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A PHYLOGENETIC OVERVIEW OF THE GENUS *VERTIGO* O. F. MÜLLER, 1773 (GASTROPODA: PULMONATA: PUPILLIDAE: VERTIGININAE)

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ABSTRACT

We document global phylogenetic pattern in the pupillid land snail genus *Vertigo* by analyses of nDNA (ITS1 and ITS2) and mtDNA (CytB and 16S) sequence from 424 individuals representing 91 putative specific and subspecific *Vertigo* taxa. nDNA and mtDNA data were separately subjected to neighbor-joining, minimum evolution, maximum likelihood and Bayesian reconstruction methods, with conclusions being drawn from shared topological structures. Six highly supported, reciprocally monophyletic subgeneric level clades were identified: *Vertigo*, *Alaea*, ***Boreovertigo*** new subgenus, *Isthmia*, *Staurodon* and *Vertilla*. 88 species or subspecies were also confirmed, nine of which are new and formally described herein: ***V. beringiana***, ***V. chiricahuensis***, ***V. chytryi***, ***V. genesioides***, ***V. kodamai***, ***V. kurilensis***, ***V. lilljeborgi vinlandica***, ***V. pimuensis*** and ***V. pisewensis***. Thirteen taxa were synonymized: *V. arthuri basidens*, *V. arthuri hubrichti*, *V. arthuri paradoxa* (= *V. arthuri*); *V. allyniana* (= *V. modesta*); *V. andrusiana* (= *V. columbiana*); *V. conecuhensis* (= *V. alabamensis*); *V. dedecora tamagonari* (= *V. dedecora*); *V. elatior*, *V. idahoensis* (= *V. ventricosa*); *V. eogea* (= *V. ovata*); *V. modesta insculpta* (= *V. modesta concinnula*), *V. modesta microphasma*, *V. modesta sculptilis* (= *V. modesta castanea*). Qualitative observations of conchological features, ecological preferences and geographic coverage were conducted for each subgenus and genetically supported species or subspecies-level taxon. These demonstrated that: (1) a suite of diagnostic shell features usually exists to demarcate each species-level taxon; (2) shell features were incapable of defining genetically validated subgenera; (3) all subgenera had transcontinental ranges; (4) $^1/_3$ of all species possess continental or trans-continental ranges, with very few having range extents < 1,000 km; (5) all subgenera and fully $^2/_3$ of global *Vertigo* species and subspecies are found in North America, more than 2.5 times the number found in central and eastern Asia, the second most diverse region. This is similar to several other molluscan groups, such as the polygyrid land snails and unionid bivalves for which North America is the global biodiversity hotspot.

Key words: phylogenetics, conchology, biogeography, ecology, mtDNA, nDNA, new species, new subspecies, taxonomy.

INTRODUCTION

Land snails of the genus *Vertigo* (Pupillidae: Vertigininae) have cylindrical-ovoid shells that generally range from 1.5–3.0 mm in length and possess a rounded aperture with 0–6 + lamellae at maturity (Pilsbry, 1948). Historically, the genus has been regarded as predominantly Holarctic, where *Vertigo* are an important component of many terrestrial gastropod faunas, often constituting 10% or more (up to 70%) of both species and individuals within many North American (Nekola, 2014), Fennoscandian (Valovirta, 1968; Waldén, 1981), and central Asian (Horsák et al., 2010) assemblages. However, Nekola & Coles (2016) have recently shown that at least some *Afripupa*, *Nearctula*, *Ptychalaea*, *Staurodon* and *Sterkia* should also

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be regarded as *Vertigo* and that the genus has a worldwide distribution.

Vertigo feature prominently in many lists of species of conservation concern, with over a quarter of the European *Vertigo* being listed in Annex II of the Habitats Directive of the Bern Convention (Speight et al., 2003), approximately half of the North American *Vertigo* being listed as Globally Threatened or higher in the NatureServe database (NatureServe, 2015), and half of the Japanese *Vertigo* being listed in the Japan Red Data Book (Japanese Ministry of the Environment, 2012).

In spite of its significant contribution to terrestrial gastropod biodiversity, taxonomic treatments of the genus tend to be old or parochial, with arguably the last global consideration being found in Volume 25 of the *Manual of Conchology* (Pilsbry, 1919). Since that time, only regional and national overviews have been published, for example, North America (Pilsbry, 1948; Nekola & Coles, 2010), Europe (Speight et al., 2003, and contributions therein), Poland (Pokryszko, 1990) and Russia (Schileyko, 1984).

Anatomy is of limited use in the Pupillidae due to radular and genitalic convergence and the high incidence of aphally (Pokryszko, 1987, 1990; Gittenberger & van Bruggen, 2013). Thus, taxonomic concepts have been almost entirely based on conchological features. However, given the non-insignificant incidence of ecophenotypic and biogeographic plasticity in conchological features in the closely related *Pupilla* (Nekola et al., 2015), the ability of shell features to accurately document evolutionary relationships and species diversity patterns must be questioned.

The logical source for quasi-independent assessment of such conchologically based concepts is DNA sequence data. Nekola et al. (2009) considered species-level taxonomy in the North American *Vertigo gouldii* group (*sensu* Pilsbry, 1948) using both mtDNA and nDNA sequences. This work demonstrated that although some conchological traits were plastic within a species (for example palatal lamellae, callus, and crest strength within *Vertigo arthuri* and related forms), in general each validated species-level taxon did possess a unique combination of conchological traits, allowing for reliable diagnoses from shells alone. However, these features were also too evolutionarily mutable to allow for accurate supraspecific classification.

Here we expand this work to present an empirically driven overview of global *Vertigo* taxonomy based on DNA sequence data, conchology, and ecological preferences. We conclude with an overview of updated genus-level evolutionary, ecological and biogeographic patterns.

MATERIALS AND METHODS

Taxonomic Coverage

We considered all species and subspecies of Holarctic *Vertigo* that appear to have recognizably distinct shells, plus representatives of taxa historically assigned to *Afripupa*, *Nearctula*, *Ptychalaea*, *Staurodon*, *Sterkia* and *Vertilla* (Appendix). Eighteen recent putative Holarctic *Vertigo* could not be included as follows: *Vertigo bermudensis* Pilsbry, 1919, *V. marki* Gulick, 1904, and *V. numellata* Gulick, 1904, from the island of Bermuda have not been seen alive in over a century (John Slapcinsky, *personal communication*). *Vertigo californica cyclops* (Sterki, 1890), *V. ovata mariposa* Pilsbry, 1919, and *V. sterkii* Pilsbry, 1919, from California, U.S.A., have all been sought from their last known stations, but living populations have not been relocated. *Vertigo californica guadalupensis* Pilsbry, 1927, was not considered as we have yet to conduct field work on Guadalupe Island. We have not included *V. ovata diaboli* Pilsbry, 1919, from Texas as only dead river drift material is known. During field work on Honshu, we were unable to locate material referable to the holotype of *V. japonica* Pilsbry & Hirase, 1904, and found only dead shells of *V. japonica tosana* Pilsbry, 1919. The inherent dangers to western scientists working in the tribal areas of northern Pakistan prevented location of living *V. nangaparbatensis* Pokryszko et al., 2009, and *V. superstriata* Pokryszko et al., 2009. None of the archived museum material for these two species contains mummified tissue suitable for DNA extraction and analysis. We did not visit mainland China to obtain live material of *V. teilhardi* Ping & Yen, 1933. Specimens of Caribbean *Sterkia* (*Metasterkia*) suitable for DNA extraction were also not available and it remains unknown whether they represent *Vertigo.* The North American Pacific Coast members of this (former) genus, which have been shown to be *Vertigo* (Nekola & Coles, 2016), are included in this study. Argentinean *V. frenguelli* Parodiz, 1957, was not included because it is only known from subfossil shells.

The following were excluded because their stated conchology was so indistinct from other named taxa that unequivocal *a priori* identification/selection (see below) was impossible: *Vertigo andrusiana sanbernardinensis* Pilsbry, 1919, represents small or immature *V. occidentalis*, as confirmed by the continual variation noted between these two taxa in S. S. Berry collections of the early 20th Century, in particular Lot 1679 of the Barry Roth Collection. We have also been unable to locate extant pure colonies of *V. a. sanbernardinensis* in the San Bernardino Mountains. *Vertigo heldi* (Clessin, 1877) appears to simply represent parasitized *V. pygmaea* individuals, as indicated by the fact that nowhere does *V. heldi* exist as anything other than rare individuals within large *V. pygmaea* populations that possess juvenile-looking but aberrantly large shells characteristic of parasite infection. Given the original description of *Vertigo hydrophila* (Reinhardt, 1877), we are unsure how it would differ from either *V. eogea*, *V. ovata* or *V. lilljeborgi*. Following Pilsbry (1948), we do not recognize *V. modesta corpulenta* (Morse, 1865) or *V. modesta parietalis* (Ancey, 1887), as these represent the endpoints of continuous variation within many *V. modesta* populations. We agree with Hubricht (1974) that the lectotype of *V. wheeleri* Pilsbry, 1928 (ANSP 144810), represents a small individual of *V. rugosula*. Likewise, the Cuban *V. torrei* Aguayo & Jaume, 1935, which we have observed (ANSP 167405, ANSP 160201) also represent *V. rugosula*. We follow Pilsbry (1919) in treating *V. neglecta* Poey, 1856, of Cuba as an eroded beach-drift shell of *V. ovata*.

Specimen Identification and Selection

Specimens used for DNA sequence analyses were primarily obtained from collections made by the authors from 2000–2016. A total of 424 individuals were included (Appendix). Our selection of analyzed material is grounded in the fact that taxonomic concepts within the genus have until now been limited to conchology. Thus, we made *a priori* taxonomic assignments of all specimens using currently recognized diagnostic conchological features as reported by Pilsbry (1919, 1920, 1948), Kerney & Cameron (1979), Schileyko (1984), Nekola & Coles (2010) and Horsák et al. (2013b). The names used in the Appendix reflect these *a priori* assignments and not their *post hoc* taxonomic status. We also selected for analyses individuals of forms that fell outside of the shell features and/or the ecology and distribution of known species and thus represented potential undescribed taxa. Three to six individuals per taxon were analyzed (with some exceptions) representing the full known range of variation in conchology, geography and ecology. Paratype or topotype individuals and material sourced from within 200 km of the type location included: *V. alabamensis conecuhensis* (VH8), *V. alpestris* (T16 & H37), *V. angustior* (VH78), *V. arizonensis* (NS1), *V. arthuri basidens* (NS8), *V. arthuri paradoxa* (NS39), *V. binneyana* (VH69), *V. botanicorum* (paratypes: B3, B55, B56), *V. catalinaria* (topotypes: C5, C11), *V. clappi* (VH55), *V. clementina* (topotypes: C42, C43, OG15), *V. concinnula* (VH96), *V. cristata* (NS44), *V. cupressicola* (topotype: C1), *V. dedecora* (topotype: VH28), *V. dedecora tamagonari* (topotype: VH23), *V. diegoensis* (C3, C23), *V. eogea* (J1), *V. extima* (B77), *V. genesii* (topotype: B99), *V. hachijoensis* (topotype: VH103), *V. hebardi* (topotype: VH1), *V. hinkleyi* (NS53), *V. inserta* (topotypes: NS30, T9), *V. kushiroensis* (topotypes: VH61, J13), *V. longa* (topotypes: C4, C27–C30), *V. malleata* (paratype: VH9), *V. marciae* (paratype: VH4), *V. meramecensis* (T10), *V. modesta castanea* (B104), *V. modesta insculpta* (topotype: B105), *V. modesta microphasma* (topotype: B106), *V. nylanderi* (NS36), *V. occidentalis* (B96), *V. oralis* (VH14), *V. perryi* (VH89), *V. ronnebyensis* (topotype: B84), *V. substriata* (T18), *V. tridentata* (VH46), *V. trinotata* (topotype: C2) and *V. ventricosa* (B91).

Throughout the manuscript, the acronyms used to identify institutions which house given lots are reported as in the Global Registry of Biodiversity Repositories (http://grbio.org/find-biorepositories).

DNA Extraction, PCR Amplification and Sequence Determination

Live specimens were allowed to desiccate at ambient temperature and humidity, were preserved in absolute ethanol, or in a few cases used before death. DNA was prepared using the Omega BioTek Mollusk DNA Extraction Kit. Because of the poor diffusion of proteinase into and extracted DNA out of these tiny, tightly coiled shells, shell destruction was required to allow sufficient DNA yield for reliable polymerase chain reaction (PCR) success. In addition, significant shell degradation was noted following proteinase exposure. Thus (with few exceptions), specimens were taken from lots containing multiple examples of each taxon, with all specimens used for DNA preparation being imaged at 20x magnification prior to shell destruction (Nekola et al., 2009). An archive of all shell images is available upon request.

The internal transcribed spacers (plus flanking sequence) of the nuclear ribosomal RNA complex (ITS1 and ITS2) and mitochondrial Cytochrome B (CytB) and 16S ribosomal RNA (16S) were amplified using standard PCR techniques. To obtain maximum success, we used an assortment of primer designs obtained not only from the published literature but also developed by the authors (Table 1). PCR products were sequenced in both forward and reverse directions using Perkin Elmer ABI Big Dye termination and standard protocols. We obtained unambiguous CytB sequence from 420 individuals, 16S from 416 individuals, ITS1 from 401 individuals and ITS2 from 415 individuals (Appendix).

Phylogenetic Analyses

The various primers used to amplify each gene generated amplicons of different length. We selected for analysis the longest sequence common across all amplicons of a given gene (excluding primer sequence) and, using Clustal X, aligned each to the respective target: CytB between CytB397f and CytB811r; 16S between 16Sar and 16Sbr; ITS1 between 18srDNA and LSU1rc; and ITS2 between LSU1 and LSU3. Amplicon and sequence lengths given later in the text refer to these common regions. We found that insertion-deletion patterns were simple and provided alignments that could have been easily accomplished by eye. Following this, CytB and 16S sequences were concatenated, and ITS1 and ITS2 sequences were analyzed as a single construct by omitting 27 invariant bases from the upstream end of ITS1, nine invariant bases from the downstream end of ITS2 and 81 invariant bases from the intervening 5.8S region. Base substitutions quoted in the text refer to the “sense” strand throughout. FASTA files of the aligned ITS1 + ITS2 and CytB + 16S sequence are available upon request.

Phylogenetic analyses were conducted on various data subsets. For subgenus-level analyses, a single representative individual per taxon was selected, preferably a paratype, topotype or individual sourced from within 200 km of the type location. If such specimens were unavailable we chose an individual that presented typical conchology. We used such pruned data because our experience suggests that support values appear to be partially a function of clade size. Since the number of specimens per taxa varied among the various subgeneric groups, we did not trust comparison of support values between different subgeneric clades until this potential confounder was controlled. Because of potential nomenclatural issues related to improper introduction of new taxonomic names, we also limited subgeneric analyses only to previously described taxa. Subsequently, mtDNA and nDNA trees were generated separately for each subgenus, using data from all specimens falling within that subgenus. To ensure that this two-step approach did not introduce analytical artifacts, we also conducted phylogenetic reconstructions using the entire ITS1 + ITS2 and CytB + 16S datasets. The topologies and support values from these entire-dataset trees proved to be essentially identical across all highly supported nodes.

To identify robust topological features, we used four different phylogenetic reconstruction methods, each employing very different analytical assumptions, and confined our interpretation to well-supported, shared structures. Mega v6.0 was used to conduct neighbor-joining (NJ), minimum evolution (ME) and maximum likelihood (ML) analyses separately for the nuclear and mitochondrial data. NJ analysis used maximum composite distance including transitions and transversions with pairwise gap deletion. ME analysis used the close-neighbor interchange search option with the random addition of ten replicate trees. ML analysis used all sites and was based on the Tamura-Nei substitution model, a five-category gamma distribution for substitution rates and the nearest neighbor interchange ML heuristic method. In all cases support values were estimated from 1,000 bootstrap replicates. Additionally, Bayesian trees were generated using MrBayes v3.2.6 (Huelsenbeck & Ronquist, 2001), using a GTR substitution model assuming gamma-shaped rate variation over 2,000,000 generations with a sampling frequency of once each 10,000 generations. Throughout this work, all support values are reported as the number of cases out of 100 in which observed clade membership could be recovered from randomized data subsets.

Taxonomic Assignment

We identified subgenera as highly supported, reciprocally monophyletic supraspecific clades.

TABLE 1. Primer designs and cycling protocols used for PCR reactions.

