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Research Article

Integrative taxonomic consideration of the Holarctic *Euconulus fulvus* group of land snails (Gastropoda, Stylommatophora)

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While among the most common Holarctic land snails, species of the *Euconulus fulvus* group have been subject to considerable recent taxonomic controversy. Based on 76 *Euconulus* populations collected across Eurasia and North America, we empirically evaluated these competing taxonomic hypotheses through an integration of nDNA and mtDNA phylogenetics, shell morphometrics and various qualitative traits. Our results support the existence of five taxa: *Euconulus alderi* (Atlantic Europe to western North America), *E. fresti* sp. nov. (North America), *E. fulvus fulvus* (Europe), *E. fulvus egenus* (central Asia to Atlantic North America), and *E. polygyratus* (north-eastern North America). Each species-level entity possessed a unique suite of observable shell features allowing for accurate identification without need of DNA sequence information. Our data did not support the recent erection of *E. callopisticus*, *E. praticola*, and *E. trochiformis* to species-level status. This work also helps illustrate the importance of using consensus across DNA and shell/soft body features in assessing species-level taxonomy and in determining those features which allow for accurate identification. It furthermore documents the importance of basing taxonomic work on samples drawn from across the entire geographic and ecological range of the study group.

http://zoobank.org/urn:lsid:zoobank.org:pub:97985479-EDF8-4B94-A825-AC42BF31F597

Key words: *Euconulus*, morphometrics, phylogenetics, species delimitation, taxonomy, terrestrial gastropod

Introduction

Land snails of the genus *Euconulus* Reinhardt, 1883 are frequent across the Holarctic both in modern (Cameron, Pokryszko, & Horsák, 2010; Horsák, 2006; Nekola, 2014) and fossil (Juřičková, Horsák, Horáčková, Abraham, & Ložek, 2014; Ložek, 2001) assemblages. These species are characterized by their minute size and simple shell morphology, having conical, closely coiled shells of brown to amber colour, generally ranging from 2.3–3.5 mm in diameter (Kerney & Cameron, 1979; Pilsbry, 1946). The genus is considered native across the Holarctic (Pilsbry, 1946), and introduced in other parts of the world (Stanisic, Shea, Potter, & Griffiths, 2010). The taxonomy of the genus and its phylogenetic position have been subject to ongoing debate (Baker, 1963; Hausdorf, 1998; Hyman, Ho, & Jermiin, 2007), with over 20 *Euconulus* species being described according to the worldwide malacological literature and

databases (e.g., Baker, 1963; Galli, 2016; Kerney & Cameron, 1979; MolluscaBase, 2019; Pilsbry, 1946). Our former research suggests that except for the south-eastern USA, the Holarctic representatives of the genus appear restricted to a monophyletic clade containing taxa closely allied with *E. fulvus* (Müller, 1774) (Horsáková, Nekola, & Horsák, 2019), which we hereafter call the *E. fulvus* group.

Throughout the 20th century three members of the *E. fulvus* group were generally believed to exist in Eurasia: upland *E. fulvus* and *E. fulvus alaskensis* (Pilsbry, 1899) (Kamchatka; Pilsbry, 1946), with pale bodies, light yellow shells, and dull lustre, and wetland *E. alderi* (Gray, 1840) with darker bodies and shinier, darker shells. This changed with publication of the Check-list of the Non-marine Molluscan Species of Northern, Atlantic and Central Europe (CLECOM; Falkner, Bank, & von Proschwitz, 2001; Falkner, Ripken, & Falkner, 2002) with *E. trochiformis* (Montagu, 1803) being considered a senior synonym of *E. alderi*, *E. praticola* (Reinhardt, 1883) being used for most continental *E. alderi* populations, and

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E. callopisticus (Bourguignat, 1880) being considered a valid species-level entity. Although clear diagnostic traits were not given to support these concepts, the data presented in Falkner et al. (2001, 2002) suggest that *E. praticola* occurs across continental and oceanic Europe, *E. trochiformis* is intermediate between *E. praticola* and *E. fulvus* and presumably limited to Atlantic regions, and *E. callopisticus* possesses shells taller than *E. praticola* and occurs in the Mediterranean region. While this approach has been followed in some recent works (e.g., Gargominy, Prié, Bichain, Cucherat, & Fontaine, 2011; Groh & Weitmann, 2007), it has also been rejected by others (e.g., Cameron, 2003) in part because no effort was made to confirm that type *E. callopisticus* and *E. trochiformis* match the above concepts (Welter-Schultes, 2012). The use of *E. praticola* in preference to *E. alderi*, without acceptance of *E. callopisticus* and *E. trochiformis*, has also been adopted by some European authors (e.g., Čejka, Dvořák, Horsák, & Šteffek, 2009; Horsák, Juřičková, & Picka, 2013; Körnig, Hartenauer, Unruh, Schnitter, & Stark, 2013; Zettler et al., 2006).

In North America this group was historically thought to represent only *E. fulvus* and *E. f. alaskensis* (Pilsbry, 1946). While the range of the former was believed to cover all but the south-eastern quarter of the continent, the latter was thought limited to the Western Cordillera. Subsequently two species were added. Based on comparison with European material Frest (1990) reported *E. alderi* from Iowa fens. This entity eventually was reported throughout the north-central/north-eastern USA (Nekola, 1998, 2002, 2004, 2008) and adjacent eastern Canada (Nekola, 2009) with populations from British Columbia and Ontario being considered *E. praticola* (Forsyth, 2004; Forsyth & Oldham, 2016). Additionally, while *Euconulus polygyratus* (Pilsbry, 1899) was originally described as a subspecies of the south-eastern USA *E. chersinus* (Say, 1821), and without empirical validation risen to species rank (Grimm, 1971), previous DNA sequence analysis confirmed its species-level status and showed it to be a member of the *E. fulvus* group (Horsáková et al., 2019).

The frequency of the *E. fulvus* group across the Holarctic combined with its contentious taxonomy suggests that a formal revision is warranted. We have previously taken an integrative approach that considers consensus among mtDNA and nDNA sequences, conchology, ecology, and biogeography to determine the number of biologically supported taxa (e.g., *Pupilla* – Nekola, Coles, & Horsák, 2015; *Vertigo* – Nekola et al., 2018). By applying this methodology to *Euconulus*, we can determine not only the actual number of empirically defensible taxonomic concepts but also provide robust information regarding their geographic and ecological

range and identify those conchological features which provide accurate species-level assignments.

Our goal in this contribution is to present an empirically supported species-level taxonomy of the *E. fulvus* group in which we formally conduct the nomenclatural acts – including a description of a new species – suggested by, but not undertaken in, our previous work concerning the delimitation of cryptic species (Horsáková et al., 2019).

Materials and methods

Taxonomic coverage

Analysed material was primarily obtained from collections made by the authors from 2000–2018. These represent approximately 900 *Euconulus* populations from Eurasia (Michal Horsák collection) and 1000 from North America (Jeffrey Nekola collection). Specimen selection was grounded in the fact that taxonomic diagnoses within this genus have until now been limited to a small suite of conchological criteria with unknown utility. Using the most liberal assignment of species status for both Europe (Falkner et al., 2002) and North America (NatureServe, 2018) we selected material in order to cover known conchological and geographic variation of all putative taxa (*E. alderi/trochiformis*, *E. callopisticus*, *E. fulvus*, *E. f. alaskensis*, *E. praticola*, *E. polygyratus*) using the diagnostic traits indicated in Falkner et al. (2002), Frest (1990), Horsák et al. (2013), Pilsbry (1946), and Welter-Schultes (2012). We excluded a potentially distinct lineage from Japan due to the very limited number of observed populations in combination with their considerable observed genetic variation. Resolution of their status is left to future investigators.

In addition, we also analysed 12 *E. callopisticus* (and images of a syntype which could not be loaned) from the Bourguignat collection (Natural History Museum of Geneva, Switzerland; MHNG 103698, 103700 and 103701) and images of two *E. trochiformis* syntypes from the Montagu collection (Royal Albert Memorial Museum & Art Gallery, Exeter; EXEMS Moll4313; see Oliver & Morgenroth, 2018). Because it was not possible to use this material for DNA analyses (all were over a century old, were mostly empty, with any remaining dried tissue requiring either shell destruction or degradation to extract DNA – see Nekola et al., 2018) they were only used for morphological evaluation and morphometry.

DNA sequence and phylogenetic analysis

A total of 76 specimens were used in the phylogenetic analyses, representing the known geographic and ecological range of all currently recognized Eurasian and North American *nomens* including: 7 *E. alderi/E.*
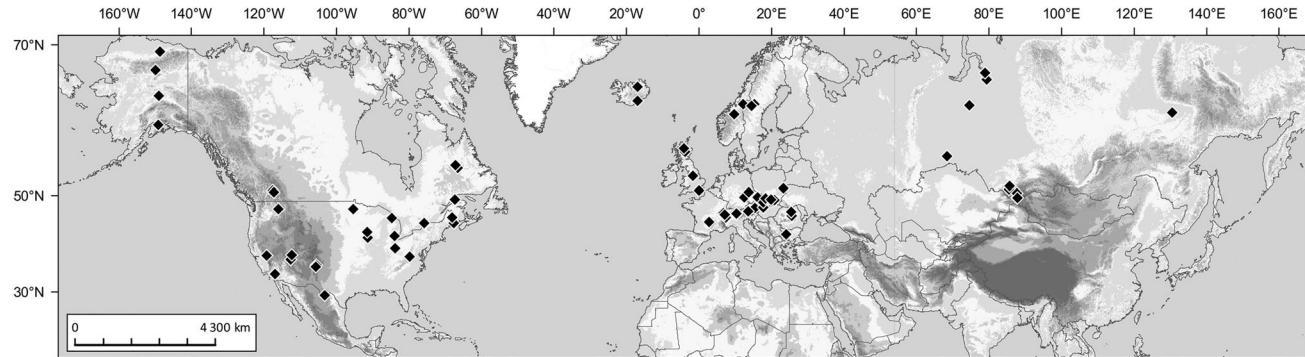
Figure 1. Geographic location for analysed *Euconulus fulvus* group specimens. Detailed sample information is provided in Supplementary Material – Appendix S1.

Table 1. Forward (F) and reverse (R) primer sequences used for PCR with anneal temperatures and primer design authors.

Region	Sequence	Anneal	Source
COII (F)	5′–AAATAATGCTATTTCATGAYCAYGC–3′	45 °C	Hugall, Moritz, Moussalli, & Stanisic (2002)
COII (R)	5′–GCTCCGCAAATCTCTGARCAYTG–3′	45 °C	Hugall et al. (2002)
16S (F)	5′–GCGCTGTTTATCAAAAACAT–3′	52 °C	Palumbi et al. (2002)
16S (R)	5′–CCGGTYTGAACTCAGATCAYGT–3′	52 °C	Palumbi et al. (2002)
ITS1 (F)	5′–TAACAAGGTTTCCGTATGTGAA–3′	52 °C	Armbruster & Bernhard (2008)
ITS1 (R)	5′–TCACATTAATTCTCGCAGCTAG–3′	52 °C	Nekola et al. (2018)
ITS2 (F)	5′–CTAGCTGCGAGAATTAATGTGA–3′	52 °C	Wade & Mordan (2000)
ITS2 (R)	5′–GGTTTCACGTACTCTTGAAC–3′	52 °C	Nekola et al. (2018)

trochiformis, 9 *E.* aff. *alderi*, 2 *E. callopisticus*, 29 *E. fulvus*, 3 *E. f. alaskensis*, 20 *E. praticola*, and 6 *E. polygyratus* (Fig. 1, Supplementary Material – Appendix S1). An individual of *E. trochulus* (Reinhardt, 1883) from Oklahoma, USA (representing the *E. chersinus* group *sensu* Pilsbry, 1946) was used for outgroup comparison.

