**0.0483**	**0.0365**	**0.0058**	1.0000	–

Umbilicus Width/Number of Whorls	*P. binneyana*	*P. electrina*	*P. hammonis*	*P. petronella*	*P. radiatella radiatella*	*P. radiatella hesperia*
P. binneyana	–	–	–	–	–	–
P. electrina	1.0000	–	–	–	–	–
P. hammonis	1.0000	0.12998	–	–	–	–
P. petronella	1.0000	1.0000	0.13749	–	–	–
P. radiatella radiatella	1.0000	1.0000	**0.02856**	1.0000	–	–
P. radiatella hesperia	**0.00456**	**<0.001**	0.09473	**<0.001**	**<0.001**	–

Expansion Rate: Early (C2/C1)	*P. binneyana*	*P. electrina*	*P. hammonis*	*P. petronella*	*P. radiatella radiatella*	*P. radiatella hesperia*
P. binneyana	–	–	–	–	–	–
P. electrina	0.70621	–	–	–	–	–
P. hammonis	0.70621	<0.001	–	–	–	–
P. petronella	0.07403	0.40128	**<0.001**	–	–	–
P. radiatella radiatella	1.0000	**0.0167**	1.0000	**<0.001**	–	–
P. radiatella hesperia	0.70621	**0.00169**	1.0000	**<0.001**	1.0000	–

Expansion Rate: Late (C3/C2)	*P. binneyana*	*P. electrina*	*P. hammonis*	*P. petronella*	*P. radiatella radiatella*	*P. radiatella hesperia*
P. binneyana	–	–	–	–	–	–
P. electrina	0.7293	–	–	–	–	–
P. hammonis	0.1712	0.6615	–	–	–	–
P. petronella	1.0000	0.3935	**0.0420**	–	–	–
P. radiatella radiatella	0.1712	0.7293	1.0000	**0.0344**	–	–
P. radiatella hesperia	**0.0109**	**0.0303**	0.7293	**0.0012**	0.7403	–

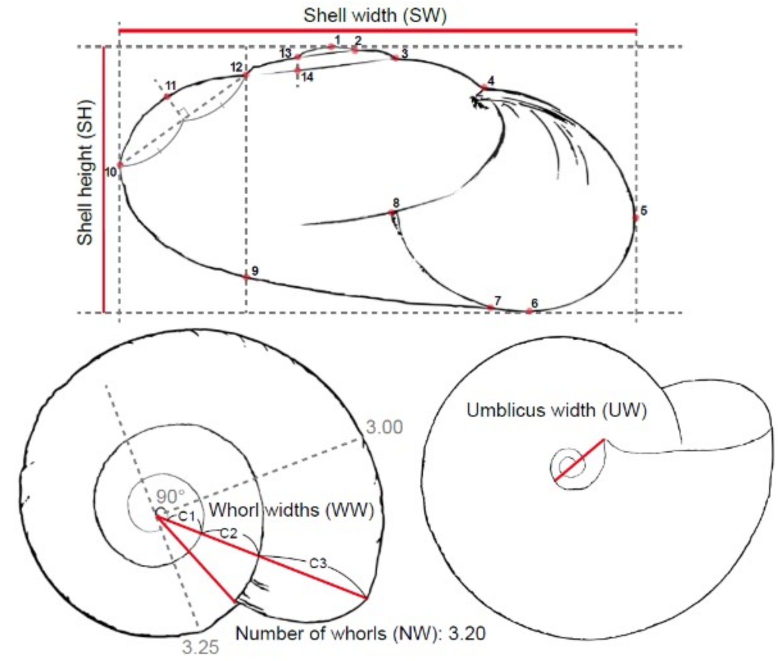

Fig. S1. Schematic of morphometrics used in this study.

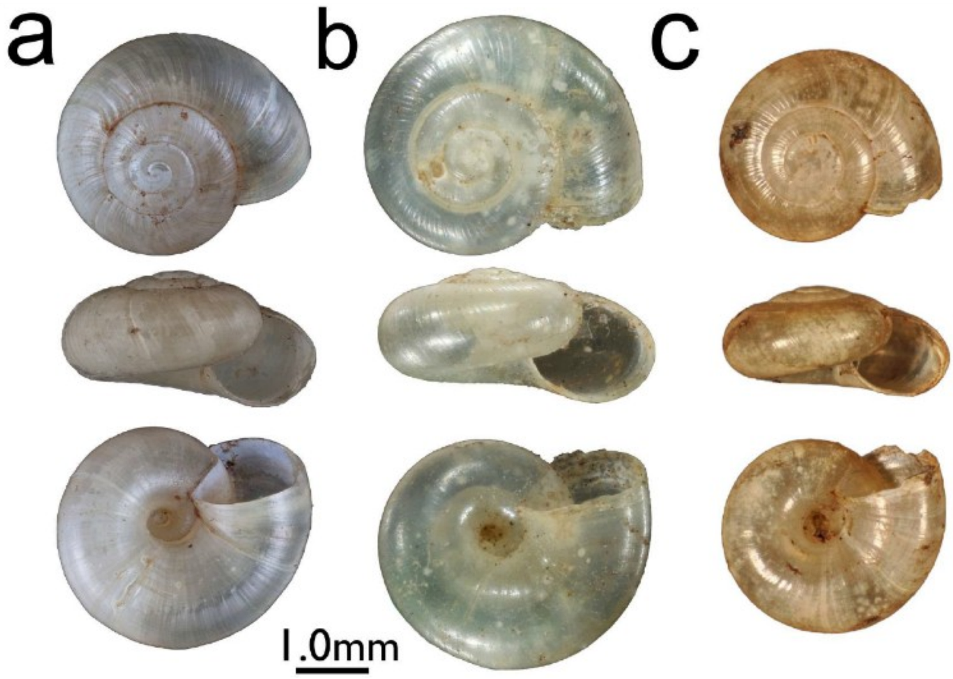

Fig. S2. Type specimens used in morphometrics in this study. **a.** Neotype of *Helix hammonis* Strøm, 1765 (Naturhistorisk Museum, Oslo, Norway, NHMO-D27826). **b.** Lectotype of *Helix viridula* Menke, 1830 (Naturmuseum Senckenberg Frankfurt, Germany, SMF166599). **c.** Lectotype of *Vitrea radiatula* var. *radiata* Pilsbry and Y. Hirase (Academy of Natural Sciences of Philadelphia, USA, AMS85788) from ANSP Malacology collection website (http://clade.ansp.org/malacology/collections/index.html).