Amplicon/ Name	Sequence	Annealing T (°C)	Target	Source
CytB				
CytB397f	5' – YWYTRCCTTGGRGGRCARATATC – 3'	47	Mollusca	Dahlgren et al., 2000
CytBfV	5' – TGAGGTGCAACAGTNATTAC – 3'	47	*Vertigo* (*Vertigo*)	Author Design
CytBfVU	5' – GGNCAAATRTCATTTTGAGGNGC – 3'	47	*Vertigo* (universal)	Author Design
CytBfext	5' – CATATTGGTCGGGGRTTATACTA – 3'	47	*Vertigo* (longer amplicon)	Author Design
CytB811r	5' – GCRWAYARAAARTAYCAYTCWGG – 3'	47	Mollusca	Dahlgren et al., 2000
CytBrV	5' – GCAAATAAAAAATATCATTCAGG – 3'	47	*Vertigo* (*Vertigo*)	Author Design
CytBrVU	5' – TGATCGTAAAATRGCATATGCA – 3'	47	*Vertigo* (universal)	Author Design
16S				
16Sar	5' – GCGCTGTTTATCAAAAACAT – 3'	52	Universal	Palumbi, 1996
16SfV	5' – CACCTGTTTAACAAAAACA – 3'	52	*Vertigo*	Author Design
16SfVjap	5' – CGACTGTTTAGCAAAAACA – 3'	52	*Vertigo* (*Isthmia*)	Author Design
16SfVG	5' – TAAGGAACTCGGCAAAMAT – 3'	52	*Vertigo* + *Gastrocopta*	Author Design
16Sbr	5' – CCGGTYTGAACTCAGATCAYGT – 3'	52	Terrestrial Gastropod	Tongkerd et al., 2004
16SrPUm	5' – GGCTTACGCCGGTCTGAACTC – 3'	52	*Vertigo* + *Gastrocopta* + *Pupilla*	Author Design
ITS1				
18srDNA	5' – TAACAAGGTTTCCGTATGTGAA – 3'	52	Terrestrial Gastropod	Armbruster & Bernhard, 2000
LSU1rc	5' – TCACATTAATTCTCGCAGCTAG – 3'	52	Terrestrial Gastropod	Author Design
ITS2				
LSU1	5' – CTAGCTGCGAGAATTAATGTGA – 3'	52	Terrestrial Gastropod	Wade & Mordan, 2000
LSU3	5' – ACTTTCCCTCACGGTACTTG – 3'	52	Terrestrial Gastropod	Wade & Mordan, 2000
LSU3rm	5' – GGTTTCACGTACTCTTGAAC – 3'	52	Terrestrial Gastropod	Author Design

Variation within and between subgenera was calculated in Mega v6.0 as the average number of nucleotide base differences using maximum composite likelihood including transitions and transversions with pairwise gap deletion.

Potential species-level classifications within each verified subgenus were accomplished by identifying highly supported reciprocally monophyletic clades between the nDNA and mtDNA trees. The members of each of these clades were then qualitatively analyzed in terms of their conchology (see below), ecological preferences and biogeography. From this, unique species-level concordances were identified. Species-level taxa were considered valid only when a consensus was apparent across mtDNA sequence, nDNA sequence and conchology. We also used ecology and biogeography to further inform these species-level taxa. Initial (*a priori*) identities were revised in those few cases where assignment based on shell features alone did not follow this consensus approach.

Subspecific taxa were generally designated in those cases where highly supported reciprocally monophyletic clades existed within the more rapidly evolving mtDNA data but significant variation was not present in the more slowly evolving nDNA data. We have chosen to term as shell forms those conchologically based entities that did not possess distinct DNA.

We identified potential cases of mtDNA or nDNA introgression or incomplete sorting by noting incongruence in topological position between the mtDNA and nDNA trees. In these cases, we used the consensus of conchology, ecology and biogeography to determine which DNA source reflected expected sequence.

We have not used any of the methods for species demarcation based on single-locus analyses of base-pair variation (e.g., generalized mixed Yule-coalescent functions) because they universally require generation of ultrametric trees. As this process assumes constant evolutionary rates across all clades, these methods do not provide accurate results when base-pair substitution rates are clade-specific, as is the case in the data presented below.

Conchology, Ecology and Biogeography Characterization

Qualitative documentation of conchological trends and variability for each putative DNA-supported species was accomplished by critical observation of lots from the Nekola, Coles and Horsák collections. Except for the rarest taxa, we examined at least 150 shells from ten different populations representing the ecological and biogeographical ranges of each taxon. Typical expression and variability of sixteen shell traits were noted: height (mm), width (mm), overall shell shape, suture depth, striae architecture, luster, color, the strength and appearance of the apertural crest, callus, sinulus, angular lamella, parietal lamella, columellar lamella, basal lamella, palatal lamellae, depression of shell over the palatals, plus any other pertinent identification features. The definition of any unfamiliar terms may be found in Nekola & Coles (2010) and Pilsbry (1919), notably "sinulus" (see Pilsbry, 1919: 100: "The outer [apertural] margin has an indentation barely above its middle, forming a well-marked sinulus …" Pilsbry, 1919, also referred to this feature as a "biarcuate aperture"). Ecological preference and biogeography are based on personal field observations as well as information reported in Pilsbry (1919, 1948), Kerney & Cameron (1979), Nekola & Coles (2010), Horsák et al. (2013b), and papers published in Speight et al. (2003).

SUBGENERIC CLASSIFICATION

The subgenera erected within *Vertigo* have previously been based solely on conchological criteria, primarily shell chirality and apertural lamellae architecture. This subject has been reviewed by Pokryszko & Stworzewicz (2001) from which the following summary is taken – although it should be remembered their focus was limited to the historical concept of *Vertigo* and as such did not consider the larger genus as informed by DNA sequence data (Nekola & Coles, 2016).

Isthmia Gray, 1821, was erected to encompass species with dextral shells. *Alaea* Jeffreys, 1830, was also erected to encompass dextral *Vertigo*. Jeffreys noted that members of this subgenus generally had a thickened callus on the apertural wall and peg-shaped lamellae. *Vertilla* Moquin-Tandon, 1855, encompassed all sinistral *Vertigo* but Pilsbry & Vanatta (1900) removed *V. pusilla* O. F. Müller, 1774, as it is the type species of the genus. *Vertilla* was subsequently defined by the presence of well-developed parietal and angular lamellae with the angular not connected to the peristome, a subvertical columellar lamella spirally entering the aperture, and the upper palatal lamella being longer than the lower (Pilsbry, 1919). Schileyko (1984) elevated *Vertilla* to generic rank. *Angustula* Sterki, 1888, was erected to encompass *V. milium* and the sinistral *V. angustior*, but because the original diagnosis disagreed with the actual appearance of these species, Pilsbry (1919) redefined *Angustula* to represent species with a crescent-shaped columellar lamella possessing a downward-curving inner end and a long lower palatal lamella which deeply entered the aperture. Under this framework, *Angustula* consists only of *V. milium*, *V. bermudensis* and *V. hibbardi* F. C. Baker, 1938 – a Pliocene fossil species. *Nearctula* Sterki, 1892, was erected without any diagnosis to encompass an idiosyncratic assortment of western and northern North American species. This concept was subsequently refined (Pilsbry, 1948) to encompass striate or rib-striate species lacking an apertural crest and possessing no shell depressions over the palatal lamellae. While Turgeon et al. (1998) recognized *Nearctula* at the generic level, this action has not been supported by subsequent DNA sequence analyses (Nekola et al., 2009; Nekola & Coles, 2016). *Haplopupa* Pilsbry, 1898, is a monotypic subgenus erected without any diagnosis to encompass the Californian *V. dalliana* Sterki, 1890. *Vertillaria* Pilsbry, 1919, is a monotypic subgenus erected to encompass *V. oscariana* Sterki, 1890. It is differentiated from other members of the genus by possessing an oblong shell, a blunt, vertical columellar lamella and by lacking angular, basal and upper palatal lamellae. *Alloptyx* Pilsbry, 1953, is a monotypic subgenus erected to encompass *V. hinkleyi* Pilsbry, 1920. Although noted to be close to *Vertilla*, Pilsbry (1953) differentiated *Alloptyx* by the shape of its columellar lamella. In addition, based on apertural lamellae architecture, *Angustella* Steklov, 1967, and *Ungulidenta* Popova & Schileyko, 1981, were erected to encompass Neogene fossil material from central Asia.

Pokryszko & Stworzewicz (2001) concluded that only two subgenera were taxonomically valid: *Vertilla* (*V. angustior*, *V. hinkleyi*, and the three central Asian fossil forms) and *Vertigo s. str.* (all other members of the genus). They differentiated *Vertilla* based on its very long upper palatal lamella that deeply enters the shell.

In addition, Pilsbry (1948) erected seven informal taxonomic groups within the North American fauna consisting of species with similar conchological traits but whose limits he was unable to circumscribe. Two represent synonyms of previously listed entities: *Vertigo hinkleyi* group = *Alloptyx* and the *Vertigo californica* group = *Nearctula*. The remainders represent novel categories. The *Vertigo gouldii* group included strongly striate species with 4–6 apertural lamellae. The *Vertigo modesta* group comprised species with weakly striate to smooth shells and 0–5 apertural lamellae. The *Vertigo ovata* group comprised species that lacked distinct striae and possessed 4–9 or more apertural lamellae. The *Vertigo pygmaea* group comprised species with dull, weakly striate shells that possessed 4–5 apertural lamellae. Lastly, the *Vertigo tridentata* group was erected to include species that lacked sharp shell striation yet also possessed 3–4 apertural lamellae.

Supraspecific Groupings based on DNA Sequence Analyses

Independent documentation of supraspecific groupings in *Vertigo* were based on DNA sequence analyses limited to a single representative of each previously described taxon. Target amplicon lengths varied as follows: CytB (367 base pairs); 16S (439–448 base pairs); ITS1 (591–681 base pairs); and ITS2 (618–763 base pairs). A total of 193 variable sites were noted in CytB (53% of total), 210 (47%) in 16S, 243 (36%) in ITS1, and 227 (30%) in ITS2.

Phylogenetic reconstructions recovered closely similar tree topologies across all four methods, particularly for highly supported nodes. The ITS1 + ITS2 construct identified six subgeneric-level clades with high (> 95) support in at least Bayesian (and often ML, NJ, and ME) reconstructions (Fig. 1), each of which possessed diagnostic nucleotide sequence and/or amplicon lengths. The mtDNA CytB + 16S data in general identified these same six divisions (Fig. 1), however with lower resolution and support likely due to higher rates of mutation saturation.

Available names exist for five of these subgeneric clades: *Vertigo s. str.*, *Alaea*, *Isthmia*, *Staurodon* and *Vertilla*. The sixth corresponds to the *Vertigo modesta* group of Pilsbry (1948). Because it was never formally defined as a supraspecific entity, we define it below as ***Boreovertigo*** n. subgen. Three species in the nDNA tree (*V. lilljeborgi*, *V. parcedentata* and *V. pseudosubstriata*) fall outside of these highly supported subgenera. As detailed below, we have provisionally assigned these to their nearest topological neighbors.

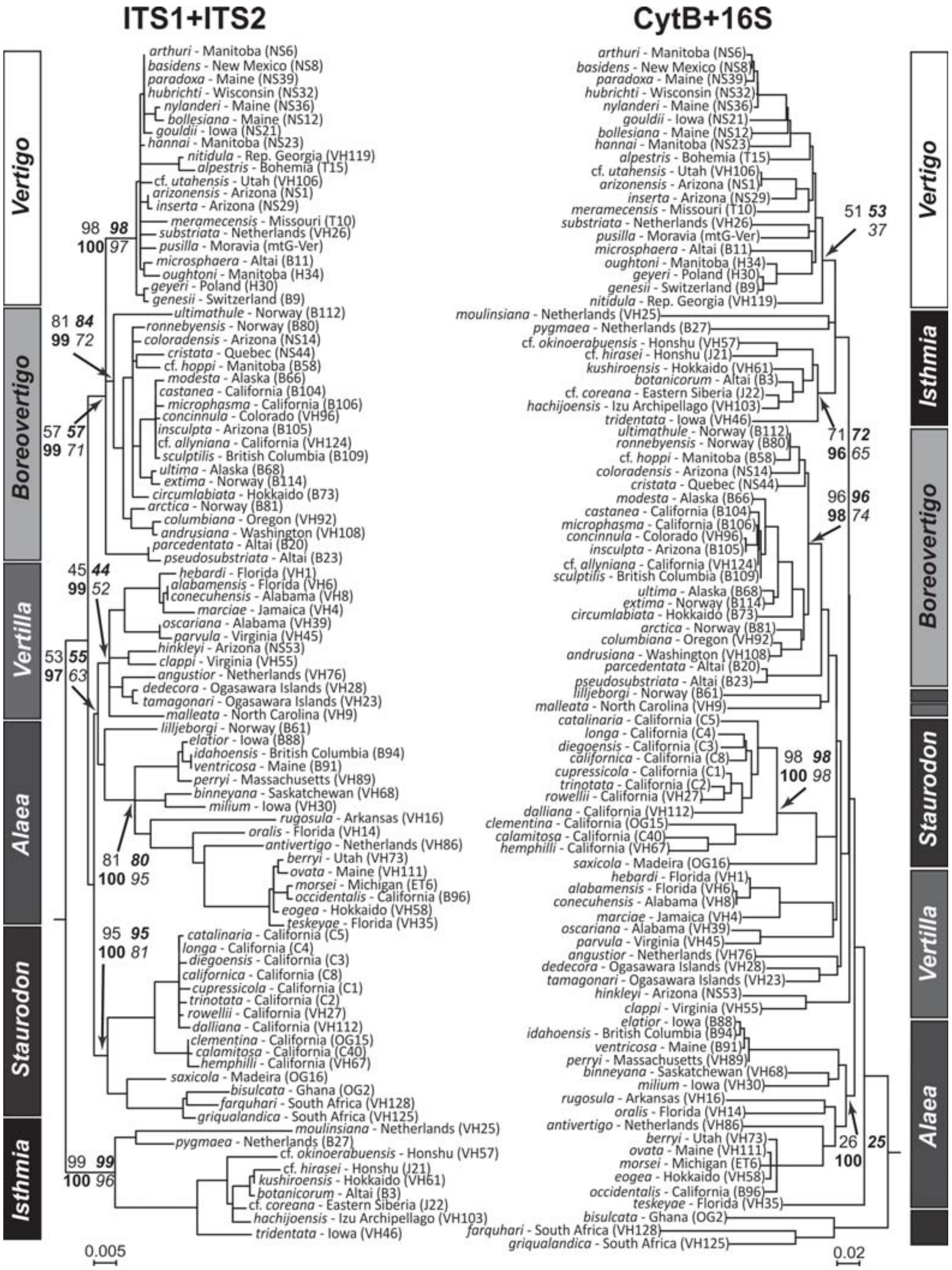


FIG. 1. Subgenus level maximum-likelihood phylogenetic tree reconstructions in *Vertigo* based on separate analyses of concatenated ITS1 + ITS2 and CytB + 16S data. Nodes with strong to moderate support have been labeled by four values: The upper left (normal font) is for Neighbor Joining. The upper right (***bold italic font***) is for Minimum Evolution. The lower left (**bold font**) is for Bayesian. The lower right (*italic font*) is for Maximum Likelihood.

The ITS1 + ITS2 Bayesian tree also suggests with high support that *Vertigo* and ***Boreovertigo*** are sister as are *Alaea* and *Vertilla*. While lumping would eliminate two subgeneric groups, we have not opted for this approach as it is not replicated with high support in the other reconstruction methods nor in the mtDNA tree, especially in terms of ***Boreovertigo***. Other differences noted in the CytB + 16S tree are: (1) *Vertilla* does not exist as a single highly supported clade, but of five individual, non-coalescing branches; (2) *Isthmia* comprises two clades, one with *V. moulinsiana* and *V. pygmaea*, the other with the remaining species; (3*)* *V. bisulcata*, *V. farquhari* and *V. griqualandica* are not part of the same clade as the rest of *Staurodon*; and (4) *V. lilljeborgi* is clustered with *V. malleata* and not with *Alaea*.

Mean genetic variation in the ITS1 + ITS2 construct within each of the six subgeneric level clades ranged from 7.7 bases in *Vertigo s. str.* to 28.4 in *Alaea*, with *Vertilla* (20.7), *Staurodon* (21.1) and *Isthmia* (25.5) also expressing high levels of intra-subgenus variability. In CytB + 16S intra-subgenus mean variation ranged from 37.7 bases in ***Boreovertigo*** to 73.8 in *Staurodon*. Mean pairwise variation between subgenera (Table 2) in ITS1 + ITS2 ranged from 22.9 bases (*Vertigo s. str.* vs. ***Boreovertigo***) to 51.1 (*Isthmia* vs. *Staurodon*), and in CytB + 16S from 69.6 bases (***Boreovertigo*** vs. *Vertilla*) to 93.5 (*Staurodon* vs. *Isthmia*).

The supported *Vertigo* subgenera and associated synonyms are as follows:

Vertigo s. str.
O. F. Müller, 1774

Type species: *Vertigo pusilla* O. F. Müller, 1774, by monotypy (ICZN Opinion 335, 1955: 50, 59).

Synonyms: “*Vertigo gouldii* group” (in part) of Pilsbry (1948) and Nekola et al. (2009).

Diagnosis

A highly supported (97–100) monophyletic clade across all four reconstruction methods in the ITS1 + ITS2 construct, whose members uniquely possess 348C and a T insert 639 bases downstream of the 18srDNA primer of the ITS1 region. The ITS1 amplicon varies between 638 and 651 bases; the ITS2 amplicon varies between 700 and 702 bases.

Range

Holarctic arctic to temperate; extending south into Japan, the Caucasus and the mountains of northern Mexico.

Ecology

While most species inhabit upland forest and rock outcrop habitats, some also occur in lowland forest, open wetland and tundra sites.

Boreovertigo, n. subgen.

Type species: *Pupa modesta* Say, 1824.

Synonyms: “*Vertigo modesta* group” (in part) of Pilsbry (1948).

Diagnosis

A moderately to highly supported (72–99) monophyletic clade across all four reconstruction methods in the ITS1 + ITS2 construct whose members uniquely possess A and T inserts 85 and 577 bases respectively downstream of the 18srDNA primer of ITS1. The ITS1 amplicon varies between 644 and 665

TABLE 2. Mean pairwise distances between *Vertigo* subgenera for the analyzed nDNA and mtDNA constructs, reported as nucleotide bases/construct. The lower half of the matrix represents distances in the ITS1+ITS2 construct and the upper half (demarcated by italic font) represents distances in the CytB+16S construct.