DNA extraction, PCR amplification, and DNA sequencing was performed using standard protocols (see Horsáková et al., 2019). We analysed two mitochondrial [16S ribosomal RNA (16S) and cytochrome oxidase subunit II (COII)] and two nuclear [internal transcribed spacers 1 and 2 of the ribosomal RNA gene complex (ITS1 & ITS2)] amplicons using primers and thermal profiles listed in Table 1. Geneious v. 8.0.2 (Biomatter Ltd) was used for assembling forward and reverse strands into one sequence which was manually checked for potential misreads. The protein-coding COII fragment was translated into amino acids to check for the presence of erroneous stop codons. GenBank accession numbers of all sequences used in the phylogenetic analyses are available in Appendix S1.

Multiple sequence alignments were performed in MEGA v. 6.0 (Tamura, Stecher, Peterson, Filipski, & Kumar, 2013) using ClustalX with the default parameters of the IUB weight matrix as implemented, and checked by eye for potential errors. The two mitochondrial (mtDNA) amplicons were concatenated into a single construct as were the two nuclear (nDNA) fragments. Four different phylogenetic reconstruction methods, each employing very different analytical assumptions, were then separately run on the mtDNA and nDNA constructs to identify well-supported, shared structures. Mega v6.0 was used to conduct Neighbour-joining (NJ), using maximum composite distance including transitions and transversions with pairwise gap deletion. Maximum parsimony (MP) was conducted in TNT (Goloboff, Farris, & Nixon, 2008) using traditional search with 1000 replicates of Wagner trees, one random seed, Tree Bisection and Reconnection branch-swapping algorithm and 10 trees to save per replication. ML analysis was conducted using RAxML v 8.2 (Stamatakis, 2014) while BI analysis was performed using MrBayes v3.2.6 (Huelsenbeck & Ronquist, 2001). Both the mtDNA and nDNA constructs were first partitioned into two genes each with optimum base pair substitution models being identified using jModelTest v. 2.1.10 (Darriba, Taboada, Doallo, & Posada, 2012). Internal node support was assessed via 1000 non-parametric bootstrap replicates (Felsenstein, 1985). Trees were visualized using FigTree v. 1.4.3 (http://tree.bio.ed.ac.uk/software/figtree/). Full methodology is reported in Horsáková et al. (2019).

We also conducted preliminary analyses on 10 *Euconulus* mtDNA cytochrome oxidase I (COI) sequences from France, kindly provided by Olivier Gargominy (personal communication, 19 December 2018), together with 29 COI from specimens we collected across Eurasia (data available upon request).

Shell morphometrics

Shell measurement protocols follow Horsáková et al. (2019). A total of 106 shells from 33 populations in the Czech Republic, Slovakia, Poland, Switzerland, Bulgaria, Norway, Sweden, Russia, USA, and Canada were analysed (Appendix S2), along with two syntype *E. trochiformis* and three *E. callopisticus* (see above). Photo-micrograph images of each shell were generated using an Olympus SZX7 with Olympus C-7070 Wide Zoom camera and QuickPHOTO MICRO software. All shells were measured by the authors except for the *E. trochiformis* syntypes which were imaged and measured by P. Graham Oliver at the National Museum Wales (Cardiff) using identical protocols.

Because of the lack of determinant growth and absence of well-defined conchological structures to demarcate adult individuals in *Euconulus*, we only measured shells of at least four whorls and then compiled ratios between seven conchological traits, with the number of whorls being counted following Cameron (2003). These ratios were then subjected to discriminant correspondence analysis (see Horsáková et al., 2019). Basic descriptive statistics of all directly measured traits and calculated ratios are shown in Appendix S2, and an illustration of shell measurements is shown in Appendix S3. All calculations were conducted in R version 3.5.2 (https://www.r-project.org/), using the 'ade4' (Dray & Dufour, 2007), and 'vegan' (Oksanen et al., 2017) packages.

We complemented these analyses by visually evaluating eight additional qualitative morphological characters from each individual, including: body tissue and mantle colouration, presence of a keel, sillon ('furrow' in French, used by Welter-Schultes (2012) to demarcate the spiral grooves inset into the bottom shell surface) strength, shell colour and lustre, protoconch and teleoconch microsculpture. The latter were documented using a digital Keyence VHX-5000 microscope with ZS-20 and ZS-200 objective lenses.

Species delimitation

We choose to demarcate a species as being distinct once it has become a largely independent evolutionary unit (Horsáková et al., 2019). We do not use any of the various sequence-based species delimitation methods as these may provide inaccurate results especially for groups with recent diversification histories (e.g., Wei et al., 2016), and require the making of questionable assumptions regarding evolutionary rate (e.g., Nekola, Coles, & Bergthorsson, 2009). Instead, we first searched the mtDNA and nDNA trees for jointly held, highly supported, reciprocally monophyletic groups containing the same individuals. The conchological, geographic,

and ecological ranges for each were then subjected to morphometric and qualitative evaluation. Such groups are considered to represent valid species-level entities when unique patterns occur across a consensus of data. *A priori* species identifications were then updated based on these integrative findings.

Results

Phylogenetic reconstruction

DNA sequence data were obtained for 75 specimens in the mitochondrial and 76 specimens in the nuclear construct (Supplementary Material – Appendix S1). Amplicon lengths were 379–381 bp for 16S, 502 for COII, 652–664 for ITS1, and 862–890 for ITS2. Twenty-five variable base pair positions were identified in 16S, 109 in COII, 22 in ITS1, and 21 in ITS2. Because NJ, MP, ML, and BI all generated essentially the same topologies we used only ML to illustrate phylogeny (Fig. 2). Support values were generally higher in the mtDNA dataset presumably due to greater base pair variability.

Four reciprocally monophyletic clades showing high support in both the mtDNA and nDNA trees were observed: (1) Eurasian *E. alderi/trochiformis*, *E. callopisticus*, *E. praticola*, and far western North American *E.* aff. *alderi*; (2) North American *E.* aff. *alderi* east of the Cascade/Sierra Nevada Mountains; (3) *E. polygyratus*; (4) European *E. fulvus*. The remaining Asian and North American *E. fulvus* fell into multiple weakly defined, somewhat geographically structured clades, which we choose to interpret as representing a single poorly defined subspecies due to their uniformly very low support, inconsistency of placement between nDNA and mtDNA clades, lack of identifiable diagnostic macro-scale features unique to individual clades, and evidence for hybridization (for full reasoning see Horsáková et al., 2019; and Discussion in the present study). Within-group variability ranged from 3.2–13.5 bases in COII + 16S and 0.3–2.6 bases in ITS1 + ITS2. Between group variability ranged from 23.7–32.2 bases in COII + 16S and 2.8–6.8 bases in ITS1 + ITS2 (Supplementary Material – Appendix S4).

Material initially identified as *E. alderi/trochiformis* was polyphyletic, with western/Atlantic populations being strongly associated with *E. callopisticus* and *E. praticola* and alpine populations being strongly associated with *E. fulvus*. This pattern was replicated in preliminary reconstructions limited to COI sequence from eastern France and Eurasia (results available upon request). Additionally, material initially identified as North American *E.* aff. *alderi* was polyphyletic, with most populations representing a highly supported
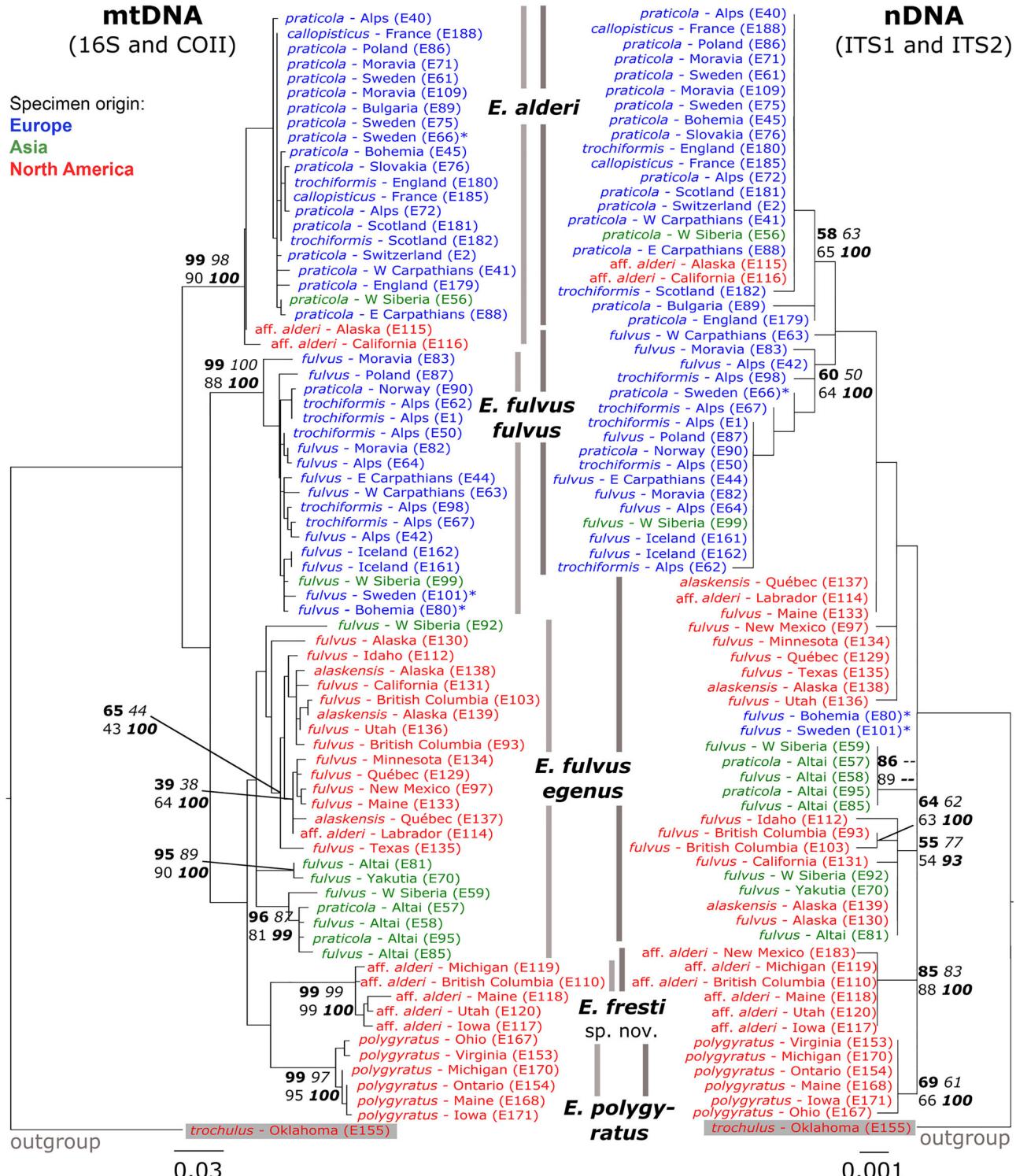
Figure 2. Maximum likelihood tree for the *Euconulus fulvus* group based on mtDNA (16S + COII) (left) and nDNA (ITS1 + ITS2) (right). Support values of >70% for NJ (upper left, **bold font**), MP (upper right, *italic font*), ML (lower left, normal font), and in posterior probabilities of >95% for BI (lower right, ***bold italic font***) are shown next to the corresponding nodes. Only highly supported nodes in at least one of the methods are labelled. Colours represent individual source: blue – Europe, green – Asia, red – North America.

distinct clade. However, an eastern taiga specimen was strongly associated with non-European *E. fulvus*, and far western/arctic specimens were strongly associated with *E. alderi/trochiformis*.

Morphometric comparison

Single quantitative shell measurements demonstrated considerable overlap and were generally ineffective in distinguishing groups (Table 2a). However, multivariate ordination of measured ratios did illustrate partitioning (Fig. 3.1). The principal axis of variation was most closely associated to the ratio between shell size (height or width) and the number of whorls (e.g., coiling tightness/expansion rate; $r^2 = 0.967$), with *E. polygyratus* possessing much tighter coils and reduced coil expansion (Table 3a). As a result, individuals of the same diameter possess 1–2 more whorls than other group members. This species was so distinct that it forced the remaining groups to overlap in a non-informative way. Discriminant analysis was thus repeated following removal of *E. polygyratus*. In this new analysis (Table 3b, Fig. 3.2) the first axis was again most correlated with coiling ratio ($r^2 = 0.918$). For both analyses the second axis was poorly explained by any single trait, and represented a complex combination of shell height, width, and aperture measurements. While it was most correlated in the full analysis with aperture height to body whorl height ratio and in the reduced analysis to shell height to width ratio, these factors explained little observed variation ($r^2 = 0.179$ and $r^2 = 0.217$, respectively). For this reason the second axis is best seen as not reflecting any particular calculated shell ratio.

In cases of morphometric overlap qualitative morphological features were found to clearly separate groups (Table 2b). In comparison with *E. fulvus*, European *E. alderi/trochiformis* and North American *E.* aff. *alderi* have darker red-brown shells with a more shiny lustre, reduced teleoconch microsculpture, stronger sillons, and a darker body. Eurasian/western North American *E. alderi/trochiformis* differ from North American *E.* aff. *alderi* in possession of a uniform dark mantle, rounded margin, stronger protoconch microsculptural ribs and weak to absent teleoconch microsculpture. North American *E.* aff. *alderi* is characterized by a mottled mantle, prominent keel, weak to absent protoconch sculpture, and more prominent microsculpture (especially spiral lines) on the teleoconch. No features allowed for definitive separation of European and non-European *E. fulvus*, with all trait characters being observed across all groups. However, European *E. fulvus* tended to have a tighter coiling ratio with more constant rate of whorl expansion with uniform grey mantle

Table 2. Summary of quantitative and qualitative conchology in *Euconulus fulvus* group members.

A. Quantitative Variation

Taxon	Shell width mm (min–max)	Shell height mm (min–max)	Max. no. of whorls	Shell width/No. of whorls (min–max)	Shell height/No. of whorls (min–max)
E. alderi	2.44–3.53	1.74–2.78	5.30	0.57–0.69	0.42–0.52
E. fresti sp. nov.	2.18–2.70	1.59–2.14	5.00	0.52–0.61	0.38–0.43
E. fulvus fulvus	2.48–3.36	1.66–2.79	5.30	0.56–0.65	0.39–0.53
E. fulvus egenus	2.60–3.44	1.89–2.70	5.00	0.57–0.72	0.42–0.55
E. polygyratus	2.49–2.90	1.95–2.54	6.60	0.41–0.46	0.35–0.38

B. Qualitative Variation

Taxon	Shell colour	Shell lustre	Protoconch structure	Teleoconch structure	Sillons (bottom grooves)	Body colour	Mantle pattern	Keel on body whorl
E. alderi	brownish-red	glossy	coarse growth ribs	reduced to weak; irregular ribs	strong sparse	greyish black	uniform	almost absent
E. fresti sp. nov.	brownish-red	glossy	smooth to very weak spiral lines	distinct spiral lines, fine thread-like ribs	strong sparse	greyish black	mottled	prominent
E. fulvus fulvus	yellowish	silky to dull (glossy*)	ribs and spiral lines equal	strong; sharp dense ribs (weak*)	weak dense (moderate sparse*)	pale grey/ yellowish	usually uniform (mottled*)	almost absent
E. fulvus egenus	yellowish	silky to semi-glossy	strong to weak ribs and/ or spiral lines	absent to weak spiral lines, weak to sharp ribs	weak dense to moderate sparse	pale grey/ yellowish	usually mottled	usually weak
E. polygyratus	yellowish	dull	smooth to very weak	fine spiral lines, fine ribs	weak to absent	pale grey/ yellowish	mottled	weak

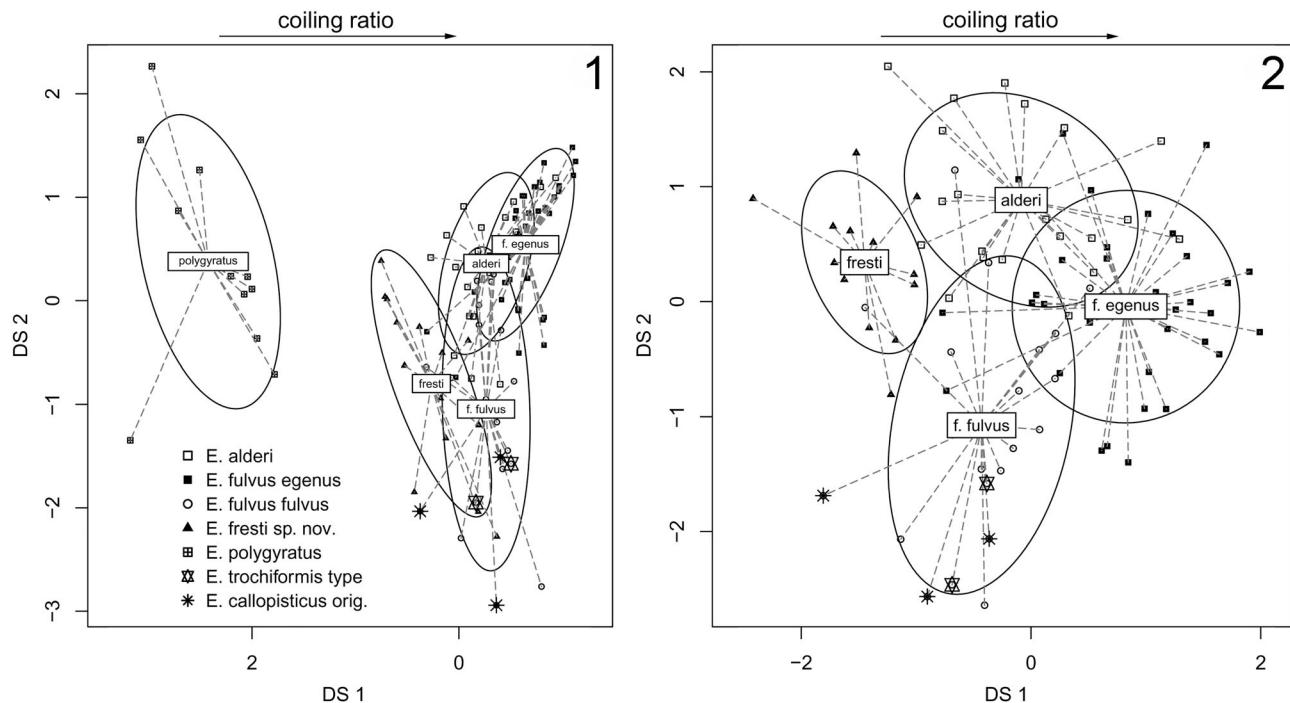*High mountain wetland populations only.

Figure 3. Placement of measured shells along the first two discriminant analysis axes: (1) all shells; (2) *E. polygyratus* removed. Ellipses represent the 95% confidence interval for that entity. Numbers of measured shells/populations: *E. alderi* = 27/7, *E. fulvus fulvus* = 16/6, *E. fulvus egenus* = 35/12, *E. fresti* sp. nov. = 14/5, *E. polygyratus* = 14/4. Two syntype shells of *E. trochiformis* from Montagu collection (EXEMS) and three shells of *E. callopisticus* from Bourguignat collection (MHNG) were also used.

Table 3. Multiple regressions of shell characteristics and specimen scores on the first two discriminant axes (DS 1 and DS 2): (a) all shells; (b) *E. polygyratus* removed. Regression coefficients; the fit of each shell characteristic into the ordination space, i.e., variation in the characteristic explained by specimen scores on the first two DS axes in multiple linear regression (r^2); and significance (P) of the result based on 4999 permutations are shown. The highest regression coefficients of significant variables ($P < 0.05$) to each axis are in bold.

A) All five taxa	DS 1	DS 2	r^2 (%)	*P*
Shell width/no. of whorls	**0.983**	0.185	96.7	<0.001
Shell height/no. of whorls	0.886	0.464	81.8	<0.001
Shell height/shell width	−0.796	0.605	53.7	<0.001
Body whorl height/shell height	0.943	−0.334	56.9	<0.001
Aperture width/shell width	0.922	0.386	41.4	<0.001
Aperture width/shell height	0.946	−0.325	63.4	<0.001
Aperture height/body whorl height	−0.033	**0.999**	17.9	<0.001
B) Without *E. polygyratus*				
Shell width/no. of whorls	**0.995**	−0.100	91.8	<0.001
Shell height/no. of whorls	0.976	0.217	68.6	<0.001
Shell height/shell width	0.189	**0.982**	21.7	<0.001
Body whorl height/shell height	−0.486	0.874	1.6	0.498
Aperture width/shell width	0.754	0.657	31.2	<0.001
Aperture width/shell height	0.532	−0.847	10.2	0.001
Aperture height/body whorl height	0.860	0.510	18.1	<0.001

tissue, while non-European *E. fulvus* tended to possess more lax coiling with an initial low and then more rapid rate of whorl expansion and mottled mantle tissue.

Systematic treatments

Based on these results we choose to recognize four species and one subspecies within the *E. fulvus* group.

Identification key for the *Euconulus fulvus* group

1(2) Coiling tight (i.a), shell width-number of whorls ratio <0.5, aperture lunate (i.b), spire domed (i.b)……………………..***E. polygyratus***

2(1) Coiling lax (ii.b), shell width-number of whorls ratio >0.5, aperture elliptical, spire conic (ii.d)..go to 3

3(6) Shell yellowish, teleoconch with dull lustre (ii.a, iii.a) and strong microsculpture, pale animal, sillons usually weak and dense (ii.c)..go to 4

4(5) European, solid mantle (ii.a) /except for high Alpine fen populations (ii.b)/, weak sillons (ii.c), whorl expansion rate tending to be slower and continuous….......***E. fulvus fulvus***

5(4) Central Asian-North American, mottled mantle (iii.a), stronger sillons, whorl expansion rate tending to be faster and discontinuous…………........................***E. fulvus egenus***

6(3) Shell brownish red, teleoconch with glossy lustre and weak microsculpture, black animal, sillons strong and sparse (iv.c, v.d)..go to 7

7(8) Mottled mantle (iv.a), shells always keeled (iv.b), protoconch with reduced to absent microsculpture, teleoconch microsculpture weak with spiral lines being stronger than ribs, lower coiling ratio (iv.b)..***E. fresti*** sp. nov.

8(7) Solid mantle (v.a, b), only immature shells keeled, protoconch with radial ribbing, teleoconch microsculpture weak to absent, higher coiling ratio (v.c)...............***E. alderi***
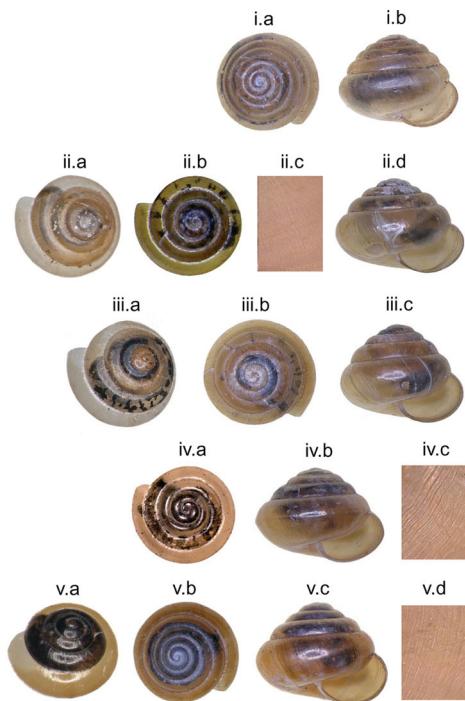
Figure 4. Taxonomic key for *Euconulus fulvus* group members based on shell features validated through DNA sequence analysis. All illustrated shell identifications were confirmed through DNA sequence.