	Vertigo	***Boreovertigo***	*Vertilla*	*Staurodon*	*Alaea*	*Isthmia*
Vertigo		*70.4*	*75.9*	*89.2*	*78.0*	*71.7*
Boreovertigo	22.9		*69.6*	*83.1*	*76.0*	*71.3*
Vertilla	31.4	31.6		*87.6*	*80.2*	*80.4*
Staurodon	36.3	34.9	36.2		*92.4*	*93.5*
Alaea	39.2	40.0	35.5	42.9		*80.7*
Isthmia	42.1	44.1	47.1	51.1	49.2	

bases and the ITS2 amplicon varies between 700 and 702 bases.

Range

Holarctic arctic-boreal, ranging south into the mountains of the southwestern U.S.A., Scotland, central Europe, southern Siberia and Hokkaidō.

Ecology

Found across a wide moisture gradient, from upland forests to open wetlands. A number of taxa tolerate or prefer low pH and low base-status soils.

Remarks

Two principally central Asian species, *V. parcedentata* and *V. pseudosubstriata*, are included in spite of the fact that they are almost as genetically distinct from ***Boreovertigo*** as they are from *Vertigo s. str.* We have placed them provisionally into ***Boreovertigo*** due to their similar conchology and ecological preferences to *V. modesta* and related species, and because we have not yet been able to conduct DNA sequence analysis on *V. nangaparbatensis* and *V. superstriata* of Pakistan which might better resolve the relationship.

Vertilla

Moquin-Tandon, 1855

Type species: *Vertigo angustior* Jeffreys, 1830.

Synonyms: *Ptychalaea* Boettger, 1889 – type species: *Pupa flexidens* Reuss, 1861; *Vertillaria* Pilsbry, 1919 – type species: *Vertigo oscariana* Sterki, 1890; *Alloptyx* Pilsbry, 1953 – type species: *Vertigo hinkleyi* Pilsbry, 1920; *Angustella* Steklov, 1967 – type species: *Vertigo bicolumellata* Steklov, 1967; *Ungulidenta* Popova & Schileyko, 1981 – type species: *Vertigo olchonica* Popova & Shileyko, 1981.

Diagnosis

A poorly to highly supported (44–99) monophyletic clade across all four reconstruction methods in the ITS1 + ITS2 construct whose members uniquely possess 466G downstream of the 18srDNA primer of the ITS1 region. The ITS1 amplicon varies between 630 and 640 base pairs, and the ITS2 amplicon varies between 618 and 702 base pairs.

Range

Neotropics and temperate Holarctic.

Ecology

Found across a wide variety of habitats including upland and lowland forests, rock outcrops, calcareous wetlands, acidic bogs and pinelands.

Alaea

Jeffreys, 1830

Type species: *Pupa antivertigo* Draparnaud, 1801.

Synonyms: *Angustula* Sterki, 1888 – type species: *Pupa milium* Gould, 1840; "*Vertigo ovata* group" (in part) of Pilsbry (1948).

Diagnosis

A moderately to highly supported (80–100) monophyletic clade across all four reconstruction methods in the ITS1 + ITS2 construct whose members possess an ITS1 amplicon varying between 591 and 645 base pairs and an ITS2 amplicon varying between 618 and 630 base pairs (699 in *V. lilljeborgi*; see below).

Range

Northern hemisphere tropical to boreal.

Ecology

Most species are denizens of open to forested wetlands; a few also range into upland forests and grasslands.

Remarks

Vertigo lilljeborgi (Westerlund, 1871) has seventy additional bases in the ITS1 + ITS2 construct as compared to other members of *Alaea*. However, Bayesian reconstructions include this taxon (support value = 87); its conchology and ecology are also convergent with other *Alaea* species. We have thus included it in the subgenus.

Staurodon
Lowe, 1852

Type species: *Pupa saxicola* R. T. Lowe, 1852.

Synonyms: *Sterkia* Pilsbry, 1898 – type species: *Pupa calamitosa* Pilsbry, 1889; *Nearctula* Sterki, 1892 – type species: *Pupa californica* Rowell, 1861; *Afripupa* Pilsbry, 1919 – type species: *Pupa griqualandica* Melvill & Ponsonby, 1893; "*Vertigo californica* group" of Pilsbry, 1948.

Diagnosis

A moderately to highly supported (81–100) monophyletic clade across all four reconstruction methods in the ITS1 + ITS2 construct whose members possess an ITS1 amplicon varying between 641 and 681 base pairs and an ITS2 amplicon varying between 700 and 763 base pairs.

Range

Madeira; sub-Saharan Africa; western North America (British Columbia to Baja California). This subgenus is likely present in the Caribbean, Central and South America.

Ecology

Found in tropical, subtropical and temperate forest as well as coastal fog-belt scrub.

Remarks

Schileyko (1998) placed *Staurodon* as a subgenus within *Vertigo*, but presented no empirical data to support this contention. Note that although the type species of *Afripupa* and *Sterkia* reside in this subgenus, this result has not yet been confirmed for all taxa historically referred to these genera.

Isthmia
Gray, 1821

Type species: *Helix* (*Isthmia*) *cylindrica* Gray, 1821 [= *Vertigo pygmaea* (Draparnaud, 1801), as per Pokryszko & Stworzewicz (2001)].

Synonym: "*Vertigo tridentata* group" (in part) of Pilsbry (1948).

Diagnosis

A highly supported (96–100) monophyletic clade across all four reconstruction methods in the ITS1 + ITS2 construct whose members uniquely possess an A insert 617 bases downstream of the 18srDNA primer of the ITS1 region and a GA insert at 496–497 bases downstream of the LSU1 primer of the ITS2 region. The ITS1 amplicon varies between 594 and 639 base pairs; the ITS2 amplicon region varies between 623 and 683 base pairs.

Range

Northern Hemisphere tropical to temperate, with *V. moulinsiana* perhaps penetrating into equatorial Africa (Ton de Winter, *personal communication*).

Ecology

Upland and lowland habitats; often living above ground on graminoid vegetation and low herbs.

DISCUSSION OF SUBGENERA

Four salient points can be drawn from these subgeneric-level analyses:

(1) Even though both nuclear and mitochondrial DNA sequence data establish six well-supported monophyletic supraspecific clades, there is no consistent concordance of these with conchology, especially in terms of apertural architecture. It is not surprising, therefore, that previous attempts to assign subgenera within *Vertigo* (and genera within the Vertigininae) on the basis of conchology have been inconsistent and unreliable. Two examples illustrate this point:

a. the presence of a sharply striate shell surface and possession of 4–6 apertural lamellae, which Pilsbry (1948) used to demarcate the "*Vertigo gouldii* group" (e.g., *Vertigo s. str.*), does not provide accurate supraspecific taxonomic assignments. Not only do all other subgenera possess at least some members that share these traits, but additionally some *Vertigo s. str.* members have smooth shells with 0–3 apertural lamellae (e.g., *V. genesii* and *V. oughtoni*). The subgenus type (*V. pusilla*) not only lacks sharp striae but is also sinistral.

b. The very long, deeply entering upper palatal lamella that Pokryszko & Stworzewicz (2001) use to delimit *Vertilla* is shared by species in other subgenera (e.g., *V. bisulcata*, *V. farquhari* and *V. griqualandica* in *Staurodon*), with most members of *Vertilla* actually lacking this trait (most evidently for *V. hebardi*, *V. malleata*, *V. marciae*, *V. oscariana* and *V. parvula*).

Although conchology does not allow for accurate classification of supraspecific groups, some oft-violated trends can be identified: for instance, *Vertigo s. str.* shells tend to be ovate and range from 1.6–2.0 mm in height. ***Boreovertigo*** tend to have weakly to strongly striate ovate shells that are usually > 2.0 mm tall. *Vertilla* shells tend to be small (1.2–1.8 mm in height). *Alaea* species tend to have broadly ovate dark red-brown shells with a glassy shell surface. Many *Staurodon* species are strongly striate on the shell surface. *Isthmia* species tend to have ovate shells with a shallow suture, reduced (or absent) striae and a dull surface luster due to microscopic periostracal scales (Horsák & Pokryszko, 2010). Examination of Figures 3, 10, 13, 15, 19 and 23 will further illustrate these points.

(2) Ecological preferences may be more useful than conchology in defining subgenera. Although overlap certainly exists, *Vertigo s. str.* are characteristic of upland forest and shaded rock outcrops; *Alaea* generally represent wetland species; *Isthmia* are often found in grasslands and/or in herb-dominated forest ground layers; *Staurodon* are upland and often xeric-adapted; ***Boreovertigo*** and *Vertilla* often tolerate or require acidic soils.

(3) In contrast to previous classifications, none of the subgenera defined on the basis of DNA sequence are monotypic with no fewer than nine taxa being found within each. Monotypic or near-monotypic subgeneric-level branches can either be empirically assigned to one of the remaining clades with moderate support (*V. lilljeborgi*) or likely represent an undersampled clade (*V. parcedentata* and *V. pseudosubstriata*). These results significantly alter the evolutionary picture of the genus. Rather than having most subgenera being represented by only one or two relict taxa, in reality active evolutionary diversification appears present across the genus.

(4) All subgenera possess transcontinental ranges. *Vertigo s. str.* and ***Boreovertigo*** extend from Europe across central and East Asia to North America. *Vertilla* possess a highly disjunct distribution, occurring in the Caribbean, southeastern and southwestern North America, Europe, and western Pacific island archipelagos. Potential fossil representatives are also known from central Asia. *Isthmia* is known from southeastern North America and across Eurasia, with populations perhaps extending into Congo-Kinshasa. *Alaea* also extends across all of North America and Eurasia, extending south into the western hemisphere tropics. *Staurodon* occurs throughout the North American Pacific coast east to Madeira and sub-Saharan Africa, although it should be mentioned that species found within each of these regions represent distinct monophyletic clades.

Such immense ranges are likely due to two factors: first, small snails like *Vertigo* that are capable of uniparental reproduction (Pokryszko, 1987) evidently have great passive dispersal abilities, probably as a result of migratory bird vectors (Gittenberger et al., 2006). Rapid passive dispersal into deglaciated lands at the end of the Pleistocene can easily explain transcontinental distributions of species-level entities in *Vertigo s. str.*, ***Boreovertigo*** and *Alaea*. Transcontinental subgeneric ranges made up of various species are probably related to ancient biotic homogenization – likely during periods of the middle Tertiary when contiguous broad-leaved temperate/semitropical forest extended across much of the northern latitudes (aka the Arcto-Tertiary forest; Wen 1999) – with vicariance-like distribution patterns being generated by subsequent loss of geographically intermediate habitats and populations. This is perhaps most clearly observed in *Vertilla* for which extant members are scattered across the northern hemisphere tropical to temperate zones with potential fossil material being known from regions that no longer support the subgenus. Similar processes are likely responsible for the apparently disjunct transcontinental distributions of *Staurodon*, *Isthmia*, some components of *Vertigo s. str.* and *Alaea*. The prevalence of such broad-ranging ancient lineages suggests that the excellent passive dispersal abilities of *Vertigo* have allowed them to rapidly expand over global extents during favorable periods, and then to persist – and diversify – in favorable regional habitats that have subsequently become isolated following global environmental change.

SUBGENUS *VERTIGO S. STR*.

Analysis of the subgenus *Vertigo* is based on 123 individuals for CytB + 16S and ITS1 + ITS2. The CytB segment was 367 bases and the 16S segment was 443–448 bases, with a total of 240 variable sites along the entire CytB + 16S construct. The analyzed ITS1 segment was 603–616 bases, the analyzed ITS2 segment was 673–675 bases, with a total of 114 variable sites along the entire ITS1 + ITS2 construct. Support values tended to be higher in CytB + 16S than ITS1 + ITS2, with by far the greatest support (generally > 90) being achieved in Bayesian reconstructions.

In combination with conchology and ecological preferences, these analyses suggest at least 22 valid species-level entities within the subgenus (Tables 3, 4, Figs. 2, 3). Seventeen already possess names (*V. alpestris*, *V. arizonensis*, *V. arthuri*, *V. bollesiana*, *V. genesii*, *V. geyeri*, *V. gouldii*, *V. hannai*, *V. inserta*, *V. meramecensis*, *V. microsphaera*, *V. nitidula*, *V. nylanderi*, *V. oughtoni*, *V. pusilla*, *V. substriata* and *V*. cf. *utahensis*); five are new and formally described below (***V. beringiana***, ***V. chiricahuensis***, ***V. chytryi***, ***V. genesioides*** and ***V. kodamai***).

Mean within-species variability ranged in ITS1 + ITS2 from none in ***V. chytryi***, *V. geyeri*, *V. hannai*, *V. nitidula* and *V*. cf. *utahensis* to 6.0 bases in ***V. genesioides***, although it should be noted that variability is at least partially related to number of analyzed specimens combined with their geographic coverage, and these have not been held constant. Species with individuals residing both in the normal and divergent ITS1 + ITS2 clades (see below) ranged from 6.9 bases (*V. meramecensis*) to 10.4 (***V. chiricahuensis*** / *V.* cf. *chiricahuensis*). In CytB + 16S within-species variability ranged from 1 (***V. chytryi***) to 28.6 (***V. chiricahuensis*** / *V.* cf. *chiricahuensis*) bases. Mean pairwise variation between species ranged in ITS1 + ITS2 from 2 bases (*V. alpestris* vs. *V. nitidula*) to 19.4 (*V. alpestris* vs. *V. gouldii*) and in CytB + 16S from 5.3 (*V. arthuri* vs. *V. nylanderi*) to 66.4 (*V. microsphaera* vs. *V. meramecensis*) bases (Table 3).

The most strongly supported clade (98–100 in all reconstruction methods) in ITS1 + ITS2 represent a subset of *V. meramecensis*, *V. gouldii*, *V.* cf. *chiricahuensis* and ***V. kodamai***, creating polyphyly for these taxa. However, in CytB + 16S each of these taxa remained monophyletic and highly supported. We have chosen to ignore this divergent ITS1 + ITS2 cluster for two reasons: (a) The topological placement of species within the “normal” and “divergent” ITS1 + ITS2 clades were largely similar and replicate their arrangement within the CytB + 16S tree. (b) Illumina genomic data from a single Iowa *V. meramecensis* individual demonstrates that multiple ITS1 sequence configurations exist, with most copies (or pseudogenes) being referable to other Iowa *meramecensis* but with some having the first half of their ITS1 comparable to the Virginia specimen occupying the divergent cluster. Definitive resolution of taxonomic patterns in this group using nuclear DNA will require use of additional genes.

While many of the species in the subgenus existed as unresolved branches in ITS1 + ITS2, in CytB + 16S, a larger number of well-supported supraspecific clades can be identified – at least in Bayesian reconstructions. We see the following as being useful:

(1) The *Vertigo genesii* group (*V. genesii*, ***V. genesioides***, *V. geyeri*, *V. oughtoni*, *V. microsphaera* and *V. substriata*). In ITS1 + ITS2 across all four reconstruction methods these species were shown at low to high support to represent two independent clades, one (36–91) containing *V. microsphaera*, ***V. genesioides*** and *V. oughtoni*, and the other (58–100) *V. genesii* and *V. geyeri*. The association of *V. genesii*, ***V. genesioides***, *V. geyeri* and *V. oughtoni* was highly supported (90–100) across all four reconstruction methods in CytB + 16S. Additionally, Bayesian analysis linked these species with moderate support (75) to *V. microsphaera* and *V. substriata*.

(2) The *V. alpestris* group (*V. alpestris*, ***V. beringiana***, *V. nitidula* and *V. pusilla*) had moderate to high support (71–100) in ITS1 + ITS2. In CytB + 16S *V. alpestris* and ***V. beringiana*** were grouped at high support (98–100) across all reconstruction methods, with *V. nitidula* having a separate branch and being the most divergent of any species within the subgenus. Bayesian CytB + 16S reconstructions suggest association of these three species with moderate support (86) to *V. pusilla*.

Two remaining groups were evident from the CytB + 16S data but not ITS1 + ITS2.

(3) The *V. arizonensis* group (*V. arizonensis*, ***V. chiricahuensis***, *V. inserta* and *V.* cf. *utahensis*) existed with high support (>/= 91) across all reconstruction methods in CytB + 16S; Bayesian analysis also strongly (100) included *V. meramecensis*. In ITS1 + ITS2 three distinct highly supported groupings were apparent in Bayesian analysis, including *V. arizonensis* and *V. inserta* (100), *V.* cf. *utahensis* (100), and a poorly supported (55) assemblage of ***V. chiricahuensis***, ***V. chytryi*** and ***V. kodamai***. In ITS1 + ITS2 *V. meramecensis* was always shown to be an independent branch unrelated to the other members of this group.