Their valid names are: *E. alderi*, *E. fresti* sp. nov., *E. fulvus*, *E. fulvus egenus*, and *E. polygyratus*. To assist identification, results have been summarized via an illustrated taxonomic key (Fig. 4).

Family **Euconulidae** H.B. Baker, 1928
Genus ***Euconulus*** Reinhardt, 1883

Euconulus Reinhardt, 1883: 86.
Type species. *Helix fulva* Müller, 1774.

Euconulus alderi (Gray, 1840)

Helix alderi Gray in Turton & Gray, 1840: 148.

Type locality. Great Britain

Synonyms. *Hyalina praticola* Reinhardt, 1883: 40, type locality: Germany – Brandenburg.

Material examined. Twenty-two populations from Europe (Austria, Bulgaria, Czech Republic, France, Poland, Romania, Slovakia, Sweden, Switzerland, and United Kingdom), Asia (Russia: Western Siberia) and North America (USA: Alaska and California); for details see Supplementary Material – Appendix S1.

Phylogenetics. *Euconulus alderi* exists as a monophyletic clade across all reconstruction methods in both the nDNA and mtDNA constructs (Fig. 2). Preliminary analysis of COI from France and other Eurasian populations also supported the presence of only *E. alderi* and *E. fulvus fulvus*. Our data were unable to establish with high support the most closely related sister taxon to *E. alderi*.

Conchology. This species is characterized by dark, cinnamon-brown shell with a shiny surface, strongly reduced teleoconch microsculpture, protoconch microsculpture limited to rounded, widely spaced radial ribs, and a dark animal with uniform mantle colour (Figs 4 [v.a-c], 5.1). It typically possesses strong sillons (Table 2, Figs 4 [v.d], 7.2). *Euconulus fulvus* differs in possessing a yellow, duller shell with sharper and denser microsculptural ribs on both the teleoconch and protoconch and a grey animal body. While European *E. fulvus fulvus* sillons are typically weaker, considerable overlap is observed with *E. fulvus egenus*. *Euconulus alderi* differs from the similar North American *E. fresti* sp. nov. in possessing a greater coil expansion rate, rounded margin, stronger protoconch microsculpture, weaker teleoconch microsculpture, and possession of uniformly coloured mantle tissue.

Ecology. *Euconulus alderi* is restricted to base-rich wetlands, ranging from open fens to wet riparian and other swampy forests.

Biogeography. Atlantic Europe east across the Eurasian and Alaskan taiga and tundra to the west shore of Hudson's Bay in the North American arctic and south along the Western Cordillera to the southern Sierra Nevada in California.

Nomenclatural notes. Falkner et al. (2002) erect species from the Atlantic/Alpine (*E. trochiformis*), continental Europe (*E. praticola*), and eastern France (*E. callopisticus*) to replace *E. alderi*; however, none were empirically supported by either genetic or conchological data. While British material referable to the Falkner et al. (2002) concept of *E. trochiformis* possesses DNA sequence solidly rooted in the highly supported *E. alderi* clade, material corresponding to *E. trochiformis* in the sense of Falkner et al. (2002) from high altitude alpine habitats is actually *E. fulvus*. Furthermore, even if genetic partitioning had existed, *nomens* were incorrectly applied because type material for both *E. callopisticus* and *E. trochiformis* actually represents *E. fulvus*. As a result, the earliest available *nomen* representing this entity is *E. alderi*, with the original description stating: "Mr. Alder observes that … it is darker coloured and with very delicate and beautiful concentric striae on the base, only visible with a high magnifier, which induced him at first to consider it distinct …" (Turton & Gray, 1840).

Euconulus fresti sp. nov.
Figs 3, 6, 7.1

GenBank accessions: MK266537; MK266543-6; MK299610; MK299616-9; MK299700; MK299707-10; MK299793; MK299800-3; MN706207; MN706200-3.

Diagnosis. Glossy dark cinnamon-brown shell, strong sillons, overall appearance similar to *E. alderi* but with tighter coiling, mottled mantle tissue, keeled margin on shells of all ages, weak to absent protoconch microsculpture and distinct teleoconch microsculpture of spiral lines with weak ribs. Within the *E. fulvus* group, this species uniquely possesses 350 T in the aligned ITS2 sequence (Supplementary Material – Appendix S5).

Description. Shell height 1.9–2.1 mm, width 2.5–2.7 mm (holotype 1.9×2.6 mm); width vs. number of whorls 0.52–0.61 (holotype 0.54), height to width ratio 0.7–0.8 (holotype 0.75). Shell dark red-brown with glossy lustre, squat-conical shape, moderate suture, aperture crescent-shaped with a simple edge, no umbilicus, 4.8–5.0 whorls in fully adult individuals (holotype 4.75), relatively tightly coiled with whorl width increasing at a constant $1.5–1.8\times$ rate per rotation, keeled periphery present even in fully adult individuals (Fig. 4 [iv.b]). Protoconch microsculpture reduced to absent, limited (when present) to very weak spiral lines (Figs 6 [i], 7.1); teleoconch microsculpture of distinct spiral lines with weaker thread-like ribs (Fig. 6 [ii–iii]). Sillons strong and sparse (Figs 4 [iv.c], 6 [iv], 7.1, 4 [iv.c]). Animal body almost black with a dark-grey mottled mantle (Fig. 4 [iv.a]).

Figure 5. Live individuals of *Euconulus alderi* (1), *E. fulvus fulvus* (2–3) and *E. fulvus egenus* (4): 1, Slovakia; 2, Crimea; 3, Northern Norway; 4, Western Siberia, Russia. Photo: R. Coufal (1, 3), S. Leonov (2), M. Horsák (4).
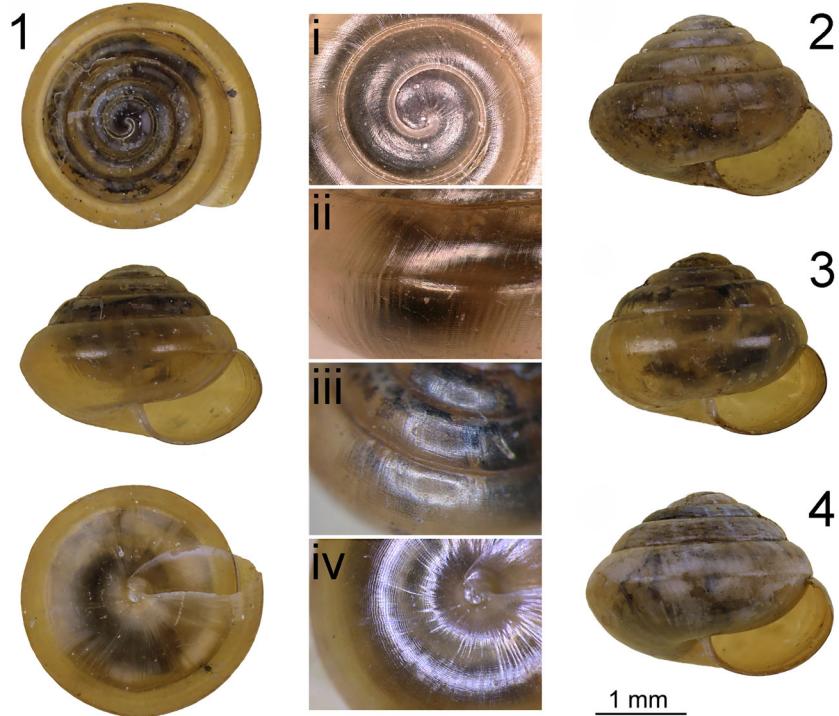
Figure 6. *Euconulus fresti* sp. nov.: (1) holotype (ANSP 478687) and (2) paratype (ANSP 478688) from type locality, Martelle Fen, Iowa, USA; (3) paratype (ANSP 478690) from Mystic River calcareous seep, Utah, USA; (4) a specimen from Maxton Plains sedge wetland, Michigan, USA. Middle images illustrate shell microsculpture: (i and iv) holotype (ANSP 478687); (ii) paratype (NMW.Z.2019.021.1) from Kelly Creek Fen, British Columbia, Canada; (iii) paratype (ANSP 478690) from Mystic River seep, Utah, USA.

Holotype (Figs 6.1, 6 [i and iv], 7.1). ANSP 478687, Martelle Fen, Jones County, Iowa USA: sedge mat in pasture (42°2′27″N, 91°19′36″W); 27 October 2002, J.C. Nekola.

Paratypes. Twenty shells (ANSP 478688), 5 shells (FMNH 344774), 5 shells (UMMZ 305776), 5 shells (NHMUK 20190694) collected with holotype; 5 shells (ANSP 478689), Wesley School, Washington County, Maine USA: rich *Thuja–Fraxinus–Acer rubrum* swamp (44°55′39″N, 67°39′32″W); 16 September 2007, J.C. Nekola; 12 shells (ANSP 478690), Mystic, Kane County, Utah, USA: calcareous seep near the East Fork Virgin River (37°22′28″N, 112°35′40″W), 6 October 2009, J.C. Nekola; 7 shells (ANSP 478691), 6 shells (NMW.Z.2019.021.1), Kelly Creek Fen, Incomappleux River valley, British Columbia, CANADA: rich open sedge mat (50°55′17″N, 117°34′38″W), 29 August 2011, M. Horsák, J.C. Nekola & B. Coles Coles; 11 shells (ANSP 478692), Tiplady Fen, Livingston County, Michigan, USA: marly sedge mat (42°25′51″N, 83°58′45″W), 11 October 2008, J.C. Nekola.

Other examined non-Type material. NMW.Z.2005.011.00781, NMW.Z.2005.011.01547 representing approximately 200 shells from Minnesota and Maine, USA. Also 208 lots representing 6320 individuals from Alberta, British Columbia, Iowa, Maine, Manitoba, Massachusetts, Michigan, Minnesota, Nevada, New Hampshire, New Mexico, New York, Ontario, Utah, Vermont, and Wisconsin in the Nekola collection.

Etymology. The specific epithet honours Terrence J. Frest (Supplementary Material – Appendix S6), the first researcher to recognize the existence of this species. Terry was a tireless field researcher and one of the most ardent champions of North American terrestrial gastropod conservation during the latter decades of the 20th century.

Phylogenetics. This species exists as a highly to very-highly supported monophyletic clade across all reconstruction methods in both the nDNA and mtDNA constructs (Fig. 2). While the phylogenetic reconstructions based on mtDNA suggest a sister-group relationship with *E. polygyratus*, the data were insufficient to resolve the relationship with high support (observed values <50). The potential validity of this sister relationship, however, is suggested by shared
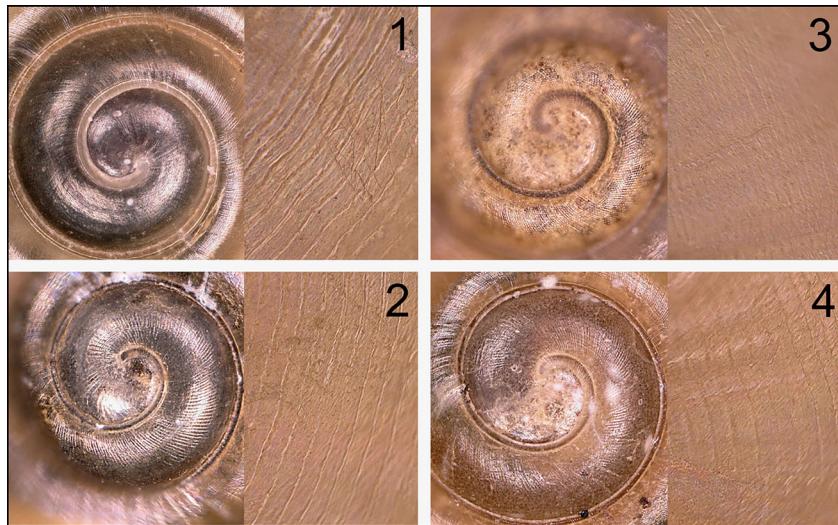
Figure 7. Comparative protoconch (left image) and shell bottom (right image) microsculpture for: (1) *E. fresti* sp. nov. (NMW.Z.2019.021.1); (2) *E. alderi*; (3) *E. fulvus fulvus*; (4) *E. fulvus egenus*.

reduced protoconch microsculpture and higher coiling ratio as compared to *E. alderi* and *E. fulvus*.