TABLE 3. Mean pairwise distances between *Vertigo* (*Vertigo*) species for the analyzed nDNA and mtDNA constructs, reported as nucleotide bases/construct. The lower half of the matrix represents distances in the ITS1 + ITS2 construct and the upper half (demarcated by *italic font*) represents distances in the CytB + 16S construct.

	arthuri	*hannai*	***chytryi***	*nylanderi*	*arizonensis*	cf. *utahensis*	*inserta*	*bollesiana*	*substriata*	*pusilla*	*geyeri*	*genesii*	*oughtoni*	*microsphaera*	***beringiana***	***genesioides***	***chiricahuensis***	*meramecensis*	***kodamai***	*gouldii*	*alpestris*	*nitidula*
arthuri		*40.6*	*44.7*	*5.3*	*55.3*	*56.6*	*48.2*	*36.1*	*56.4*	*55.0*	*46.9*	*47.8*	*49.9*	*56.7*	*53.9*	*44.0*	*56.4*	*61.5*	*39.3*	*38.2*	*51.7*	*55.5*
hannai	2.2		*39.9*	*40.7*	*53.8*	*54.1*	*43.8*	*42.2*	*59.3*	*54.0*	*55.6*	*55.3*	*57.8*	*57.7*	*48.6*	*52.5*	*51.9*	*59.4*	*39.8*	*41.9*	*49.9*	*47.6*
chytryi	3.2	3.0		*44.5*	*52.2*	*53.0*	*42.9*	*45.3*	*52.3*	*48.9*	*46.7*	*46.4*	*47.2*	*55.8*	*53.5*	*42.9*	*51.2*	*51.0*	*37.2*	*46.6*	*48.8*	*50.2*
nylanderi	3.4	5.3	5.5		*52.8*	*54.5*	*49.1*	*36.0*	*57.7*	*56.1*	*47.7*	*48.7*	*50.8*	*55.9*	*54.8*	*45.0*	*54.6*	*61.7*	*38.4*	*38.0*	*52.8*	*53.9*
arizonensis	3.8	3.7	4.7	6.9		*9.3*	*30.1*	*51.9*	*56.1*	*53.3*	*57.9*	*57.1*	*57.0*	*57.9*	*50.8*	*52.1*	*24.3*	*50.4*	*44.1*	*56.6*	*50.8*	*56.3*
cf. *utahensis*	4.2	4.0	5.0	7.3	5.7		*33.8*	*52.3*	*57.3*	*54.7*	*59.2*	*58.4*	*57.7*	*59.2*	*50.6*	*53.9*	*26.6*	*52.8*	*44.4*	*56.8*	*52.1*	*56.8*
inserta	4.4	4.2	5.2	7.5	1.9	6.2		*46.1*	*53.4*	*51.6*	*52.8*	*52.7*	*52.3*	*56.6*	*49.8*	*47.8*	*26.1*	*43.6*	*36.7*	*51.3*	*48.4*	*49.9*
bollesiana	4.4	6.3	6.3	3.4	6.9	8.3	7.5		*57.8*	*51.9*	*53.4*	*51.1*	*51.8*	*57.6*	*48.6*	*47.0*	*51.5*	*51.4*	*37.2*	*41.9*	*47.8*	*46.3*
substriata	4.4	4.3	5.3	7.5	5.9	6.3	6.5	8.5		*47.6*	*50.6*	*51.0*	*54.5*	*56.9*	*56.6*	*50.6*	*58.0*	*60.8*	*50.1*	*58.7*	*51.5*	*59.3*
pusilla	4.8	4.6	5.6	7.9	6.3	6.6	6.8	8.9	6.9		*56.0*	*55.4*	*56.3*	*58.6*	*44.6*	*52.0*	*54.6*	*55.3*	*49.5*	*49.7*	*24.3*	*50.2*
geyeri	5.2	5.0	6.0	8.3	6.7	7.0	7.2	9.3	7.3	7.6		*10.4*	*15.3*	*56.8*	*58.8*	*14.5*	*58.0*	*56.3*	*44.3*	*55.1*	*57.8*	*53.1*
genesii	5.8	5.4	6.6	8.9	7.3	7.6	7.8	9.9	7.9	8.2	3.0		*19.6*	*55.6*	*56.7*	*17.6*	*57.3*	*54.6*	*44.8*	*55.3*	*56.0*	*52.7*
oughtoni	6.8	6.7	7.7	9.9	8.3	8.7	8.9	10.9	8.9	9.3	9.7	10.3		*55.7*	*53.8*	*13.0*	*57.4*	*54.8*	*48.7*	*56.1*	*57.0*	*53.4*
microsphaera	6.9	6.0	7.8	10.0	8.4	8.8	9.0	11.0	9.0	9.4	9.8	10.0	9.4		*58.2*	*52.4*	*60.4*	*66.4*	*47.1*	*57.5*	*58.4*	*60.6*
beringiana	7.5	7.4	8.4	10.6	9.0	9.4	9.6	11.6	9.6	10.0	10.4	11.0	12.0	10.2		*52.5*	*51.9*	*53.6*	*43.9*	*53.3*	*30.8*	*58.8*
genesioides	8.0	7.0	8.6	11.1	9.5	9.8	10.0	12.1	10.1	10.4	10.2	10.2	9.1	8.0	10.4		*52.3*	*50.8*	*43.9*	*50.8*	*52.0*	*49.6*
chiricahuensis	8.2	8.0	7.8	10.5	9.5	10.0	10.0	10.9	9.9	10.6	11.0	11.6	12.7	12.8	13.4	13.4		*53.4*	*43.9*	*56.4*	*51.7*	*58.2*
meramecensis	8.2	8.0	9.0	11.1	10.5	10.8	11.0	12.1	9.9	10.6	11.0	11.6	12.7	12.8	13.4	13.8	13.2		*48.1*	*60.4*	*54.4*	*55.1*
kodamai	8.5	8.4	8.4	11.3	10.0	10.4	10.6	12.1	9.9	11.0	11.4	12.0	13.0	13.2	13.8	14.2	9.4	12.9		*41.6*	*44.0*	*48.8*
gouldii	9.0	9.7	10.7	12.1	11.4	11.7	11.9	13.1	11.4	12.0	11.9	12.5	14.4	14.4	15.1	15.4	12.1	14.2	11.5		*49.0*	*55.0*
alpestris	11.8	12.0	13.0	14.9	13.7	13.0	14.2	15.9	14.3	14.6	15.0	15.6	16.7	16.7	11.4	16.4	17.9	17.9	18.2	19.4		*54.2*
nitidula	12.2	12.0	13.0	15.3	13.7	13.0	14.2	16.3	14.3	14.6	15.0	15.6	16.7	16.8	11.4	16.4	17.6	17.8	17.9	19.1	2.0	

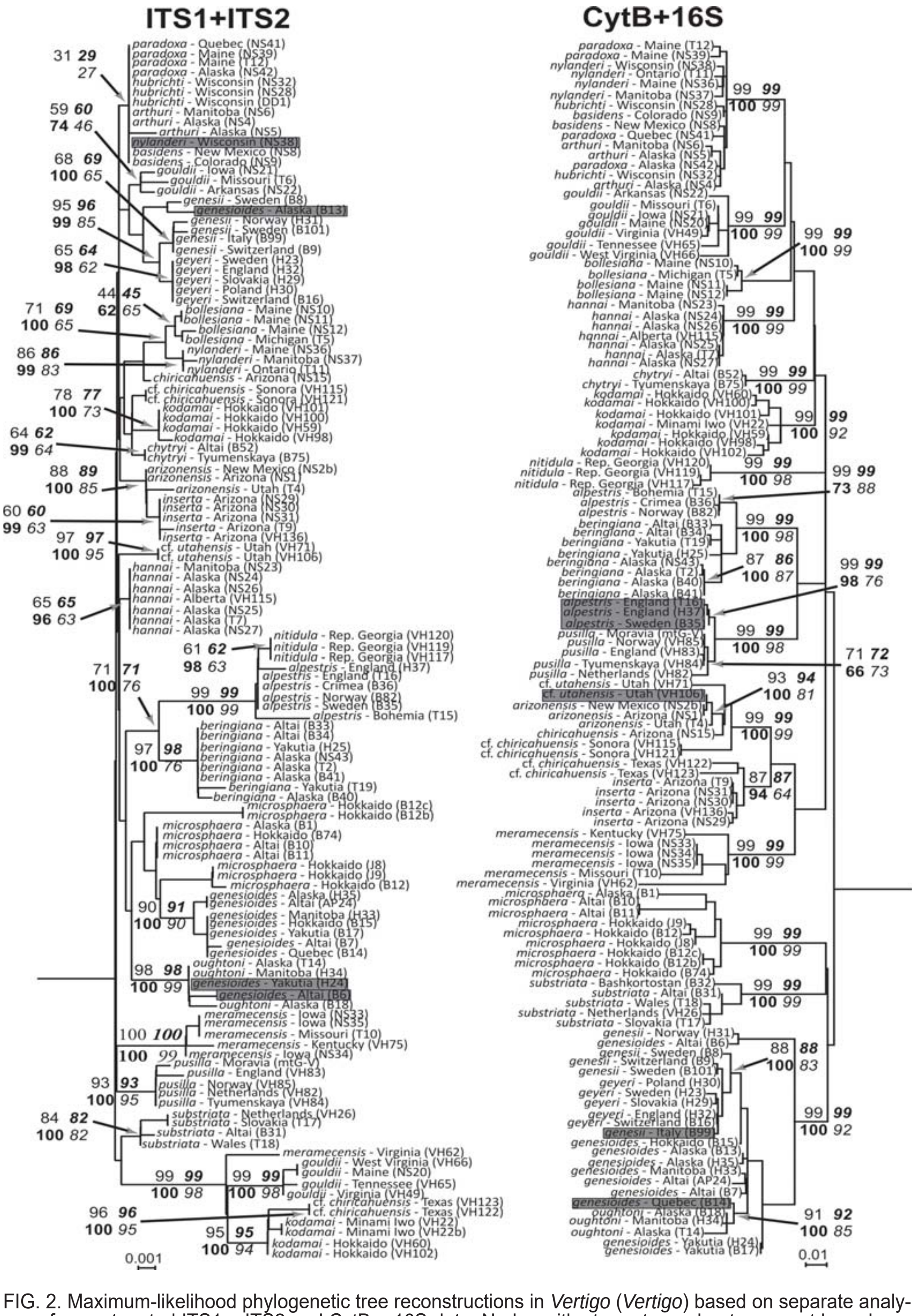


FIG. 2. Maximum-likelihood phylogenetic tree reconstructions in *Vertigo* (*Vertigo*) based on separate analyses of concatenated ITS1 + ITS2 and CytB + 16S data. Nodes with strong to moderate support have been labeled by four values: The upper left (normal font) is for Neighbor Joining. The upper right (***bold italic font***) is for Minimum Evolution. The lower left (bold font) is for Bayesian. The lower right (*italic font*) is for Maximum Likelihood. A grey box demarcates specimens that show incongruence in topologic location between the ITS1 + ITS2 and CytB + 16S trees, and likely represent examples of genetic introgression or incomplete sorting.

(4) The *V. gouldii* group (*V. gouldii*, *V. hannai*, *V. bollesiana*, *V. nylanderi*, *V. arthuri*, ***V. chytryi*** and ***V. kodamai***) was moderately supported (85) in Bayesian CytB + 16S reconstructions but was not recovered – or possessed little support (< 37) – in the other three reconstruction methods. No evidence for grouping of these species existed in ITS1 + ITS2. However, it should be noted that Bayesian analysis supported a strong association of *V. bollesiana* and *V. nylanderi* (100), and suggested a weak linkage (55) between ***V. chytryi***, ***V. kodamai*** and ***V. chiricahuensis***.

Below, we consider the phylogenetics, conchology, ecology and biogeography of each supported species-level taxon.

VERTIGO GOULDII GROUP

Vertigo (*Vertigo*) *arthuri*
Martens, 1882
Figs. 3 (second row), 7N

Vertigo bollesiana var. *arthuri* Martens, 1882: 140.

Type Locality: Little Missouri, North Dakota, U.S.A.

Synonyms: *V. briarensis* Leonard, 1972: 79, type locality: Briar Bluff South Section, Petersburg Silt, Henry County, Illinois, U.S.A. (fossil) (= *V. brierensis* auctt.); *V. coloradensis basidens* Pilsbry & Vanatta, 1900: 604, type locality: Bland, New Mexico, U.S.A.; *V. gouldii hubrichti* Pilsbry, 1934: 99, type locality: Loess of St. Mona, St. Louis County, Missouri, U.S.A. (fossil); *V. hubrichti variabilis* Frest, 1991: 32, figs 11B, 13, no types designated; *V. iowaensis* Frest, 1991: 38, figs. 11C, 15, no types designated; *V. occulta* Leonard, 1972: 78, type locality: Long Lake Section, Banner Formation, Schuyler County, Illinois, U.S.A. (fossil); *V. gouldii paradoxa* Sterki, in Nylander, 1900: 103, type locality: Woodland, Aroostook County, Maine, U.S.A.

Phylogenetics

Although there was only poor support for monophyly in this species in ITS1 + ITS2 (< 31), all but a single Alaskan specimen possessed identical sequence. In CytB + 16S, this species was represented by a very strongly supported clade (99–100) across all four analyses. The CytB + 16S of *V. nylanderi* existed as a poorly to moderately supported (52–70) subclade within this group in NJ, ME and ML reconstructions.

→

FIG. 3. Shells of *Vertigo* (*Vertigo*). Bracketed DNA specimen codes precede each entry. Top row (left to right): *Vertigo gouldii*, [26] Deer Creek, Fillmore Co., Minnesota, U.S.A. (43.7322°N, 92.3443°W); [VH49] Falling Springs NE, Alleghany Co., Virginia, U.S.A. (37.8810°N, 79.9176°W). *Vertigo meramecensis*, [T10] 11-Point River, Oregon Co., Missouri, U.S.A. (36.7931°N, 91.3334°W). *Vertigo pusilla*, [VH82] Katwijk, Netherlands (52.1826°N, 4.408°E). *Vertigo hannai*, [B115] Waiparous River, Alberta, Canada (51.3681°N, 114.9905°W). ***Vertigo chytryi***, [B75] Nizhnie Aremzyany, Tyumenskaya, Russia (58.5269°N, 68.6815°E). Second row (left to right): ***Vertigo kodamai***, [VH98] Samani, Hokkaidō, Japan (42.1815°N, 143.0003°E). *Vertigo bollesiana*, [T5] Maxton Plains, Chippewa Co., Michigan, U.S.A. (46.0749°N, 83.6569°W). *Vertigo arthuri*, [NS7] Leithead Addition, Pembina Co., North Dakota, U.S.A. (48.8147°N, 97.8878°W). *Vertigo arthuri* form *basidens*, [17] Bland, Sandoval Co., New Mexico, U.S.A. (35.7474°N, 106.4593°W). *Vertigo arthuri* form *paradoxa*, [NS39] Caribou, Aroostook Co., Maine, U.S.A. (46.8590°N, 68.0119°W). *Vertigo arthuri* form *hubrichti*, [NS32] Potawatomie State Park, Door Co., Wisconsin, U.S.A. (44.8774°N, 87.4250°W). *Vertigo nylanderi*, [T11] Wolford Bog, Leeds & Grenville Co., Ontario, Canada (44.9230°N, 75.7738°W). Third row (left to right): *Vertigo arizonensis*, [T4] Bullion Canyon, Piute Co., Utah, U.S.A. (38.4171°N, 112.3126°W). *Vertigo inserta*, [NS30] Bear Wallow, Pima Co., Arizona, U.S.A. (32.4211°N, 110.7302°W). *Vertigo* cf. *utahensis*, [VH106] Bullion Canyon, Piute Co., Utah, U.S.A. (38.4171°N, 112.3126°W). ***Vertigo chiricahuensis***, [NS15] Buena Vista Peak, Cochise Co., Arizona, U.S.A. (31.9176°N, 109.2722°W). *Vertigo* cf. *chiricahuensis*, [VH121] Sierra el Tigre, Sonora, Mexico (30.6003°N, 109.2199°W). *Vertigo* cf. *chiricahuensis,* [VH122] Mt. Livermore, Jeff Davis Co., Texas, U.S.A. (30.6386°N, 104.1616°W). Fourth row (left to right): *Vertigo substriata*, [VH26] Zuid-Kennemerland, Driehuis, Netherlands (52.4413°N, 4.6267°E). *Vertigo nitidula*, [VH119] Sairme, Imereti, Republic of Georgia (41.9274°N, 42.7498°E). *Vertigo alpestris*, Björkliden, Lappland, Sweden (68.3900°N, 18.6730°E) [B35]. ***Vertigo beringiana***, [B34] Aktash, Altai, Russia (50.3080°N, 87.6487°E). *Vertigo* cf. *chiricahuensis*, [VH123] Tobe Canyon, Jeff Davis Co., Texas, U.S.A. (30.6371°N, 104.1781°W). Bottom row (left to right): *Vertigo microsphaera*, [B12] Tsukiji, Urakawa, Hokkaidō, Japan (42.1717°N, 142.7649°E). *Vertigo geyeri*, [H30] Chełmski, Brzeźno, Poland (51.1568°N, 23.6000°E). *Vertigo genesii*, [B99] Pocol, Belluno, Italy (46.5207°N, 12.0985°E). ***Vertigo genesioides***, [H35] Dalton Highway, Alaska, U.S.A. (69.3100°N, 148.7300°W). *Vertigo oughtoni*, [H34] Goose Creek Road, Churchill, Manitoba, Canada (58.7264°N, 94.1171°W).


gouldii
meramecensis
pusilla
hannai
chytryi
kodamai
bollesiana
arthuri
basidens
paradoxa
hubrichti
nylanderi
arizonensis
inserta
cf. utahensis
chiricahuensis
cf. chiricahuensis
substriata
nitidula
alpestris
beringiana
cf. chiricahuensis
microsphaera
geyeri
genesii
genesioides
oughtoni
1 mm

Conchology

Vertigo arthuri shares with *V. nylanderi* a more deeply inserted lower as compared to the upper palatal lamella, a feature unique in the subgenus to these two species (Table 3). *Vertigo arthuri* differs from *V. nylanderi* by its weak to absent sinulus and peg-shaped columellar lamella. Apertural callus and crest strength, and the presence/absence of a basal and/or angular lamella have been historically used to split *V. arthuri* into seven additional taxa. However, these traits show continual variation not only across the geographic and ecological range of this species, but also within single populations – especially in southeastern Ontario. As a result *V. briarensis*, *V. basidens*, *V. hubrichti*, *V. hubrichti variabilis*, *V. iowaensis*, *V. occulta* and *V. paradoxa* represent at best only shell forms of *V. arthuri*.