Comparisons with other species. *Euconulus fresti* sp. nov. is consistently differentiated from *E. alderi* based on its weaker protoconch microsculpture, stronger teleoconch microsculpture, keeled margin, and mottled mantle (Figs 6, 7, Table 2). *Euconulus polygyratus* differs in its dull yellowish shell, unmarked shell bottom, narrower whorls, and pale animal body. While *E. fresti* sp. nov. typically has tighter coiling than *E. fulvus egenus*, it can be difficult to distinguish in some wetland and cool, humid forest *E. fulvus egenus* populations that possess reduced microsculpture, shinier lustre, tighter than normal coiling ratio, and keeled margins. However animal colour in these individuals remains grey, their shells remain yellowish, with microsculptural ribs on the protoconch always being stronger than any spiral lines.

Geographic distribution. Maine, southern Ontario, southern Manitoba, British Columbia and the Yukon to New York, Ohio, and Iowa down the Rocky Mountains to southern Utah and northern New Mexico (Fig. 8). In the east it does not appear to range north of the St. Lawrence, and only rarely into the southern taiga fringe in Manitoba; however it is present in Yukon taiga. It is entirely absent from the Arctic. While not yet recorded from the Canadian Maritime Provinces, given its abundance in adjacent Maine *E. fresti* sp. nov. presumably occurs throughout New Brunswick and Nova Scotia. It is also likely present in aspen parkland and adjacent grassland landscapes of Saskatchewan and Alberta.

Ecology. Very similar to *E. alderi*, being particularly common in open sedge mats of fens, rich conifer/ash swamps, sedge meadows, and shrub carrs. It is most likely to co-occur with *E. fulvus egenus* in the latter habitat.

Nomenclatural notes. This species has previously been reported as *E. alderi* from the USA and eastern Canada (Frest, 1990; Nekola, 1998, 2002, 2003, 2004, 2008, 2009, 2012, 2014) and from British Columbia and Ontario as *E. praticola* (Forsyth, 2004; Forsyth & Oldham, 2016). In our earlier work (Horsáková et al., 2019) it was referred to as *E.* aff. *alderi*.

Euconulus fulvus fulvus (Müller, 1774)

Helix fulva Müller, 1774: 56.

Type locality. Denmark – Frederiksdal near København.

Synonyms. *Helix trochiformis* Montagu, 1803: 427, type locality: England – Wiltshire near river Avon; Lackham wood, Devonshire; *Zonites callopisticus* Bourguignat in Servain, 1880: 30, type locality: France – near Lyon.

Material examined. Nineteen populations from Europe (Austria, Czech Republic, Iceland, Norway, Poland, Romania, Slovakia, Sweden, and Switzerland), Asia (Russia: Western Siberia) and North America (USA: Alaska and California); for details see Supplementary Material – Appendix S1. In addition, 12 shells of *E. callopisticus* (and images of a syntype which could not have been loaned) from the Bourguignat collection (MHNG 103698, 103700, and 103701) and two syntype
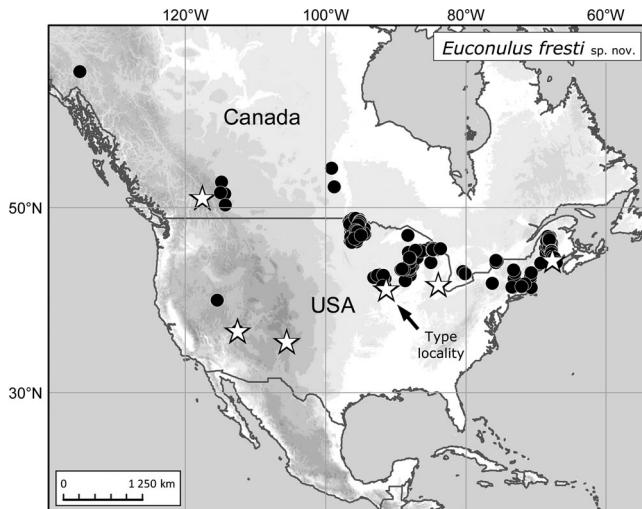
Figure 8. Distribution of *Euconulus fresti* sp. nov. Sites marked with stars were used for molecular analyses.

shells of *E. trochiformis* from the Montagu collection (EXEMS Moll4313) were also examined and found to represent *E. fulvus fulvus*. With respect to *E. callopisticus* we also thoroughly revised our own southern European material (46 lots in the Horsák collection from France, Switzerland, and Italy).

Phylogenetics. *Euconulus fulvus fulvus* exists as a monophyletic clade across all reconstruction methods in both the nDNA and mtDNA constructs (Fig. 2), with an exception of one ambiguously assigned specimen in the nDNA tree (E63). Such anomalous sequence in the nuclear rRNA gene complex has been found to be taxonomically uninformative in other pulmonate land snail groups (Nekola et al., 2018). The placement of Bohemian and Swedish specimens outside of this clade in nDNA tree is likely due to hybridization with *E. fulvus egenus* (perhaps during the Pleistocene; see Horsáková et al., 2019). The data were not sufficient to resolve with high support the phylogenetic relationships of *E. fulvus fulvus* with other species in the group. The monophyletic nature of *E. fulvus fulvus* was also supported in preliminary analysis of COI sequence from eastern France and across Eurasia.

Conchology. This taxon is most easily separated from *E. alderi* and *E. fresti* sp. nov. by its typically lighter shells with stronger protoconch and teleoconch microsculpture, resultant duller lustre, weaker sillons, and grey animal body (Table 2b, Figs 4 [ii.a–d], 5.2, 7.3). While no definitive traits separate all *E. fulvus fulvus* from *E. fulvus egenus*, *E. fulvus fulvus* individuals tend to possess a tighter coiling ratio, more constant whorl expansion, weaker sillons, and a uniformly

coloured mantle. However, some European *E. fulvus fulvus* possess laxer coiling, discontinuous whorl expansion, strong sillons and mottled mantle tissue (Fig. 5.3). Considerable variability is also noted in spire height and other conchological traits. This plasticity appears at least partially responsible for erection of *E. callopisticus* and *E. trochiformis* (Figs 3, 9). It should also be mentioned that ecophenotypic variability is substantial with populations from high-elevation and high-latitude habitats developing a darker shell with less prominent teleoconch microsculpture and dark-grey mottled mantle tissue (Figs 4 [ii.b], 5.3, 9.viii). Because these populations appear intermediate between *E. alderi* and *E. fulvus fulvus*, they correspond to the concept of *E. trochiformis* in Falkner et al. (2002). This led to our initial misidentification of these individuals and polyphyleticism for *E. trochiformis* in the phylogenetic trees.

Ecology. This species occurs in a wide variety of upland forest, shrubland, heath, and grassland habitats across the soil acidity gradient. It is one of the more acid-tolerant species in the European fauna. It also colonizes acid wetland sites, especially at high elevations and latitudes.

Biogeography. This species ranges across western Eurasia from Iceland and Atlantic Europe to just east of the Urals.

Nomenclatural notes. Examination of *E. callopisticus* and *E. trochiformis* types (Figs 3, 9) documents that both are junior synonyms of *E. fulvus fulvus* and should not be associated with *E. alderi* and its synonyms.

Euconulus fulvus egenus (Say, 1825)
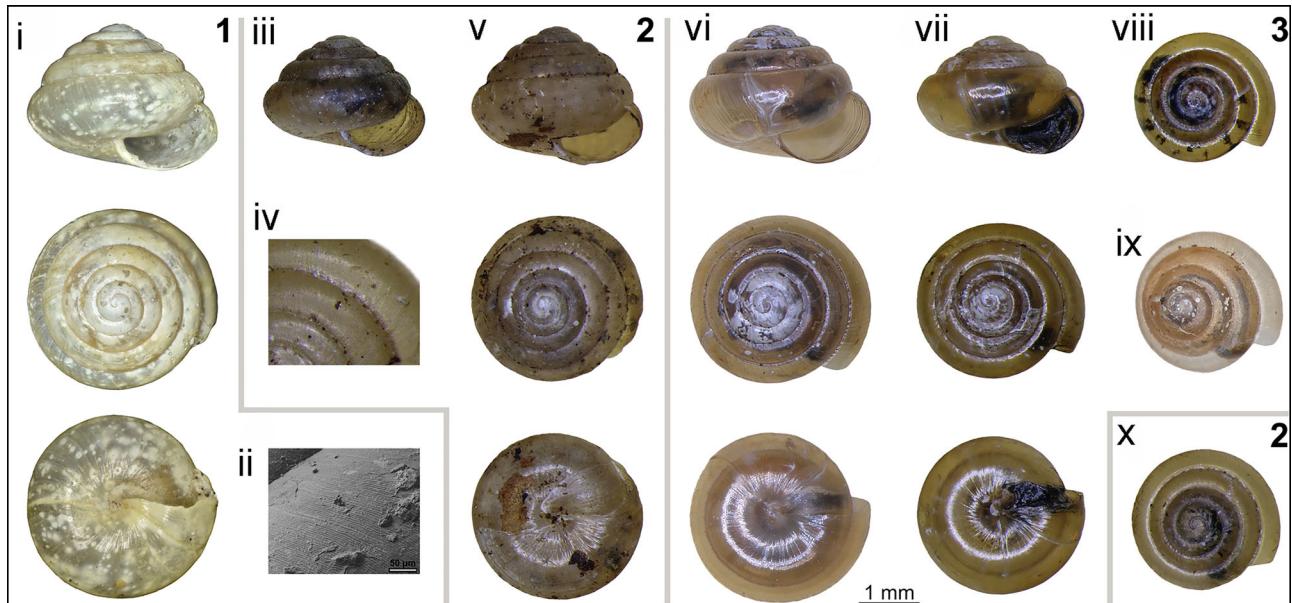
Helix egena Say, 1825: 120.

Figure 9. Shell variation of European *Euconulus fulvus* and its junior synonyms: 1, *E. trochiformis*, syntype shell from the series no. EXEMS Moll4313: i, 2.61 × 3.35 mm (height × width); ii, teleoconch top microstructures in SEM; 2, *E. callopisticus*, original collections: iii, MHNG-MOLL-103700, 1.98 × 2.72 mm; iv, teleoconch top microstructures of the shell from MHNG-MOLL-103701 and v, the same collection, 2.26 × 2.87 mm; vi, MHNG-MOLL-103700; 3, *E. fulvus*: vii, mountain spruce forest, Moravia, Czech Republic, 2.30 × 3.09 mm; viii, mountain alkaline fen, Passo della Nuovena, Switzerland, 1.93 × 2.81 mm; ix, mountain alkaline fen, Zermatt, Switzerland; x, mountain spruce forest, Moravia, Czech Republic.

Type locality. USA – Bank of the Delaware River about 10 miles from Philadelphia.

Synonyms. *Conulus fulvus alaskensis* Pilsbry, 1899: 116, type locality: USA – Dyea Valley and Point Romanoff, Alaska.

Material examined. Twenty-three populations from Asia (Russia: Altai, Yakutia, and Western Siberia) and North America (Canada: Québec, British Columbia, and Labrador; USA: Alaska, California, Idaho, Maine, Minnesota, New Mexico, Texas, and Utah); for details see Supplementary Material – Appendix S1.

Phylogenetics. This taxon is represented by multiple weakly defined, somewhat geographically structured clades, covering central Asia across Beringia to North America (Fig. 2). As explained in detail in Horsáková et al. (2019), these cannot be considered biologically valid species because of their uniformly very low support, inconsistent specimen assignment between the nDNA and mtDNA clades, and lack of any diagnostic macro-scale features. Since evidence also exists of hybridization between central Asian populations and *E. fulvus fulvus* (see Horsáková et al., 2019), we consider only a single species to be present, with the non-European populations being designated as a subspecies.

Conchology. While no unique conchological features demarcate *E. fulvus egenus*, it tends to differ from *E. fulvus fulvus* by possessing more lax coiling, a more discontinuous whorl expansion rate (being initially slow and then rapidly increasing around the second whorl), stronger sillons, more frequent presence of a keel, and possession of strongly mottled mantle tissue (Table 2b, Figs 4 [iii.a–c], 5.4, 7.4). However individuals demonstrating these traits can be found across the entire species range. Individuals sourced from wet taiga and other humid, cool habitats (such as algific talus slopes in the USA upper Midwest) sometimes resemble *E. fresti* sp. nov. in terms of tighter coiling, reduced shell microsculpture, and shinier lustre. However these always maintain a lighter shell colour, grey animal body, and always have the microsculptural ribs being stronger than any spiral lines. Shells from the central Asian clade often possess the tighter coiling ratio of *E. fulvus fulvus* but the mottled mantle of *E. fulvus egenus*.

Ecology. One of the most catholic upland snails, being found from forests to grasslands across the entire soil moisture and acidity gradient.

Biogeography. Ranges from east of the Urals in central Asia to the Atlantic coast in the north-eastern USA and Canada, north into the arctic tundra and south into Mexico along the Rocky Mountains.

Nomenclatural notes. We have chosen *egenus* as the name for this entity because it appears to represent the earliest *nomen* applied to any non-European *E. fulvus* population. Note that the specific epithet was modified to '*egenus*' to accommodate the gender shift of the generic epithet from *Helix* to *Euconulus*. Although material identified as *Helix egena* by Say no longer exists at ANSP, given the original description ('It is much broader than the *H. chersina*') it can represent nothing else: In this part of Pennsylvania only three *Euconulus* can potentially exist (Hubricht, 1985) – *E. fulvus*, *E. fresti* sp. nov., and *E. polygyratus.* Prior to Grimm (1971) *E. polygyratus* was considered a form of *E. chersinus*. As shown above, *E. fulvus egenus* possesses much broader shells and whorls than either of these species.

Euconulus polygyratus (Pilsbry, 1899)

Conulus chersinus polygyratus Pilsbry, 1899: 116.

Type locality. Grand Rapids, Michigan.

Material examined. 6 populations from North America (Canada: Ontario; USA: Iowa, Maine, Michigan, Ohio, and Virginia); for details see Supplementary Material – Appendix S1.

Phylogenetics. This species exists as a monophyletic clade across all reconstruction methods in both the nDNA and mtDNA constructs (Fig. 2). All phylogenetic reconstructions based on the mtDNA construct suggest with very low support (values <50) a sister-group relationship with *E. fresti* sp. nov.

Conchology. Elevated to a full species by Grimm (1971), its shells are highly distinct from any other member of the *E. fulvus* group by their very slow whorl expansion rate allowing for 1–2 additional whorls to exist for a given diameter (Figs 3, 4 [i.a]). It is also distinguished by its strongly lunate aperture, domed spire (Fig. 4 [i.b]), reduced microsculpture, and absence of sillons (Table 2b).

Ecology. This species is characteristic of rich upland, often rocky forest.

Biogeography. Ranges from the Atlantic Provinces of Canada west through the Great Lakes to north-central Minnesota and south to north-eastern Iowa, northern Illinois, the Ohio River valley and Maryland. It extends south along the crest of the Appalachians to western North Carolina.

Discussion

Global diversity of *Euconulus*

The review of literature sources and data in online databases (Baker, 1963; Falkner et al., 2002; Galli, 2016; Kerney & Cameron, 1979; MolluscaBase, 2019; Pilsbry, 1946; Poppe & Poppe, 1994–2019) revealed approximately 20–30 extant *Euconulus* species worldwide, with some being considered endemic, e.g., to Japan (Clench & Turner, 1962), Hawaii (Johnson, 1996), and Bermuda Islands (Bieler & Slapcinsky, 2000). However, an actual species diversity of this genus is very difficult to estimate mainly for two reasons. First, taxonomists often tended to oversplit these continental-range species based on their local forms, such as seen for *E. callopisticus* and *E. trochiformis* in our study. Second, the delimitation of the genus itself is problematic due to its simple shell morphology, making it similar to other genera, mainly *Kaliella* and *Parakaliella*. Thus, some of the putative *Euconulus* species might in fact belong to these related genera and vice versa (see Baker, 1963). For instance in Japan, the species *Parakaliella harimensis* (Pilsbry, 1901) remarkably resembles *E. fulvus* in all superficial morphological features (K. Kimura, personal communication, 19 January 2019; Kawase, Nishio, & Ichihara, 2013; Kawase & Ichihara, 2018). To resolve all these taxonomic issues will require a comprehensive phylogenetic analysis including all of the putative taxa related to *Euconulus*. Our discussion is therefore limited to the Holarctic species within the *E. fulvus* group, which are now well phylogenetically supported and taxonomically clarified.

Our data clearly show that only two *Euconulus* species are present in Europe, *E. alderi* and *E. fulvus*, with both *E. callopisticus* and *E. trochiformis* simply representing junior synonyms of *E. fulvus*, and *E. praticola* being a junior synonym of *E. alderi*. A potential occurrence of other species in Europe, including a putative undescribed Corsican endemic (Falkner et al., 2002), seems very unlikely, given the high and potentially confusing phenotypic plasticity of *E. fulvus* along with the typically large ranges expressed by *Euconulus* species.

The erection of these junior synonyms was probably related to an overemphasis on some morphological traits in isolation along with poor understanding of intraspecific plasticity within the genus. Such conchologically-based over-splitting is not unique to *Euconulus* but is rather common among shelled terrestrial gastropods in general (Elejalde, Muñoz, Arrébola, & Gómez-Moliner, 2005; Emberton, 1995; Köhler & Burghardt, 2016).

The extra-tropical Asian fauna also includes only two species, *E. alderi* and *E. fulvus*, with both subspecies of

the latter, *E. fulvus fulvus* and *E. fulvus egenus*, being present in Western Siberia). *Euconulus fulvus* has also been reported as an exotic from Australia (Stanisic et al., 2010), New Zealand (Climo, 1979), and South America (e.g., Maceira, Miquel, Espinosa, Virgillito, & Lauranzon, 2013; Silva, 2007). Our identification of a genetically distinct lineage within the *E. fulvus* group in Japan (Horsáková et al., 2019) indicates that a thorough revision of the entire group within East Asia is necessary once additional material has been secured.

In North America four species occur (*E. alderi*, *E. fulvus egenus*, *E. fresti* sp. nov., and *E. polygyratus*) with the latter two being endemic to the continent. Besides these, the *E. chersinus* group – consisting of multiple additional genetically validated, yet taxonomically still unresolved species (Horsáková et al., 2019) – is also endemic to south-eastern North America. Thus as also seen in pupillid microsnails (Nekola et al., 2018), the North American *Euconulus* fauna is over three times as species-rich as the European. However, across all terrestrial gastropods the European fauna alone is at least three times as rich as the North American (Nekola, 2014; Welter-Schultes, 2012). Why some microsnails are more diversified in the otherwise more depauperate North American fauna remains undetermined, with the answer likely shedding light on important macro-evolutionary processes.

Shell trait variation

We note considerable variation within and overlap between taxa in quantitative shell traits such as number of whorls, shell height and width. Ratios of shell parameters tend to be more stable and species-specific, but still they only allow reliable identification of *E. polygyratus*. The most reasonable approach towards conchometry is therefore to analyse a suite of traits (or specifically, their ratios) in a multidimensional space, e.g., using a discriminant analysis (Horsák & Meng, 2018; Horsáková et al., 2019). Remarkable levels of variation can also be seen for qualitative traits such as shell and mantle colouration. For instance, cold-climate, wetland populations of *E. fulvus fulvus* and *E. fulvus egenus* often exhibit slightly darker and glossier shells with somewhat darker mantle pigmentation.

Because it is frequent for an individual shell from one taxon to express a single trait more characteristic of another, we recommend basing identification on a consensus across multiple quantitative and qualitative factors. For the *E. fulvus* group this includes not only the ratios between shell height, width, body whorl height and aperture height and width and the number of whorls but also qualitative traits such as protoconch and

teleoconch microsculpture, shell colour and lustre, sillon strength, animal body and mantle colour. A single shell might not be sufficient for a reliable species assignment, because occurrence of atypical specimens or aberrant forms is common (Cameron, 2016). Optimally, multiple representatives of the same population should be examined to find a consensus across morphological traits. In disputable cases, identification should always be verified with molecular data.

A similar use of shell trait consensus for robust species-level diagnoses has been previously applied to the micro-snail genera *Pupilla* and *Vertigo* (Nekola et al., 2015; 2018). Comparison of our findings across these genera illustrates two important points: (1) Traits historically used for identification do not necessarily allow for accurate species diagnoses. This can be seen in the use of raw whorl number in *Euconulus* and use of apertural lamellae architecture across *Pupilla* (Nekola et al., 2015) and in *Vertigo arthuri* Martens, 1882 shell forms (Nekola et al., 2018). (2) The utility of a given suite of traits to provide accurate species-level diagnoses appears to be group-specific. Thus, while animal and shell colour appears vital for assigning *Euconulus* species, these traits are of limited use in *Vertigo* (Nekola et al., 2018). Empirical documentation of those character suites which allow for accurate classification within a given group is thus a prerequisite for biodiversity assessment.

Robust taxonomic assignment

The present study is an example of a vital role of DNA data in land snail taxonomy. Without genetic information, we would not be able to determine the taxonomic utility of given traits, and distinguish those that are highly plastic from those taxonomically informative. While it is generally recommended to use multiple DNA markers for a robust species-level classification (e.g., Horsáková et al., 2019; Razkin et al., 2016; Sauer & Hausdorf, 2012), we consider it necessary to complement the initial molecular analyses with *post hoc* analysis of macro-scale traits to identify features useful for species-level diagnoses; this approach is applicable not only in land snails, but most other taxonomic groups.

Our data also caution against drawing taxonomic conclusions from datasets of limited taxonomic and geographic extent. If sampling had been conducted only on European *E. alderi* vs. *E. fulvus*, the presence of analogue *E. fresti* sp. nov. from North America would never have been observed. The complex nature of *E. fulvus* s. lat. would also have been unobservable without sampling multiple populations across Eurasia and North America. In fact had analysis been limited to Europe and eastern North America, two distinct

species-level taxa would have been supported via DNA sequence and conchology. The evaluation of intermediate populations across Beringia and central Asia, however, revealed introgression in conchology and presumable presence of hybridization (Horsáková et al., 2019). This pointed us towards the decision to accept the traditional concept of *E. fulvus* as one species with a Holarctic distribution, despite its polyphyly in the DNA reconstructions. However, we consider this a tentative assignment that might – and should – be subjected to further scrutiny, perhaps using large-scale genome-wide data (e.g., RADseq technology). This approach has already proven useful in resolving phylogenetic relationships and species delimitation in the minute land snail genus *Pyramidula* (Razkin et al., 2016; Razkin, Gómez-Moliner, Vardinoyannis, Martínez-Ortí, & Madeira, 2017).

Taxonomic summary

Four species and one subspecies can be distinguished within the Holarctic *Euconulus fulvus* group; three are present in Eurasia (*E. alderi*, *E. fulvus fulvus*, *E. fulvus egenus*) while four are found in North America (*E. alderi*, *E. fresti* sp. nov., *E. fulvus egenus*, *E. polygyratus*). *Euconulus fresti* sp. nov. and *E. polygyratus* are endemic to North America; *E. fulvus fulvus* to western Eurasia. *Euconulus trochiformis* and *E. callopisticus* represent junior synonyms of *E. fulvus*, while *E. praticola* represents a junior synonym of *E. alderi*. North American *E. fresti* sp. nov. resembles *E. alderi* in both morphology (dark body and glossy shell) as well as ecology (wetland-restricted), but differs in a suite of diagnostic shell and body features. *Euconulus polygyratus* represents a valid species within the *E. fulvus* group. Earlier taxonomic over-splitting is likely linked to an overemphasis of single shell traits, as well as poor understanding of intraspecific conchological plasticity within this genus.