Ecology

Primarily a species of upland forest, taiga and rock outcrops. In the east, it is particularly abundant in upland northern white cedar stands and strays into the drier parts of adjacent wetlands. Along the shore of the St. Lawrence in Atlantic Maritime Canada, it can also be found in calcareous maritime turf. In the Upper Mississippi Valley, this species is limited to algific talus and other cool talus slopes and rock outcrops. In the northern plains and northwestern North America, it is especially common in aspen forest and parkland. In the western mountains, it is limited to herb-rich forest often dominated by aspen and Douglas fir.

Biogeography

North America – Newfoundland to the Alaskan interior, south to upstate New York, northeastern Iowa, northwestern Minnesota, the Black Hills of South Dakota and the Jemez Mountains of northern New Mexico.

Vertigo (*Vertigo*) *bollesiana* (Morse, 1865)

Fig. 3 (second row)

Isthmia bollesiana Morse, 1865: 209, text figs. 4–6.

Type Locality: Maine, U.S.A.

Phylogenetics

This species was represented in ITS1 + ITS2 by a poorly to moderately supported (44–65) and in CytB + 16S by a highly supported (99–100) clade across all reconstruction methods. In ITS1 + ITS2 across all reconstruction methods, *V. bollesiana* was a member of a moderate to highly supported (65–100) clade including *V. nylanderi*.

Conchology

This species shares with *V. gouldii* five apertural lamellae with a strong basal, and the parietal pointing towards the upper palatal (Table 3). It differs from that species in its deeper depression over the palatal lamellae, shinier luster, weaker and blunter striae, and more conic shape.

Ecology

Characteristic of humid, rich forest and rock outcrop sites.

Biogeography

North America – Maritime Provinces of Canada south to Pennsylvania and west to Iowa and Minnesota.

Vertigo* (*Vertigo*) *chytryi, n. sp.

Figs. 3 (top row), 4A–G, 5O, Table 4

GenBank Accessions: KY217022-3; KY216657-8; KY217430-1; KY216293-4.

Diagnosis

Shell small, conical-ovoid, most similar to *Vertigo gouldii* of eastern North America but differing in its wider shell, more strongly conical apex, less strong and more numerous macroscopic radial striae, presence of weak spiral striae and numerous wavy microscopic radial threads covering the shell, making the surface matt.

Description

Shell: 1.9–2.2 mm tall x 1.1–1.2 mm wide (Holotype 2.1 x 1.2 mm), translucent, brown to cinnamon-brown; approximately five whorls;

upper four whorls conical; suture moderately shallow; shell luster dull from the presence of numerous microscopic radial threads covering the surface on post-neanic whorls (Fig. 4H), numerous fine larger radial striae also present (Fig. 4A–G); aperture approximately $^1/_3$ of shell height, being approximately wider than tall (Fig. 4A, 4E–G), in profile ascending slightly onto body whorl (Fig. 4B); umbilicus closed by preceding whorls (Fig. 4C); peristome interrupted by body whorl, apertural lip weakly flared (Fig. 4B, D), crest absent with no apertural thickenings or callus (Fig. 4A–H); four to five apertural lamellae present including a peg-shaped columellar, a blade-shaped parietal, blade-shaped upper and lower palatals, and a weak peg-shaped basal, although this lamella may be absent in some individuals (Fig. 4A, C, E–G); no depression on the palatal wall of aperture (4D).

Holotype (Fig. 4A–D, H): ANSP 467337, Peshcherka valley, Zalesovo District, Altai Region, Russia; Birch-fir forest; 54°08'01"N, 84°45'30"E; July 10, 2012, Michal Horsák.

Paratypes: ANSP 467337, collected with holotype: 4 shells; NMPC P6M29122, collected with holotype: 3 shells.

Other, Non-Type Material Examined: Approximately 12 specimens from the type locality. Nizhnie Aremzyany, Tobolskiy District, Tyumenskaya Oblast, Russia; Hemiboreal taiga; 58°31'37"N, 68°40'53"E; August 10, 2013 (both from the Horsák collection, Brno). Kuzneckij Alatau, near Karakda Village, Obinskij District, Kemerovo Oblast, Russia; Hemiboreal taiga; 54°20'32"N, 87°10'03"E (from the Lucie Juřičková collection, Prague).

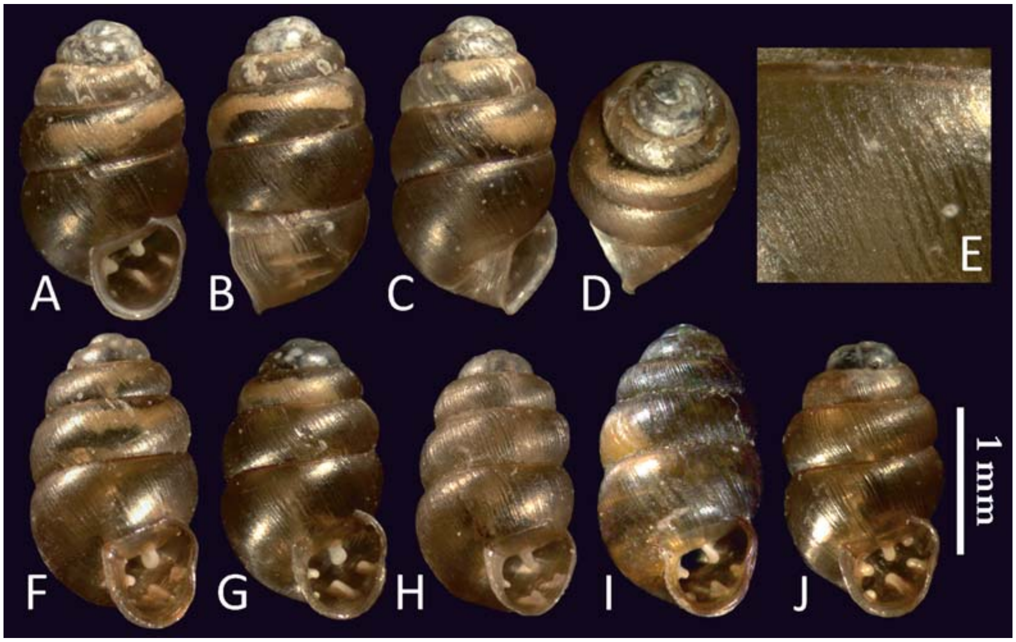


FIG. 4. ***Vertigo chytryi*** n. sp. A–E: Holotype, ANSP 467337, Birch-fir forest, Peshcherka valley, Zalesovo District, Altai Krai Republic, Russia (54.1335°N, 84.7584°E); F: [B52] Birch-fir forest, Peshcherka valley, Zalesovo District, Altai Krai Republic, Russia (54.1335°N, 84.7584°E); G: [B75] Hemiboreal taiga, Nizhnie Aremzyany, Tobolskiy District, Tyumenskaya Oblast, Russia (58.5269°N, 68.6815°E); H: *Vertigo microsphaera* [B11] Seminski Pass, Altai Republic, Russia (50.9855°N, 85.6817°E); I: *Vertigo gouldii* [26] Deer Creek, Fillmore Co., Minnesota, U.S.A. (43.7322°N, 92.3443°W); J: *Vertigo hannai* [B115] Waiparous River, Alberta, Canada (51.3681°N, 114.9905°W). When applicable, bracketed DNA specimen codes precede each entry.

TABLE 4. Conchological traits of *Vertigo* (*Vertigo*) members.

Species	Height (mm)	Width (mm)	Shell Shape	Suture Depth	Striae	Luster	Color	Crest	Callus	Sinulus	Angular	Parietal	Columellar	Basal	Palatal	Palatal Depression	Other
alpestris	1.7–2.0	1.0–1.1	Cylindrical – ovate	Shallow to moderate	Weak, blunt, scattered, irregular	Shiny	Yellow-brown	None	None	Weak	None	Blade	Peg	None	2	None	
arizonensis	1.7–1.9	0.8–0.9	Cylindrical – ovate	Moderate	Strong, sharp, numerous, regular	Dull	Yellow-brown	Weak	None	Weak	Strong	Blade	Peg	None	2 very long	Modest	
arthuri	1.6–1.8	0.7–0.9	Cylindrical – ovate	Shallow to moderate	Strong, sharp, numerous, regular	Dull	Red to yellow-brown	Weak to strong and massive	None to strong and massive	None to weak	None to strong	Blade	Peg	None to strong	2	None to modest	Lower palatal more deeply inserted than upper
beringiana	1.4–2.2	0.9–1.1	Cylindrical – ovate	Shallow to moderate	Weak, blunt, scattered irregular	Silky	Red to yellow-brown	None to weak	None	None to weak	None	Blade	Peg	None	1–2	None to weak	Upper palatal weak
bollesiana	1.5–1.7	0.8–0.9	Conic – ovate	Moderate	Weak, blunt, scattered, irregular	Shiny	Yellow Brown	None to modest	None	Modest	None	Blade	Peg	Peg	2 short	Deep	Parietal points to upper palatal
chiricahuensis	1.7–1.9	0.9–1.1	Cylindrical – ovate	Moderate to deep	Rib-like, sharp, scattered, irregular	Dull	Yellow-brown	Weak to modest	None	Modest	None	Blade	Peg	None	2	Modest	
chytryi	1.9–2.2	1.1–1.2	Ovate – cylindrical	Shallow	Threads: sharp irregular	Dull	Red-brown	Weak	None	Modest	None	Blade	Peg	Weak peg	2	Weak	
genesii	1.7–2.1	1.0–1.2	Ovate – cylindrical	Deep	Absent to weak, irregular	Glassy	Red-brown	None	None	None	None	None to weak	None or flattening	None	None	None	
genesioides	1.7–2.1	1.1–1.3	Conic – ovate	Deep	Weak: scattered, irregular	Silky	Red-brown	None	None	None	None	None to weak	None to weak	None	None	None	
geyeri	1.7–1.9	1.1–1.2	Ovate – cylindrical	Moderate	Weak: scattered, irregular	Silky	Red-brown	None to weak	None	Weak	None	Long	Peg	None	2 short	Modest	
gouldii	1.5–1.9	0.8–1.0	Cylindrical – ovate	Moderate	Numerous, strong, sharp, irregular	Dull to Silky	Brown	None to weak	None	Modest	None to very weak	Long	Peg	Peg	2	Modest	Parietal points to upper palatal

(continues)

(continued)

Species	Height (mm)	Width (mm)	Shell Shape	Suture Depth	Striae	Luster	Color	Crest	Callus	Sinulus	Angular	Parietal	Columellar	Basal	Palatal	Palatal Depression	Other
hannai	1.7–2.0	0.9–1.1	Ovate – cylindrical	Moderate	Numerous, sharp, irregular	Shiny	Red-brown	None	None	Modest	Strong	Long	Peg	Peg	2	Weak	
inserta	1.7–1.9	0.8–0.9	Cylindrical – ovate	Moderate	Numerous, sharp, irregular	Dull	Yellow to red-brown	Weak	None	Weak	Strong	Long	Peg	Peg	2	Modest	
kodamai	1.4–2.0	0.8–1.0	Ovate – cylindrical	Shallow to moderate	Numerous, sharp, irregular	Silky	Brown	Weak	None	Weak	None	Long	Peg	None	2 moderate length to long	Shallow	
meramecensis	1.8–2.0	1.0–1.2	Conical	Moderate	Strong, sharp, numerous, irregular	Dull	Red-brown	None to weak	None	None to weak	None	Long	Peg	None to Weak	2 short to moderate length	Shallow	
microsphaera	1.6–1.9	0.9–1.1	Ovate	Deep	Strong, sharp, numerous, regular	Dull	Yellow-brown	Weak	None	Modest	None	Long	Peg	None	2	None to shallow	
nitidula	1.5–2.2	0.9–1.2	Cylindrical – ovate	Moderate	Sharp, strong, irregular	Dull	Yellow-brown	Weak to modest	None to modest	Weak	Strong to none	Long	Peg	Peg to none	2 long	Shallow	
nylanderi	1.6–1.8	0.8–0.9	Ovate	Moderate	Numerous, sharp, strong, regular	Dull	Red to yellow-brown	None	None	Strong	Strong	Long	Vertical plate	Weak	2 very long	Deep groove	Lower palatal more deeply inserted than upper
oughtoni	1.8–2.2	1.1–1.2	Cylindrical – ovate	Moderate to deep	Scattered, blunt, weak, irregular	Glassy	Red-brown	None	None	None	None	Short	Short	None	1–2 short	None	Upper palatal often absent
pusilla	1.9–2.1	1.0–1.1	Conical – ovate	Moderate	Scattered, blunt, weak, irregular	Shiny	Yellow-brown	Modest to strong	Strong to none	Strong	Strong	Long	Long	Strong	2	Deep groove	Sinistral shell
substriata	1.6–1.8	0.9–1.1	Ovate	Deep	Numerous, strong, sharp, regular	Dull	Brown	Strong	Strong to none	Strong	Strong	Long	Long	Peg to none	2	Weak	
cf. *utahensis*	1.8–2.0	0.9–1.0	Ovate – cylindrical	Moderate	Numerous, sharp, regular	Dull	Brown	Strong	None	Weak	Weak to none	Long	Peg	None	2 modest	Weak	

Etymology

The specific epithet refers to Prof. Milan Chytrý of the Department of Botany and Zoology, Masaryk University, who was the P.I. responsible for the grant that allowed collection of both genetically verified populations.

Phylogenetics

Across all reconstruction methods this species existed as a moderately to highly supported clade (62–99) in ITS1 + ITS2 and a highly supported clade (99–100) in CytB + 16S. Bayesian reconstruction placed it in a poorly supported (55) ITS1 + ITS2 clade with ***V. chiricahuensis*** and ***V. kodamai***.

Comparisons with Other Species

Shell reminiscent of *V. gouldii* from eastern North America but wider with more numerous radial striae and a matt surface. The presence of a small basal lamella distinguishes it from all other known boreal central Asian species. The closest in appearance is *V. microsphaera*, which differs in its coarser and wider-spaced radial striae and deeper suture with more tumid whorls. It is also somewhat similar to the North American boreal/arctic *V. hannai*, which differs in its strong angular and basal lamellae.

Geographic Distribution

Asia – Genetically documented only from two regions separated by ca. 1,200 km in the taiga of western and southern Siberia. Novosibirsk, the largest Siberian city, lies within this range. Material collected in the Lake Baikal region by Richard Preece (personal communication) also appears to represent this species, although tissue samples for DNA analysis were unavailable. The record from Nizhnie Aremzyany was previously published as "*Vertigo* aff. *gouldii*" (Horsák & Chytrý, 2014).

Ecology

Found in moderately alkaline, plant species-rich hemiboreal taiga either under the bark of a fallen fir log (at the type site) or in *Tilia* leaf litter.

Vertigo (*Vertigo*) *gouldii*
(A. Binney, 1843)
Figs. 3 (top row), 4I, 5P

Pupa gouldii A. Binney, 1843: 105.

Type Locality: Northeastern and Middle States [of the U.S.A.].

Phylogenetics

In ITS1 + ITS2 this species existed as a poorly to moderately well supported clade (46–74) and in CytB + 16S as a highly supported clade (99–100) across all reconstruction methods. Populations of *V. gouldii* from eastern North America typically demonstrated divergent ITS1 + ITS2 sequence, with nearest sister-groups being some ***V. kodamai***, *V. meramecensis* and *V*. cf. *chiricahuensis*. However, in CytB + 16S all specimens were members of the same highly supported monophyletic clade.

Conchology

This species shares with *V. bollesiana* an aperture with five lamellae including a strong basal and a parietal that points towards the upper palatal. *Vertigo gouldii* is distinguished by its more cylindrical shell with a duller luster, sharper and stronger striae, and a weaker depression over the palatals. A number of conchological races of *V. gouldii* exist with some shells from the southern Appalachians approaching *V. bollesiana*. These can be reliably distinguished by their duller luster, sharper striae, and less pronounced palatal depression.

Ecology

Favors rich humid forest, becoming especially common in humus accumulations associated with rock outcrops and boulders.

Biogeography

North America – Southern Québec and Ontario south to the North Carolina coast and northern Alabama west to northwestern Minnesota and the Ozark Mountains of Arkansas and Oklahoma.

Vertigo* (*Vertigo*) *kodamai, n. sp.
Figs. 3 (second row), 5A–L, Table 4

GenBank Accessions: KY217148-54; KY216760-6; KY217550-7; KY216406-13.

Diagnosis

Shell minute, cylindrical-ovoid with four apertural lamellae, similar to *Vertigo japonica*, differing by lack of strong apertural sinulus and shell striae as well as the minutely papillose sculpture of the shell surface.

Description

Shell: 1.4–2.0 mm tall x 0.8–1.0 mm wide (Holotype 1.7 x 1.0 mm), translucent, cinnamon-brown to auburn; approximately five whorls; apical whorls conical, remainder ovoid-cylindrical, more cylindrical in taller shells; suture moderately deep, whorls shouldered; shell shining but with silky luster due to moderately developed somewhat regular striae, weak or absent on protoconch, and a wrinkled-papillose microsculpture throughout

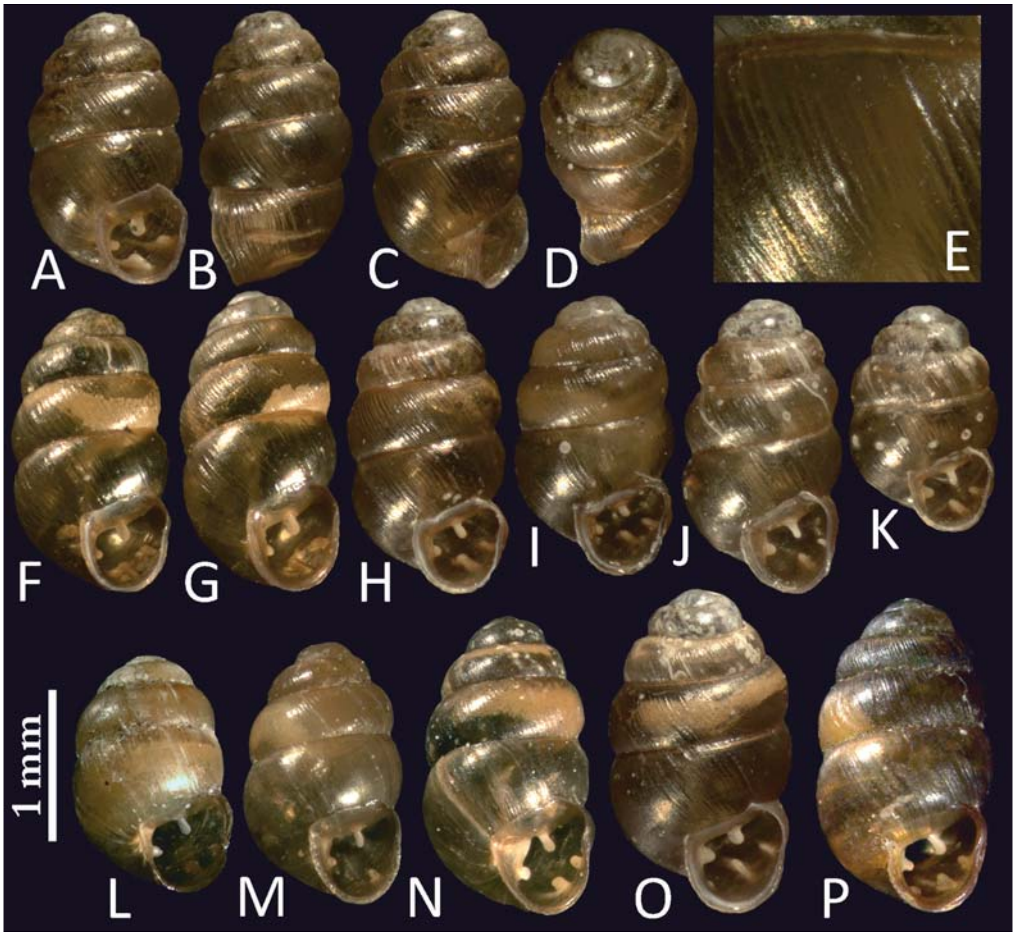


FIG. 5. ***Vertigo kodamai*** n. sp. A–E: Holotype, ANSP 467339, Kamikineusu, Urakawa District, Hokkaidō, Japan (42.2201°N, 142.9594°E); F: [VH59] Kamikineusu, Urakawa District, Hokkaidō, Japan (42.2201°N, 142.9594°E); G: [VH60] Aioi, Tsubetsu, Abashiri District, Hokkaidō, Japan (43.5104°N, 143.9862°E); H: [VH98] Samani, Samani District, Hokkaidō, Japan (42.1815°N, 143.0003°E); I: [VH102] Hobetsu-fukuyama, Yufutsu District, Hokkaidō, Japan (42.8869°N, 142.2500°E); J, K: [VH100] Cape Shirepa, Kushiro District, Hokkaidō, Japan (42.9517°N, 144.7370°E); L: [VH22] Minami Iwo, Ogasawara Islands, Tokyō, Japan (24.2385°N, 141.4695°E); M: *Vertigo* cf. *hirasei* [J21] Minami-fukasawa, Miyagi District, Japan (38.6740°N, 141.1103°E); N: *Vertigo kushiroensis* [VH61] Kushiro Marsh, Hokkaidō, Japan (43.0340°N, 144.3901°E); O: ***Vertigo chytryi*** [B52] Peshcherka valley, Zalesovo District, Altai Krai Republic, Russia (54.1335°N, 84.7584°E); P: *Vertigo gouldii* [26] Deer Creek, Fillmore Co., Minnesota, U.S.A. (43.7322°N, 92.3443°W). When applicable, bracketed DNA specimen codes precede each entry.

including striae; aperture approximately $^1/_4$ of shell height, rounded-oval, as wide as tall or slightly taller than wide (Fig. 5A, F–L); umbilicus closed by preceding whorls (Fig. 5C); peristome interrupted by body whorl but visible as a weak callus; apertural lip slightly flared (Fig. 5B, D), a weakly developed sinulus corresponding in profile to a slight forward extension of the aperture, crest absent or occasionally weakly developed basally, without apertural thickenings or callus (Fig. 5A–D, F–L); four apertural lamellae: columellar lamella peg-shaped; parietal lamella short triangular-crescent-shaped, simple or somewhat twisted; two parallel palatal lamellae, elongate, blade-shaped, of equal length, often with fine extension ~$^1/_4$ revolution into the body whorl, visible through the palatal wall (Fig. 5B); slight flattening of shell surface over palatal lamellae but without grooves or channels; animal body gray.

Holotype (Fig. 5A–E): ANSP 467339, Kamikineusu, Urakawa District, Hokkaidō Prefecture, Japan; moss on trees in rich forest on limestone hillside; 42°13'17''N, 142°57'35''E; July 22, 2012.

Paratypes: ANSP 467340, collected with Holotype: 10 shells. NMW.Z.2015.009.00034, collected with holotype: ~30 shells. ANSP 467341, Cape Shirepa, Kushiro District, Hokkaidō Prefecture, Japan; moss on trees in sweet gum, magnolia, birch, fir forest; 42°57'06''N, 144°44'13''E; July 24, 2012: 10 shells. ANSP 467342, Samani, Samani District, Hokkaidō Prefecture, Japan; moss on trees in wooded riparian corridor; 42°10'53''N, 143°00'11''E; July 22, 2012: 6 shells. ANSP 467343, Aioi, Tsubetsu, Abashiri District, Hokkaidō Prefecture, Japan; moss on trees in mesic wooded streamside; 43°30'37''N, 143°59'10''E; July 25, 2012: 10 shells.

Other, Non-Type Material Examined: Two ethanol preserved shells collected in 2007 from Minami Iwo, Ogasawara Islands, Tokyō Prefecture, Japan; tree fern leaves in summit cloud forest; 24°14'14''N, 141°27'45''E. Also, ~270 shells from 6 sites on Hokkaidō in the Nekola collection. NMW.Z.2015.009.00033, Kamikineusu, ~10 km NNE of Samani, Hokkaidō Prefecture, Japan; moss and leaf litter at base of trees – maple forest on limestone; 42°13'17''N, 142°57'35''E; July 22, 2012: 9 shells. NMW.Z.2015.009.00035, N of Samani, Hokkaidō Prefecture, Japan; moss on trees in wooded riparian corridor; 42°10'53''N, 143°0'01''E; July 22, 2012: 14 shells. NMW.Z.2015.009.00036, Shirepa: Highway 142, ~29 km E of Kushiro, Hokkaidō Prefecture, Japan; moss on trees in mixed woodland; 42°57'06''N, 144°44'13''E; July 24, 2012: ~40 shells. NMW.Z.2015.009.00037, Highway 240/Abashiri River at road pull-in, S of Tsubetsu, Hokkaidō Prefecture, Japan; moss on trees in wooded riparian corridor; 43°30'37''N, 143°59'10''E; July 24, 2012: ~50 shells. NMW.Z.2015.009.00038; junction of highways 274/610: Mu River, Hokkaidō Prefecture, Japan; moss on trees in wooded riparian corridor; 42°53'15''N, 142°15'00''E; July 26, 2012: 9 shells.

Etymology

The specific epithet refers to Kodama which are tree-dwelling spirits of Japanese folklore. Kodama tend to inhabit older and larger trees and protect the forest from harm. It is said that those who cut down trees harboring Kodama will be struck down with bad luck and misfortune.

Phylogenetics

This species was represented in ITS1 + ITS2 by a moderately to highly supported (73–100) and in CytB + 16S by a highly supported (92–100) clade across all reconstruction methods. Some populations of ***V. kodamai*** exhibited divergent ITS1 + ITS2 sequence, with these being associated with North American *V. gouldii*, *V. meramecensis* and *V.* cf. *chiricahuensis*. However, in CytB + 16S all ***V. kodamai*** populations were members of the highly supported monophyletic clade.

Comparisons with Other Species

Among the Japanese (and SE Asian) *Vertigo*, ***V. kodamai*** most closely resembles *V. japonica* in size, shape, and moderately developed suture (Pilsbry, 1919: pl. 15: figs. 1, 2). However, ***V. kodamai*** has a relatively larger aperture that lacks the very strong sinulus and associated groove on the palatal wall of *V. japonica*. *Vertigo japonica coreana* (Pilsbry, 1919: pl. 15, fig. 4) has indistinct shell striation and a lower palatal lamella markedly longer than the upper palatal lamella. *Vertigo japonica tosana* (Pilsbry, 1919: pl. 15, fig. 3) is larger, more conical in shape, much more strongly striate, and dwells among rocks in forest litter. ***Vertigo kodamai*** also somewhat resembles the European *V.*

alpestris, from which it differs in its smaller aperture and less sharp shell striae. It also bears superficial resemblance to some North American members of the subgenus *Vertigo*, such as *V. arizonensis* and *V. gouldii*. It differs from the former by lacking an angular lamella and from the latter by lacking a basal lamella and its much longer palatal lamellae blades.

Geographic Distribution

Japan – Currently known from only southern Hokkaidō and Minami Iwo in the Ogasawara Islands.

Ecology

Vertigo kodamai is obligately arboreal, being restricted to thick moss growth on tree trunks and branches in humid woodland. On Minami Iwo, it was also found foraging on tree fern leaves.

Further Taxonomic Research

It should be noted that the Minami Iwo population possessed unique ITS1 + ITS2 and CytB + 16S sequence compared with the Hokkaidō material, as well as having shorter shells with a proportionally larger aperture. However, because they were members of the same highly supported clade as the Hokkaidō ***V. kodamai***, we feel it best to remain cautious and not erect any subspecific designations until additional data are available.

Vertigo (*Vertigo*) *hannai*

Pilsbry, 1919: 114
Figs. 3 (top row), 4J

Type Locality: along Prairie Dog creek between Norton and the Republican River, Phillips County, Kansas, U.S.A. (fossil).

Phylogenetics

This species was defined by a moderately to highly supported clade (63–96) in ITS1 + ITS1 and by a highly supported clade (99–100) in CytB + 16S across all reconstruction methods.

Conchology

Within the subgenus, only this species, *V. inserta* and *V. substriata* possess strong angular and basal lamellae. *Vertigo hannai* is most readily distinguished from *V. inserta* by its more ovate shape, shining luster and weak depression over the palatal lamellae. It is most readily distinguished from *V. substriata* by its shining luster and lack of a crest.

Ecology

Occurs in taiga and tundra habitats from wetland margins through dry, rocky uplands.

Biogeography

North America – Currently ranging from northern Alaska to the southern shore of Hudson’s Bay and the foothills of the Rocky Mountains in southern Alberta. It is also known as a full glacial fossil from northern Kansas east to southwestern Ohio.

Vertigo (*Vertigo*) *nylanderi*

Sterki, 1909: 107
Fig. 3 (second row)

Type Locality: Woodland, Aroostook County, Maine, U.S.A.

Phylogenetics

This species was defined by a moderately to highly supported clade (83–99) across all reconstruction methods in ITS1 + ITS2. In CytB + 16S it existed only as a poorly supported subclade (52–70) within *V. arthuri*. All reconstruction methods identified *V. bollesiana* as sister in ITS1 + ITS2 at moderate to high support (65–100). A single Wisconsin individual exhibited typical CytB + 16S and conchology for the species yet possessed ITS1 + ITS2 typical of *V. arthuri* – which is abundant in surrounding limestone cliff habitats.

Conchology

This species and *V. arthuri* possess the only shells in the subgenus for which the lower palatal lamella is more deeply inserted into the aperture than the upper. It differs from *V. arthuri* in its longer and more deeply inserted lower palatal lamella and taller than wide columellar lamella.

Ecology

Wooded wetlands, often dominated by northern white cedar, tamarack or alder. It is quite tolerant of acidic conditions.

Biogeography

North America – Easternmost Maine west through the northern Great Lakes and central Ontario to northwestern Minnesota and central Manitoba. It is expected from the Maritime Provinces of Canada and the taiga of Saskatchewan and eastern Alberta.

VERTIGO ALPESTRIS GROUP

Even though *V. pusilla* is considered here, its connection to the rest of the group is tenuous at best and based only upon Bayesian CytB + 16S reconstructions. As a result, we have chosen to name the group after the most senior name among the remaining three taxa.

Vertigo (*Vertigo*) *alpestris*

Alder, 1838: 340
Figs. 3 (fourth row), 6I–L

Type Locality: Lipwood, near Haydon Bridge, Northumberland, England; on an old wall.

Phylogenetics

This species was represented by a very highly supported clade (99–100) across all four analyses in ITS1 + ITS2. This species was polyphyletic in CytB + 16S: one clade was sister to ***V. beringiana*** at moderate to high support (73–99), with the other being sister to *V. pusilla* at moderate to high support (76–99). Individuals from this latter clade were restricted to the Atlantic regions of Europe (British Isles into Scandinavia); presumably specimens from the type locality would have been assigned here. Because the other clade shared the same topological position with ***V. beringiana*** as illustrated in ITS1 + ITS2, we assume that the Atlantic clade is the result of an ancient introgression event for which time has been sufficient to allow differentiation from *V. pusilla*. This would not be surprising given that *V. alpestris* and *V. pusilla* often co-occur at sub-meter scales in areas of range overlap.

Conchology

A number of other members of the subgenus, including ***V. beringiana***, ***V. chiricahuensis*** and ***V. kodamai***, share with *V. alpestris* its cylindrical-ovate shape and the absence of angular and basal lamellae. It is most readily distinguished from ***V. beringiana*** by its sharper striae and more shining luster. It is distinguished from ***V. chiricahuensis*** by its shining luster and much weaker and more regular striae. It differs from ***V. kodamai*** in its more cylindrical shell, less sharp striae, and lack of a crest and palatal depression. It also differs from the related *V. nitidula* in its weaker and blunter striae and lack of both basal and angular lamellae.

Ecology

Typically limited to humus accumulations on rock outcrops and between stones on talus slopes. It also occurs in old vegetated rock walls and is limited to such habitats throughout much of Britain. It may also be found on fallen beech logs in old-growth forest.

Biogeography

Europe – British Isles and Scandinavia east to the southern Urals and Crimea.

Vertigo* (*Vertigo*) *beringiana, n. sp.

Figs. 3 (fourth row), 6A–H, Table 4

GenBank Accessions: KY216961-8; KY216604-10; KY217369-76; KY216235-41.

Diagnosis

Shell small, cylindrical-ovoid, similar to *V. alpestris* but differing by its silky luster due to the presence of wavy microscopic radial threads covering the surface. It also tends to have shallower macroscopic radial striae and less tumid whorls.

Description

Shell: 1.4–2.2 mm tall x 0.9–1.1 mm wide (Holotype 2.0 x 1.0 mm), translucent, yellowish-brown to cinnamon-brown; approximately six whorls; apical whorls conical to domed, remainder cylindrical; suture typically shallow to at most moderately deep with the whorls thus often appearing moderately compressed; shell luster silky from the presence of numerous wavy microscopic radial threads covering the post-neanic whorls (Fig. 6H), larger radial striae present but relatively shallow and indistinct (Fig. 6A–G); aperture approximately $^1/_3$ of shell height, approximately as wide as tall (Fig. 6A, E, F, G), in profile ascending slightly onto body whorl (Fig. 6B); umbilicus closed by preceding whorls (Fig. 6C); peristome interrupted by body whorl, apertural lip unflared or only slightly flared (Fig. 6B, D), crest typically absent with no apertural thickenings or callus (Fig. 6A–H); four apertural lamellae present including a peg-shaped columellar, a blade-shaped parietal, and blade-shaped upper and lower palatals (Fig. 6A, C, E–G), a very weak depression of the shell surface over the palatals may occasionally be present (Fig. 6D).

Holotype (Fig. 6A–D, H): ANSP 467344, Berg Wayside, Yukon-Koyukuk Census Area, Alaska, U.S.A.; wet-mesic alder-aspen-birch forest; 64°36'23''N, 149°05'24''W; August 3, 2007.