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Disclosure Statement

Supplemental data

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Supplemental material

Appendix S1. Taxon name, *a priori* identification (prior to revision), location, habitat information, sample code and GenBank accession number for each of the analysed *Euconulus* specimens.

Taxon / Country	*A priori* name	State / Province / region	Habitat	Latitude °N	Longitude °E	Sample code	GenBank accession number			
							16S	COII	ITS1	ITS2
Euconulus alderi										
Czech Rep.	*praticola*	Moravia	Wet meadow	48.8068	16.8382	E109	MK266536	MK299609	MK299792	MK299699
Czech Rep.	*praticola*	Moravia	*Sphagno-Tomentypnion* fen	49.7191	16.1251	E71	MK266512	MK299585	MK299768	MK299675
Czech Rep.	*praticola*	Český les	Willow shrubs on a fen margin	49.6984	12.4728	E45	MK266498	MK299571	MK299754	MK299661
France	*callopisticus*	Jura Mts.	Waterlogged mineral-rich fen	46.8941	6.3042	E185	MN685178	MN688740	MN706208	MN706201
France	*callopisticus*	Massif Central	Quaking fen with pools	45.2051	2.8487	E188	MN685179	MN688741	MN706209	MN706202
Slovakia	*praticola*	Levoča Mts.	Brown-moss rich fen	49.2052	20.7865	E41	MK266495	MK299568	MK299751	MK299658
Slovakia	*praticola*	Danube plateau	Reed-sedge wetland	47.8740	17.6709	E76	MK266515	MK299588	MK299771	MK299678
Austria	*praticola*	Niederösterreich	Wet brown-moss rich fen	47.8238	15.4713	E40	MK266494	MK299567	MK299750	MK299657
Poland	*praticola*	Lubelskie	Wet brown-moss rich fen	51.3452	23.3371	E86	MK266521	MK299594	MK299777	MK299684
Sweden	*praticola*	Jämtland	Wet calcareous fen	63.4154	14.5544	E75	MK266514	MK299587	MK299770	MK299677
Sweden	*praticola*	Jämtland	Wet calcareous fen	63.5802	15.2311	E61	MK266504	MK299577	MK299760	MK299667
Switzerland	*praticola*	Fribourg (pre-Alps)	Rich fen on a lake margin	46.8379	6.8126	E2	MK266493	MK299566	MK299749	MK299656
Switzerland	*praticola*	Graubünden (Alps)	Brown-moss rich fen	46.7772	10.2821	E72	MK266513	MK299586	MK299769	MK299676
England	*praticola*	Derbyshire	*Carex*-rich short marsh	53.3330	-1.7048	E179	MN685174	MN688736	MN706203	MN706196
England	*trochiformis*	E Sussex	*Glyceria maxima* marsh	50.8781	0.0064	E180	MN685175	MN688737	MN706204	MN706197
Scotland	*praticola*	Cairngorms	Quaking littoral fen	57.1567	-3.8822	E181	MN685176	MN688738	MN706205	MN706198
Scotland	*trochiformis*	Highland Co.a.	Fen woodland	57.6392	-4.1983	E182	MN685177	MN688739	MN706206	MN706199
Romania	*praticola*	Harghita	Calcareous fen	47.0784	25.4777	E88	MK266523	MK299596	MK299779	MK299686
Bulgaria	*praticola*	Bulgaria	Brown-moss rich fen	42.7064	24.1117	E89	MK266524	MK299597	MK299780	MK299687
USA	aff. *alderi*	Alaska	Low, marly meadow	67.4775	-149.9170	E115	MK266541	MK299614	MK299798	MK299705
USA	aff. *alderi*	California	*Juncus-Carex-Geum* wet meadow	38.2253	-119.2500	E116	MK266542	MK299615	MK299799	MK299706
Russia	*praticola*	Western Siberia	*Salix lapponum-S. phylicifolia* scrub	66.4442	79.3228	E56	MK266500	MK299573	MK299756	MK299663
Euconulus fresti sp. nov.										
Canada	aff. *alderi*	British Columbia	Extremely rich fen in river alluvium	50.9213	-117.5770	E110	MK266537	MK299610	MK299793	MK299700

Country	Subspecies	Locality	Habitat	Lat	Lon	Code				
USA	aff. *alderi*	Iowa	Heavily grazed wet sedge mat	42.0406	-91.3264	E117	MK266543	MK299616	MK299800	MK299707
USA	aff. *alderi*	Maine	Rich cedar-ash-maple swamp	44.9272	-67.6589	E118	MK266544	MK299617	MK299801	MK299708
USA	aff. *alderi*	Michigan	Rich marly sedge mat	42.4306	-83.9792	E119	MK266545	MK299618	MK299802	MK299709
USA	aff. *alderi*	Utah	Calcareous seep	37.3742	-112.5940	E120	MK266546	MK299619	MK299803	MK299710
USA	aff. *alderi*	New Mexico	Sedge meadow	36.1353	-105.5320	E183			MN706207	MN706200

Euconulus fulvus fulvus

Country	Subspecies	Locality	Habitat	Lat	Lon	Code				
Czech Rep.	*fulvus*	Krušné hory Mts.	Seepage in Ash forest	50.6673	13.6708	E80	MK266516	MK299589	MK299772	MK299679
Czech Rep.	*fulvus*	Moravia	Mountain deciduous forest	48.8550	17.6690	E82	MK266518	MK299591	MK299774	MK299681
Czech Rep.	*fulvus*	Moravia	Mountain spruce forest	49.5047	18.3761	E83	MK266519	MK299592	MK299775	MK299682
Slovakia	*fulvus*	Kysuce NR	Rich fen with willows	49.4256	18.5255	E63	MK266506	MK299579	MK299762	MK299669
Poland	*fulvus*	Orava	Fen meadow on a slope	49.3369	19.9055	E87	MK266522	MK299595	MK299778	MK299685
Austria	*fulvus*	Niederösterreich	Wet brown-moss rich fen	47.8514	15.3895	E42	MK266496	MK299569	MK299752	MK299659
Switzerland	*trochiformis*	Valais (Alps)	Brown-moss rich fen on a brook margin	45.9990	7.7551	E1	MK266492	MK299565	MK299748	MK299655
Switzerland	*trochiformis*	Valais (Alps)	Rich fen on a spring	46.0018	7.3407	E62	MK266505	MK299578	MK299761	MK299668
Switzerland	*trochiformis*	Valais (Alps)	Sloping calcareous fen	46.0072	7.7934	E50	MK266499	MK299572	MK299755	MK299662
Switzerland	*fulvus*	Bern (Alps)	Sloping calcareous fen with *Schoenus*	46.5606	7.0769	E64	MK266507	MK299580	MK299763	MK299670
Switzerland	*trochiformis*	Graubünden (Alps)	Brown-moss rich fen	46.6741	10.3523	E67	MK266509	MK299582	MK299765	MK299672
Sweden	*fulvus*	Jämtland	*Sphagno-Tomentypnion* fen	63.5802	15.2311	E101	MK266534	MK299607	MK299790	MK299697
Sweden	*praticola*	Jämtland	Sloping brown-moss rich fen	63.5684	12.2458	E66	MK266508	MK299581	MK299764	MK299671
Austria	*trochiformis*	Salzburg (Alps)	Limestone slope	47.2334	13.5067	E98	MK266532	MK299605	MK299788	MK299695
Norway	*praticola*	Dovrefjell NP	Willow shrubs on a brook margin	62.3548	9.6702	E90	MK266525	MK299598	MK299781	MK299688
Romania	*fulvus*	Harghita	Wet brown-moss rich fen	46.3176	25.5999	E44	MK266497	MK299570	MK299753	MK299660
Iceland	*fulvus*	Mývatn	Willow tundra	65.6289	-16.9928	E161	MK266571	MK299644	MK299829	MK299736
Iceland	*fulvus*	Skaftafell NP	Willow tundra	64.0264	-16.9779	E162	MK266572	MK299645	MK299830	MK299737
Russia	*fulvus*	Western Siberia	Mesic birch forest	56.5067	68.4156	E99	MK266533	MK299606	MK299789	MK299696

Euconulus fulvus egenus

Country	Subspecies	Locality	Habitat	Lat	Lon	Code				
USA	*fulvus*	Idaho	Douglas fir forest at base of open talus	47.6477	-115.9720	E112	MK266539	MK299612	MK299795	MK299702
USA	*fulvus*	California	Damp creekside with fern	34.1792	-116.9060	E131	MK266555	MK299628	MK299812	MK299719
USA	*fulvus*	Maine	Rich thuja-ash-red maple swamp	44.9272	-67.6589	E133	MK266556	MK299629	MK299814	MK299721
USA	*fulvus*	Minnesota	Aspen-ash-balsam-spruce forest	47.6211	-95.3056	E134	MK266557	MK299630	MK299815	MK299722
USA	*fulvus*	Texas	Dry rocky oak-juniper forest	29.2442	-103.2970	E135	MK266558	MK299631	MK299816	MK299723

Country	Subspecies	Location	Habitat	Latitude	Longitude	Code				
USA	*fulvus*	Utah	Aspen fringe on S-facing talus slope	38.4169	-112.3130	E136	MK266559	MK299632	MK299817	MK299724
USA	*fulvus*	New Mexico	Pine-fir forest	35.7494	-105.6590	E97	MK266531	MK299604	MK299787	MK299694
USA	*alaskensis*	Alaska	Wet mesic alder-aspen-birch forest	64.6064	-149.0900	E138	MK266561	MK299634	MK299819	MK299726
USA	*alaskensis*	Alaska	Rich upland tundra	69.3353	-148.7300	E139	MK266562	MK299635	MK299820	MK299727
USA	*fulvus*	Alaska	Spruce-alder streamside	60.9750	-149.1210	E130	MK266554	MK299627	MK299811	MK299718
Canada	*alaskensis*	Québec	Willow scrub on tundra	55.0644	-67.2347	E137	MK266560	MK299633	MK299818	MK299725
Canada	*fulvus*	Québec	Rich aspen-maple-birch forest	49.3256	-67.3700	E129	MK266553	MK299626	MK299810	MK299717
Canada	*fulvus*	British Columbia	Extremely rich fen in river alluvium	50.9213	-117.5770	E103	MK266535	MK299608	MK299791	MK299698
Canada	*fulvus*	British Columbia	Willow shrubs with shist scree	50.6368	-117.1920	E93	MK266528	MK299601	MK299784	MK299691
Canada	aff. *alderi*	Labrador	Rich *Carex-Calamagrostis* turf	54.6725	-66.6075	E114	MK266540	MK299613	MK299797	MK299704
Russia	*praticola*	Altai	*Betula* scrub on boulder accumulation	49.6288	87.6569	E57	MK266501	MK299574	MK299757	MK299664
Russia	*fulvus*	Altai	Fen shrubland in a floodplain	51.1146	85.5966	E58	MK266502	MK299575	MK299758	MK299665
Russia	*fulvus*	Altai	Lake margin	50.4742	87.6344	E81	MK266517	MK299590	MK299773	MK299680
Russia	*fulvus*	Altai	Hemiboreal forest	51.7339	85.7233	E85	MK266520	MK299593	MK299776	MK299683
Russia	*praticola*	Altai	Small woodlot	49.6426	87.8404	E95	MK266530	MK299603	MK299786	MK299693
Russia	*fulvus*	Western Siberia	Salix scrub	67.1814	78.8589	E59	MK266503	MK299576	MK299759	MK299666
Russia	*fulvus*	Western Siberia	Mesic pine-birch forest	63.4425	74.6075	E92	MK266527	MK299600	MK299783	MK299690
Russia	*fulvus*	Yakutia	Pine taiga forest	62.5671	130.5288	E70	MK266511	MK299584	MK299767	MK299674
Euconulus polygyratus										
USA	*polygyratus*	Virginia	Mesic maple-elm forest	38.0631	-79.8883	E153	MK266563	MK299636	MK299821	MK299728
USA	*polygyratus*	Ohio	Cool limestone bluff with white cedar	39.7953	-83.8364	E167	MK266576	MK299649	MK299835	MK299742
USA	*polygyratus*	Maine	Upland maple-birch-beech forest	46.0444	-68.1722	E168	MK266577	MK299650	MK299836	MK299743
USA	*polygyratus*	Michigan	Rich rocky N-facing wooded slope	45.9077	-84.7470	E170	MK266579	MK299652	MK299838	MK299745
USA	*polygyratus*	Iowa	N-facing algific slope and cliff	43.1373	-91.4782	E171	MK266580	MK299653	MK299839	MK299746
Canada	*polygyratus*	Ontario	Maple forest on limestone outcrop	44.9264	-75.7594	E154	MK266564	MK299637	MK299822	MK299729
Euconulus trochulus (outgroup)										
USA	*trochulus*	Oklahoma	Mesic wooded outcrops	36.0131	-96.9972	E155	MK266565	MK299638	MK299823	MK299730