Paratypes: ANSP 467345, collected with holotype: 15 shells. ANSP 467346, Clearwater State Recreation Area, Southeast Fairbanks Census Area, Alaska, U.S.A.; xeric upland aspen-spruce forest; 64°03'10''N, 145°25'29''W; August 11, 2007: 10 shells. ANSP 467347, Ice Cut, Dalton Highway, North Slope Borough, Alaska, U.S.A.; fern and saxifrage litter on rock talus; 69°01'09''N, 148°50'11''W; August 8, 2007: 10 shells. ANSP 467348, Khangalasskii Elanka village, Sakha Republic, Russia; scree forest with *Picea obovata*; 61°16'07''N, 128°06'21''E; August 9, 2010: 3 shells. ANSP 467349, Ust'-Aldanskii Beidinga village, Sakha Republic, Russia; *Betula*, *Larix* and *Picea obovata* forest; 62°22'28''N, 130°54'23''E; August 14, 2010: 2 shells. ANSP 467350, Camp Bolshoi Ilgumen, Altai Republic, Russia; moss-covered rocks on steep, north-facing wooded slope; 50°38'28''N, 86°21'04''E; August 5, 2011: 10 shells.

Other Non-Type Material Examined: 1,626 individuals from 17 Alaskan lots and four lots from the Altai Republic, Russia in the Nekola collection; 120 shells from 23 lots from the Altai and Sakha Republics, Russia in the Horsák collection.

Etymology

The specific epithet refers to the central/eastern Asian and western North American arctic region in which the species occurs.

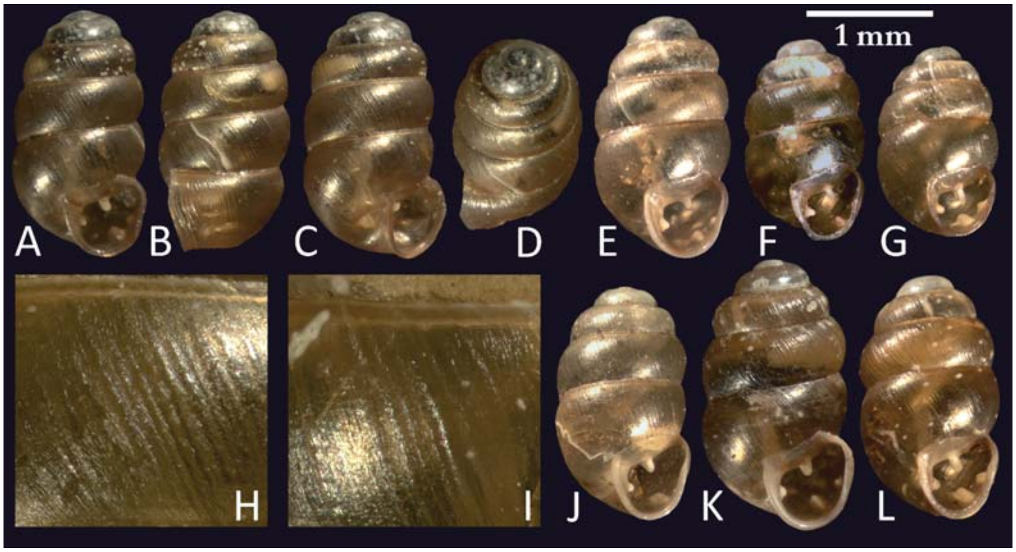


FIG. 6. ***Vertigo beringiana*** n. sp. A–D, H: Holotype, ANSP 467344, Wet-mesic alder-aspen-birch forest, Berg Wayside, Yukon-Koyukuk Census Area, Alaska, U.S.A. (64.6066°N, 149.0902°W); E: [B40] Ice Cut, Dalton Highway, North Slope Borough, Alaska, U.S.A. (69.0193°N, 148.8364°W); F: [T19] Bestyakh, Sakha Republic, Russia (61.3624°N, 128.8433°E); G: [B33] Moss-covered rocks on steep, north-facing wooded slope, Camp Bolshoi Ilgumen, Altai Republic, Russia (50.6411°N, 86.3512°E); *Vertigo alpestris.* I, J: [H57, T16] Bowston, Cumbria, England (54.3619°N, 2.7733°W); K: [B82] Signaldalen, Troms, Norway (69.1911°N, 19.9873°E); L: [B36] Mramorne, Crimea, Ukraine (44.7870°N, 34.2900°E). When applicable, bracketed DNA specimen codes precede each entry.

Phylogenetics

This species represented a moderately to highly supported (76–100) clade across all reconstruction methods in ITS1 + ITS2 and CytB + 16S. All methods across both datasets identified it as being sister to *V. alpestris* at moderate to high support (71–100).

Comparisons with Other Species

Shell reminiscent of *V. alpestris* from boreal Europe, but differs by its abundant microscopic radial threads giving the shell surface a silky – rather than shiny – luster. It also tends to have less sharp and less strong radial striae than *V. alpestris*, as well as less inflated whorls. It differs from members of the *V. ronnebyensis* group by having less numerous and sharp radial striae, and by lacking a crest on the outer apertural wall.

Geographic Distribution

Arctic-Boreal Holarctic – Interior Alaska west across boreal East Asia to the foothills of Altai Mountains in south-central Siberia. This species was previously reported as *V. alpestris* from the Altai (Horsák et al., 2010) and the Sakha Republics (Horsák et al., 2013a) and from Siberia as *V. modesta alpestris* (Sysoev & Schileyko, 2009).

Ecology

Found in a wide variety of boreal and arctic habitats including aspen, birch, and conifer forests, tundra, xeric steppe, and wooded wetland habitats. In both the far northern and southwest sections of its range it appears limited to rock outcrops.

Vertigo (*Vertigo*) *nitidula*

(Mousson, 1876)

Fig. 3 (fourth row)

Pupa (*Vertigo*) *pygmaea* var. *nitidula* Mousson, 1876: 143.

Type Locality: Tabatsquri, Georgia.

Phylogenetics

Across all reconstruction methods this species is represented by a moderately to highly supported clade (61–98) in ITS1 + ITS2, and a very highly supported clade (98–100) in CytB + 16S. It was closely allied to *V. alpestris* in ITS1 + ITS2, being a member of the same very highly supported clade (99–100) containing that species. However, in CytB + 16S all methods showed the *V. nitidula* clade basal to all other members of the subgenus.

Conchology

This species is most similar to *V. substriata*, with which it shares a striate shell with 5–6 apertural lamellae. It differs from that species in its more cylindrical shape, more irregular striae and much weaker crest. This species also demonstrates a high degree of shell variability (Walther et al., 2014) in terms of shape (cylindrical-ovate to ovate), number of apertural lamellae (4–6, with an angular and basal being sometimes absent), and the degree of crest and callus development (absent to strong).

Ecology

Montane deciduous and mixed forest and above treeline in rock fissures.

Biogeography

Asia Minor – Limited to the Caucasus.

Vertigo (*Vertigo*) *pusilla*

O. F. Müller, 1774: 124

Fig. 3 (top row)

Type Locality: Fredriksdal (N of Copenhagen), Denmark.

Phylogenetics

This species existed as a highly supported clade (93–100) across all reconstruction methods in ITS1 + ITS2 and CytB + 16S. While this clade in ITS1 + ITS2 demonstrated no affinities with any other species in the subgenus, the CytB + 16S Bayesian reconstruction suggested, with high support (92), membership in a clade including *V. alpestris* and ***V. beringiana***.

Conchology

This species is unique in the subgenus for not only possessing a sinistral shell but also in its shiny luster, reduced striae development, strongly developed callus and six strong apertural lamellae.

Ecology

Found across a wide range of forested or brushy habitats, ranging from dune scrubland to temperate and boreal forest to talus slopes and anthropogenic rock walls.

Biogeography

Western Eurasia – Atlantic shore in Iberia, the British Isles and Scandinavia east to central Siberia.

VERTIGO ARIZONENSIS GROUP

We have chosen to cover *V. meramecensis* here, even though this relationship was only supported by Bayesian (100) and ML (65) reconstructions of CytB + 16S data.

Vertigo (*Vertigo*) *arizonensis*
Pilsbry & Vanatta, 1900
Figs. 3 (third row), 7K

Vertigo coloradensis arizonensis Pilsbry & Vanatta, 1900: 601, pl. 23, fig. 9.

Type Locality: Mt. Mingus, near Jerome, Arizona, U.S.A.; 8,500 ft.

Phylogenetics

This species existed in all reconstructions as a moderately to highly supported (81–100) clade in both datasets. In ITS1 + ITS2 *V. inserta* was shown to be a moderately to highly supported (60–99) subclade. In CytB + 16S across all reconstructions *V. arizonensis* was member of a highly supported (91–100) supraspecific clade also containing ***V. chiricahuensis***, *V.* cf. *chiricahuensis*, *V. inserta* and *V.* cf. *utahensis*.

Conchology

This species is unique in the subgenus for possessing a cylindrical-ovate shell with very long palatal lamellae and a strong angular but no basal lamella. All other members of the group possess shorter palatals. The closely related *V. inserta* also differs by possessing a basal lamella; ***V. chiricahuensis*** differs in its coarse striae and lack of an angular lamella; *V.* cf. *chiricahuensis* differs in its short palatal blades; *V*. cf. *utahensis* differs in its more ovate shape, smaller aperture and short palatal blades.

Ecology

Mid- to high-elevation mixed conifer and deciduous forest, becoming abundant in humus accumulations on talus slopes.

Biogeography

North America – Guadalupe Mountains along the New Mexico/Texas border west to central Arizona and north into central Utah and southern Colorado.

Vertigo* (*Vertigo*) *chiricahuensis, n. sp.
Figs. 3 (third row), 7A–F, Table 4

GenBank Accessions: GQ921526, KY217017, KY217425, KY216288.

Diagnosis

Shell small, cylindrical-ovoid, similar to *Vertigo arizonensis* but differing by its lack of an angular lamella, shorter palatal lamellae, and coarse, widely spaced striae.

Description

Shell: 1.7–1.9 mm tall x 0.9–1.1 mm wide (Holotype 1.9 x 1.0 mm), translucent to transparent, yellow-brown; approximately five whorls; columnar-ovate; suture deep with relatively inflated whorls (Fig. 7A–D, F); dull luster with coarse, widely spaced radial striae (Fig. 7E); aperture approximately $^{1}/_{3}$ of shell height, being slightly taller than wide (Fig. 7A, F), in profile ascending onto body whorl (Fig. 7B); umbilicus closed by preceding whorls (Fig. 7C); peristome interrupted by body whorl (Fig. 7A, F); no crest, apertural thickenings or callus (Fig. 7A, B, D); four apertural lamellae present including a peg-shaped columellar, a blade-shaped parietal, and two blade-shaped palatals of normal length (Fig. 7A, B, F); a depression is present on the shell surface over the palatal wall (Fig. 7D).

Holotype (Fig. 7A–E): ANSP 467351, Buena Vista Peak, Cochise County, Arizona, U.S.A.; Mesic, N-facing boulder slope under Douglas fir; 31°55'03''N, 109°16'19''W; March 20, 2005.

Paratypes: ANSP 467352, collected with holotype: 3 shells; UF 505179, collected with holotype: 15 shells; NMW.Z.2005.011.02910, collected with the holotype: ~140 shells.

Etymology

The specific epithet refers to the Chiricahua Mountains, the location of the type (and only genetically verified) station.

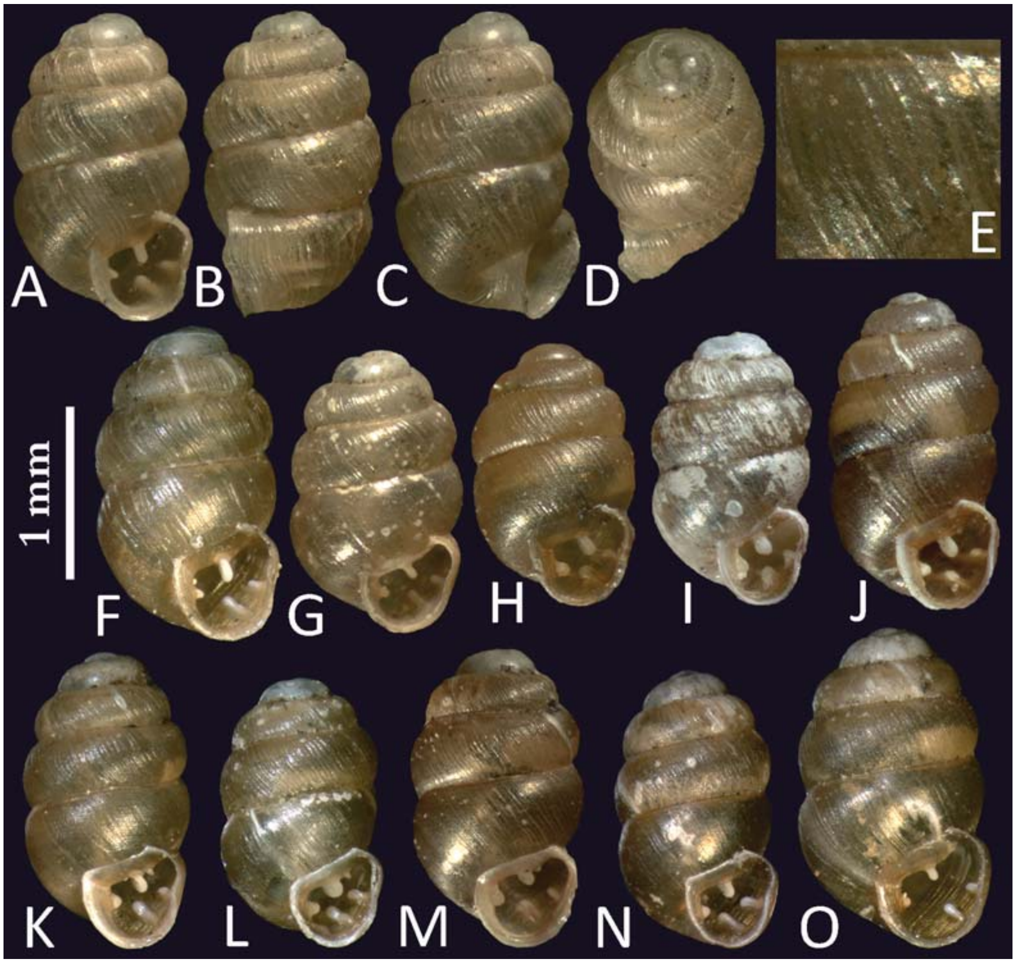


FIG. 7. ***Vertigo chiricahuensis*** n. sp. A–E: Holotype, ANSP 467351, Mesic, N-facing boulder slope under Douglas Fir, Buena Vista Peak, Cochise County, Arizona, U.S.A. (31.9176°N, 109.2722°W); F: Paratype, ANSP 467352, Buena Vista Peak, Cochise County, Arizona, U.S.A. (31.9176°N, 109.2722°W); *Vertigo* cf. *chiricahuensis.* G: ANSP 167370, Rio Piedras Verdes 2 miles below Pacheco, Chihuahua, Mexico; H: [VH115] Sierra el Tigre, Sonora, Mexico (30.6003°N, 109.2199°W); I: [VH122] Mt. Livermore, Jeff Davis Co., Texas, U.S.A. (30.6386°N, 104.1616°W); J: [VH123] Tobe Canyon, Jeff Davis Co., Texas, U.S.A. (30.6371°N, 104.1781°W); K: *Vertigo arizonensis* [31] Bland, Sandoval Co., New Mexico, U.S.A. (35.7474°N, 106.4593°W); L: *Vertigo inserta* [T9] Bear Wallow, Pima Co., Arizona, U.S.A. (32.4211°N, 110.7302°W); M: *Vertigo* cf. *utahensis* [VH106] Bullion Canyon, Piute Co., Utah, U.S.A. (38.4171°N, 112.3126°W); N: *Vertigo arthuri* form *basidens* [17] Bland, Sandoval Co., New Mexico, U.S.A. (35.7474°N, 106.4593°W); O: *Vertigo coloradensis* [NS13] Blanco River, Archuleta Co., Colorado, U.S.A. (37.1452°N, 106.8857°W). When applicable, bracketed DNA specimen codes precede each entry.

Phylogenetics

In ITS1 + ITS2 this species exhibited a poorly supported relationship with either *V. bollesiana* and *V. nylanderi* (54–55 in NJ, ME, and ML) or ***V. kodamai*** and ***V. chytryi*** (55 in Bayesian). In CytB + 16S it was part of a highly supported clade (99–100) also containing *V. arizonensis* and *V*. cf. *utahensis*.

Material from Sonora and Texas (listed in the Appendix as *V.* cf. *chiricahuensis*) demonstrated divergent DNA sequence across both datasets. The Sonoran material had ITS1 + ITS2 more closely related to ***V. chytryi*** and ***V. kodamai***, and very distinct CytB + 16S within the *V. arizonensis* – ***V. chiricahuensis*** – *V*. cf. *utahensis* clade. Both of the Texas individuals had divergent ITS1 + ITS2 sequence related to ***V. kodamai***; their CytB + 16S sequence were part of a moderately to highly supported clade (64–94) across all reconstruction methods that also included *V. inserta*. It should also be noted that although the ITS1 + ITS2 sequences for the two Texas individuals were identical, their CytB + 16S varied by 16 bases. While it seems that more than one species-level taxon is present, current data does not allow for their definitive resolution.