Appendix S2. Basic summary statistics of shell measurements and their ratios for the studied *Euconulus* species. Numbers of measured shells/populations: *E. alderi* = 27/7, from Czech Republic, Slovakia, Poland, Bulgaria, Sweden, Russia (Western Siberia) and USA (Alaska); *E. fulvus fulvus* = 16/6, from Czech Republic, Norway, Switzerland and Russia (Western Siberia); *E. fulvus egenus* = 35/12, from Russia (Altai and Western Siberia), Canada (British Columbia and Québec), and USA (Alaska, California, Texas, and Utah), **E. fresti** sp. nov. = 14/4, from USA (Iowa, Maine and Utah) and Canada (British Columbia); *E. polygyratus* = 14/4, from USA (New York, Ohio and Virginia), and Canada (Ontario). Two syntype shells of *E. trochiformis* from Montagu collection (Royal Albert Memorial Museum & Art Gallery, Exeter) and three shells of *E. callopisticus* from Bourguignat collection (Natural History Museum of Geneva) were also included, and eventually classified as *E. f. fulvus*.

		No. of whorls	Width	Height	Body height	Aperture width	Aperture height	Width/ No. of whorls	Height/ No. of whorls	Body height/ Height	Apert. width/ Width	Apert. width/ Height	Apert. height/ Body height	Height/ Width
E. alderi	Min	4.00	2442	1742	1404	1126	961	0.57	0.42	0.69	0.45	0.60	0.68	0.71
	1st Quart.	4.21	2536	1922	1483	1269	1014	0.60	0.45	0.73	0.49	0.64	0.83	0.74
	Median	4.40	2773	2105	1571	1375	1072	0.61	0.47	0.76	0.50	0.66	0.86	0.75
	Mean	4.44	2755	2108	1588	1375	1079	0.62	0.47	0.76	0.50	0.65	0.85	0.76
	3rd Quart.	4.60	2859	2218	1678	1448	1128	0.64	0.50	0.78	0.51	0.67	0.89	0.79
	Max	5.30	3530	2780	1920	1780	1300	0.69	0.52	0.81	0.53	0.71	0.92	0.84
E. fresti sp. nov.	Min	4.00	2179	1589	1260	1050	868	0.52	0.38	0.71	0.45	0.59	0.72	0.70
	1st Quart.	4.10	2339	1677	1342	1119	947	0.54	0.41	0.72	0.47	0.63	0.81	0.72
	Median	4.30	2443	1782	1389	1156	968	0.56	0.42	0.79	0.48	0.65	0.84	0.73
	Mean	4.41	2465	1829	1396	1184	971	0.56	0.41	0.77	0.48	0.65	0.83	0.74
	3rd Quart.	4.73	2594	1957	1439	1272	992	0.58	0.43	0.81	0.49	0.66	0.86	0.75
	Max	5.00	2700	2142	1513	1325	1090	0.61	0.43	0.82	0.49	0.70	0.91	0.79
E. f. fulvus	Min	4.10	2484	1655	1301	1186	899	0.56	0.39	0.66	0.46	0.57	0.66	0.65
	1st Quart.	4.25	2569	1856	1404	1228	942	0.61	0.42	0.74	0.47	0.64	0.79	0.70
	Median	4.30	2662	1897	1456	1270	1018	0.61	0.44	0.76	0.48	0.68	0.87	0.72
	Mean	4.51	2756	2010	1503	1336	1027	0.61	0.44	0.75	0.48	0.67	0.83	0.73
	3rd Quart.	4.75	2730	2010	1562	1347	1066	0.63	0.45	0.78	0.49	0.70	0.89	0.74
	Max	5.30	3360	2792	1867	1700	1230	0.65	0.53	0.84	0.51	0.73	0.93	0.86

		No. of whorls	Width	Height	Body height	Aperture width	Aperture height	Width/ No. of whorls	Height/ No. of whorls	Body height/ Height	Apert. width/ Width	Apert. width/ Height	Apert. height/ Body height	Height/ Width
E. f. egenus	Min	4.13	2596	1886	1393	1264	920	0.57	0.42	0.71	0.47	0.58	0.77	0.68
	1st Quart.	4.38	2802	2044	1568	1401	1105	0.64	0.46	0.74	0.49	0.64	0.86	0.72
	Median	4.50	3008	2236	1716	1466	1162	0.66	0.49	0.76	0.49	0.67	0.88	0.75
	Mean	4.56	3001	2238	1691	1485	1157	0.66	0.49	0.76	0.49	0.67	0.88	0.74
	3rd Quart.	4.75	3149	2410	1797	1580	1227	0.68	0.52	0.78	0.50	0.68	0.90	0.77
	Max	5.00	3444	2693	1964	1722	1330	0.72	0.55	0.81	0.52	0.74	0.96	0.84
E. polygyratus	Min	5.60	2488	1954	988	1060	683	0.41	0.35	0.48	0.41	0.46	0.72	0.78
	1st Quart.	5.75	2569	2061	1379	1192	886	0.43	0.36	0.63	0.46	0.54	0.84	0.80
	Median	6.10	2636	2191	1457	1229	925	0.44	0.36	0.65	0.46	0.57	0.87	0.82
	Mean	6.05	2656	2198	1414	1227	912	0.44	0.36	0.64	0.46	0.56	0.87	0.83
	3rd Quart.	6.25	2709	2320	1486	1288	957	0.45	0.37	0.68	0.47	0.58	0.89	0.86
	Max	6.60	2900	2539	1557	1336	1012	0.46	0.38	0.70	0.50	0.61	1.12	0.89

Appendix S3. Illustration of measurements taken for *Euconulus* shells, as conducted on one of the *E. trochiformis* syntypes.

A. Shell width
B. Shell height
C. Body height
D. Aperture width
E. Aperture height

A. 3.36mm

D. 1.70mm

B. 2.72mm

C. 1.86mm E. 1.23mm
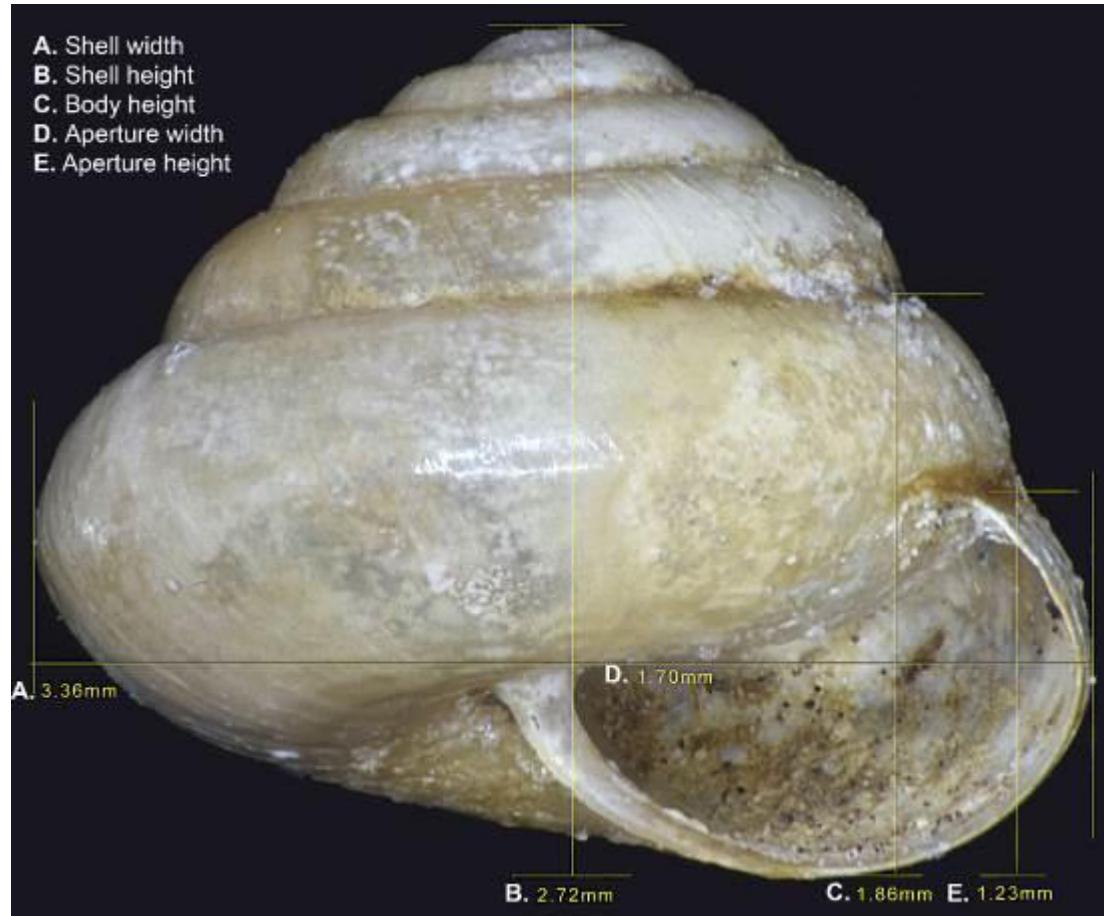
Appendix S4. Mean within-group (A) and between-group (B) distances for *Euconulus fulvus* group taxa in the analysed nDNA and mtDNA constructs, reported as nucleotide base pairs/construct. The lower half of Matrix B represents distances in ITS1+ITS2 and the upper half (demarcated by italic font) represents distances in COII+16S.

A. Within-group variability

	Mitochondrial	Nuclear
E. fresti sp. nov	6.2	*0.3*
E. alderi	3.5	*0.4*
E. fulvus fulvus	6.7	*1.5*
E. fulvus egenus	13.5	*2.6*
E. polygyratus	3.2	*0.3*

B. Between-group variability

	E. fresti sp. nov.	E. alderi	E. fulvus fulvus	E. fulvus egenus	E. polygyratus
E. fresti sp. nov		*30.8*	*31.7*	*27.8*	*24.3*
E. alderi	6.2		*32.2*	*28.9*	*28.4*
E. f. fulvus	6.8	4.7		*30.9*	*32.0*
E. f. egenus	3.9	5.3	6.0		*23.7*
E. polygyratus	3.3	5.2	5.8	2.8	

Appendix S5. Aligned ITS2 sequence of all analysed *Euconulus* specimens; the 350T is unique for *E. fresti* sp. nov. (see the attached fasta file).

For sample codes and specimen characteristics see Appendix S1.

>E1
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>E116
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>E120
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>E131
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>E162
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>E167
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Appendix S6. Terry Frest in the summer of 1989, contemporaneous with his discovery of *E.* aff. *alderi* in Iowa, USA. (photo courtesy of Edward Johannes).