Comparisons with Other Species

Shells are most readily differentiated from other southwestern U.S.A. *Vertigo* by their coarse, widely spaced striae. In addition, *V. arizonensis* (Fig. 7K) differs by possessing much longer palatal blades and a strong angular lamella; *V. inserta* (Fig. 7L) by possessing both angular and basal lamellae; *V.* cf. *utahensis* (Fig. 7M) by its more ovate shell with a wider-than-tall aperture; *V. arthuri* form *basidens* (Fig. 7N) by its strong crest; and the sympatric *V. coloradensis* by its larger shells with a shallower suture and wider aperture (Fig. 7O).

Vertigo similar to ***V. chiricahuensis*** also occur in other Sky Island systems of northern Mexico and west Texas. None of these populations exhibit the coarse striae of *V. chiricahuensis s. str.*; smaller shells from the Sierra el Tigre in Sonora are most similar (Fig. 7H). Shells with slightly less pronounced striae have also been found in the nearby Sierra Huachinera in Chihuahua (Fig. 7G). Two shell forms present in the Davis Mountains of west Texas (Fig. 7I, J) also lack coarse striae. They differ from each other in shell size and presence of an angular lamella.

Geographic Distribution

America – Currently known only from high elevation (> 2,400 m) forests in the Chiricahua Mountains of southeastern Arizona, U.S.A. It presumably occurs in similar forests of adjacent ranges. Related forms (see above) occur at lower elevations in the Sierra el Tigre in Sonora and the Sierra Huachinera in Chihuahua, Mexico, and at high elevations in the Davis Mountains of west Texas.

Ecology

At its only documented site, this species is restricted to humus accumulations between boulders on an herb-rich north-facing slope supporting Douglas fir, aspen and maple. The Sonoran material was located in humus accumulations associated with rock outcrops and agave in a mid-elevation oak forest. The Davis Mountains material was found in high elevation shaded talus and cliff base habitats.

Vertigo (*Vertigo*) *inserta*
Pilsbry, 1919
Figs. 3 (third row), 7L

Vertigo coloradensis inserta Pilsbry, 1919: 118, pl. 12, figs. 10, 11.

Type Locality: Bear Wallow, Santa Catalina Mountains, Arizona, U.S.A.

Phylogenetics

This species existed as a moderately to highly supported clade (60–99) in ITS1 + ITS2 and CytB + 16S across all reconstruction methods. It showed greatest relationship with *V. arizonensis* in ITS1 + ITS2 and with Texan *V*. cf. *chiricahuensis* in CytB + 16S.

Conchology

In the subgenus, this species shares with *V. hannai* the presence of six strong apertural lamellae in a shell lacking a strong crest or callus. It differs from that species by possession of a more cylindrical shell with dull luster and a modest palatal depression.

Ecology

While most abundant in pine needle accumulations in upland montane forest, it also occurs in humid leaf litter on seepage margins.

Biogeography

North America – Sierra el Tigre in Sonora and the Sierra Huachinera in Chihuahua north to the Mogollon Rim in east-central Arizona.

Vertigo (*Vertigo*) *meramecensis*
Van Devender, 1979: 70
Fig. 3 (top row)

Type Locality: Huzzah Creek, Crawford County, Missouri, U.S.A.

Phylogenetics

This species existed as very highly supported (99–100) clades in both datasets across all reconstruction methods. The Virginia individual was a member of the divergent ITS1 + ITS2 cluster.

Conchology

The shells of this species are easily distinguished from all others in the subgenus by their conical shape, coarse irregular striae, deep red-brown color, and parietal lamella that points towards the lower palatal. In its strongly conical shape and dark red-brown shell color it bares passing similarity to *Vertigo* (*Staurodon*) *dalliana*, the only other obligate rupicolous North American *Vertigo*.

Ecology

Strictly rupicolous, being limited to mesic, shaded, lichen and moss-covered calcareous cliffs and ledges.

Biogeography

North America – Ozark Mountains and the upper Mississippi River Valley east through the Bluegrass Plateau of northern Kentucky to the limestone valleys of western Virginia.

Vertigo (*Vertigo*) cf. *utahensis*
Sterki, 1900
Figs. 3 (third row), 7M

Vertigo columbiana utahensis Sterki in Pilsbry & Vanatta, 1900: 603, pl. 23, fig. 10.

Type Locality: Box Elder Cañon, Utah, U.S.A.; at 4,500 ft.

Phylogenetics

This species existed as a highly supported (95–100) clade across all reconstruction methods in ITS1 + ITS2. One CytB + 16S sequence existed as a unique branch in the clade containing *V. arizonensis* and ***V. chiricahuensis***, while the other had sequence characteristic of *V. arizonensis*. Given that *V. arizonensis* and *V*. cf. *utahensis* are sympatric at this site, it seems likely that the latter association is due to mitochondrial introgression.

Conchology

Shells found to date are similar to *V. arizonensis* and some *V. arthuri* form *basidens* in possessing an angular lamella while lacking a basal lamella. *Vertigo* cf. *utahensis* differs by possessing an ovate shell, small aperture, a strong crest, and palatals of medium-short length inserted to the same depth in the aperture.

Ecology

The two known populations were found in humus accumulations between boulders on the lower portions of talus slopes in aspen forest. Given conditions present at the type locality we suspect that it may range into more xeric sites.

Biogeography

North America – Currently known only from central and northern Utah, U.S.A.

Nomenclature

We have provisionally assigned our material to *V. utahensis* based on the overall shell shape and small aperture size which are similar to the *V. columbiana utahensis* holotype (ANSP 119009). However, this specimen lacks an angular lamella which is present in all our material. Because *V. utahensis* was described from only a single shell, it is impossible to assess conchological variability within the type population and thus to determine whether our form falls within this concept. Until more material is available for comparison – especially from the type locality – we feel it prudent not to erect a new name.

VERTIGO GENESII GROUP

We have chosen to cover *V. substriata* here, even though its membership is tenuous at best with the only connection being a very poorly to moderately supported (15–24 in NJ, ME & ML; 74 in Bayesian) CytB + 16S clade that also contains *V. microsphaera* but none of the other group members. We have thus named the group after the senior name among the remaining species.

Vertigo (*Vertigo*) *genesii*
(Gredler, 1856)
Figs. 3 (bottom row), 8L

Pupa genesii Gredler, 1856: 122, pl. 2, fig. 3.

Type Locality: Tyrol: above St. Jenesien, near Botzen, Italy; at 5,000 ft.

Phylogenetics

This species existed as a moderately to highly supported ITS1 + ITS2 clade (65–100) across all reconstruction methods. Although separated into two branches differing on average by six bases there is no demarcation among shells and no corresponding difference in CytB + 16S. The Italian topotype specimen – with shells, ecology, and ITS1 + ITS2 typical of the species – was found to have CytB + 16S characteristic of *V. geyeri*. This species and *V. geyeri* were shown across all reconstruction methods to be sister within the same highly supported clade in ITS1 + ITS2 (85–99) and CytB + 16S (83–100).

Conchology

Vertigo genesii lacks apertural lamellae, only rarely having a vestigial parietal lamella and a flattened columellar wall. It differs from the closely similar ***V. genesioides*** in its more ovate shell, shallower suture, and weaker to absent striae and glassy shell luster. *Vertigo genesii* differs from *V. geyeri* in its more columnar shell and lack of strong palatal and columellar lamellae.

Ecology

Calcareous flushes and wetlands in arctic, subarctic and alpine environments. Also known from calcareous springs and fens in southern Sweden.

Biogeography

Europe – England, Scotland, and Scandinavia east to Karelia, with disjunct colonies occurring at high elevations in the Alps.

Vertigo* (*Vertigo*) *genesioides, n. sp.
Figs. 3 (bottom row), 8A–J, Table 4

GenBank Accessions: KY217098-107; KY216722-31; KY217500-9; KY216363-72.

Diagnosis

Shell small, broadly conical-ovoid, most similar to *Vertigo genesii* of boreal Europe but differing in its more conical shell, an aperture > $^1/_3$ of the shell height, its less reflective surface luster due to the presence of fine radial and spiral striae, and occasional development of weak lamellae; it also differs by ranging into acidic wetland habitats.

Description

Shell: 1.7–2.1 mm tall x 1.1–1.3 mm wide (holotype 1.8 x 1.2 mm), translucent to transparent, cinnamon-brown; approximately 4–5 whorls; conical; suture moderately deep; shiny luster with a few, irregular, weak radial and spiral striae (Fig. 8E); aperture at least $^1/_3$ of shell height, being approximately as wide as tall (Fig. 8A, F–J), in profile barely ascending onto body whorl (Fig. 8B); umbilicus closed by preceding whorls (Fig. 8C); peristome interrupted by body whorl, apertural lip unflared (Fig. 8B, D) with no crest, apertural thickenings or callus (Fig. 8A–J); usually no apertural lamellae present, although occasionally a weak parietal and/or columellar may occur in some populations (Fig. 8J); palatal lamellae are never present, and there is no depression of the shell surface over the palatal wall (8D).

Holotype (Fig. 8A–D, H): ANSP 467353, Twin Lakes Road, Churchill, Manitoba, Canada; Wet *Larix-Picea* forest; 58°38'47"N, 93°49'28"W; August 23, 2003.

Paratypes: ANSP 467354, collected with holotype: 10 shells. ANSP 467355, La Grande Pointe, Côte-Nord Region, Québec, Canada; maritime turf on limestone pavement; 50°12'06"N, 63°24'05"W; August 2, 2006: 5 shells; NMW.Z.2015.009.00006: 11 shells.

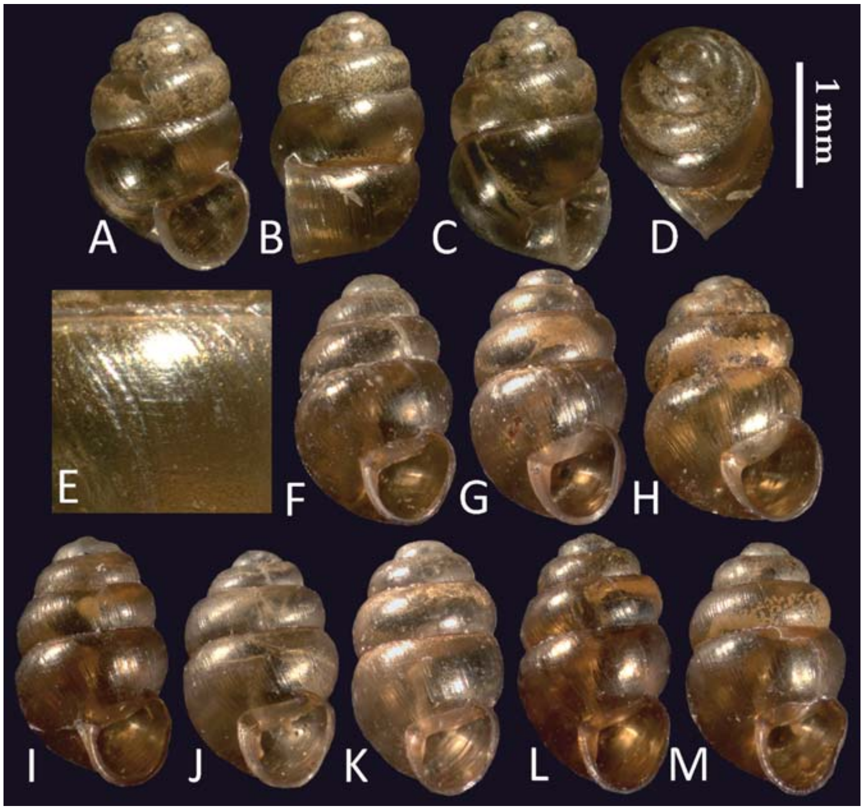


FIG. 8. ***Vertigo genesioides*** n. sp. A–E: Holotype, ANSP 467354, Wet *Larix-Picea* forest , Twin Lakes Road, Churchill, Manitoba, Canada (58.6464°N, 93.8245°W); F: [B14] La Grande Pointe, Côte-Nord Region, Québec, Canada (50.2017°N, 63.4014°W); G: [H35] Milepost 346, Dalton Highway, North Slope Borough, Alaska, U.S.A. (69.3100°N, 148.7300°W); H: [B15] Sakakimachinishi, Hamanaka, Akkeshi District, Hokkaidō, Japan (43.1108°N, 145.1068°E); I: [B7] 3 km southwest of Krasnoe village, Leninsk-Kuznetsky District, Kemerovo Oblast, Russia (54.3446°N, 85.2223°E); J: [B17] 3.5 km west of Kil'demtsy village, Sakha Republic, Russia (62.2822°N, 129.7570°E); K: *Vertigo oughtoni* [H34] Goose Creek Road, Churchill, Manitoba, Canada (58.7264°N, 94.1171°W); L: *Vertigo genesii* [B9] Tamangur Valle, Alp Astras, Switzerland (46.6741°N, 10.3522°E); M: *Vertigo geyeri* [B16] Scoul, Lac Noir, Switzerland (46.7772°N, 10.2681°E). When applicable, bracketed DNA specimen codes precede each entry.

ANSP 467356, Milepost 346, Dalton Highway, North Slope Borough, Alaska, U.S.A.; patterned peatland; 69°18'36"N, 148°43'47"W; August 9, 2007: 10 shells. ANSP 467357, Sakakimachinishi, Hamanaka, Akkeshi District, Hokkaidō, Japan; rich grassland and pond on dune slack; 43°06'39"N, 145°06'24"E; July 24, 2012: 5 shells; NMW.Z.2015.009.00008: 19 shells. ANSP 467358, 3.5 km west of Kil'demtsy village, Sakha Republic, Russia; *Betula-Larix* fen forest; 62°16'56"N, 129°45'25"E; August 3, 2010: 1 shell. ANSP 467359, 3 km southwest of Krasnoe village, Leninsk-Kuznetsky District, Kemerovo Oblast, Russia; large calcareous fen; 54°34'47"N, 85°22'24"E; July 8, 2012: 3 shells.

Other, Non-Type Material Examined: NMW.Z.2005.011.02354, 02357, approximately 40 shells from Manitoba; NMW.Z.2015.009.00015-00016, from Hokkaido, Japan, 12 shells; 46 lots representing 2537 individuals from across the species known range in boreal North America, Hokkaidō, and the Altai Republic in the Nekola collection; 25 lots representing approximately 1,300 shells from the Kemerovo region, Altai and Sakha republics, Russia in the Horsák collection.

Etymology

The specific epithet refers to the close appearance and similar ecological preferences of this species to the European *Vertigo genesii*.

Phylogenetics

This species demonstrated a highly supported (90–100) clade across all reconstruction methods in ITS1 + ITS2. Although there was no single clade defining this species in CytB + 16S, most of the specimens are found in the same general topological location. Four specimens with shells typical for the species demonstrated some form of introgression or incomplete sorting: three with typical shells and mtDNA were found to have ITS1 + ITS2 sorting with a *V. genesii* variant or *V. oughtoni*. A single Québec specimen with typical ITS1 + ITS2 and shells possessed mtDNA characteristic of *V. oughtoni*.

It should also be noted that although the Yakutian material possessed ITS1 + ITS2 typical of ***V. genesioides*** or *V. oughtoni*, they had CytB + 16S differing on average by 14 bases from other *V. genesii*, ***V. genesioides***, *V. geyeri* or *V. oughtoni*. They also possessed weak parietal and columellar lamellae.

Comparisons with Other Species

Shell most closely reminiscent of the boreal European *V. genesii*, but differing in its more conical shape, proportionately larger aperture and slightly deeper suture, and attainment of maturity in $^1/_2$–1 fewer whorls. It also differs from *V. genesii* by being more catholic in terms of its soil acidity preferences, often occurring in quite acid *Sphagnum*-dominated peatlands. It differs from both the boreal European *V. geyeri* and the North American *V. oughtoni* in its absence of palatal lamellae. It also differs from *V. oughtoni* in its broadly conical shape.

Geographic Distribution

Boreal North America to Central Asia – this species has one of the most extensive ranges of any known *Vertigo*, stretching over 12,000 km from the Atlantic coast in eastern Canada through Alaska, Hokkaidō and eastern Siberia to the Altai region of southwestern Siberia. ***Vertigo genesioides*** was previously reported from southern Siberia as *V. genesii* (Meng, 2008, 2009; Horsák et al., 2010) or *V.* aff. *genesii* (Horsák et al., 2015), from the Lake Baikal region as *V. extima* or *V. geyeri* (White et al., 2008, 2013), and from eastern North America as *V.* aff. *genesii* (Nekola & Coles, 2010).

Ecology

Forested graminoid-dominated wetlands across the soil acidity gradient from hypercalcareous limestone turf and fens to *Sphagnum*-dominated bogs and conifer swamps.

Vertigo (*Vertigo*) *geyeri*
Lindholm, 1925
Figs. 3 (bottom row), 8M

Vertigo genesii geyeri Lindholm, 1925: 241.

Type Locality: Cheremenetskoye Ozero, Russia.

Phylogenetics

This species formed a moderately to highly supported (62–98) clade across all reconstruction methods in ITS1 + ITS2, with all analyzed individuals possessing identical sequence. In CytB + 16S it formed a poorly supported (44–58) clade across all four methods.

Conchology

Vertigo geyeri differs from all others in the subgenus by its four apertural lamellae, ovate-cylindrical shell with weak and irregular striae, a relatively shiny shell and a dark red-brown color. It differs from *V. genesii* and ***V. genesioides*** by possessing well-developed columellar and palatal lamellae. It differs from *V. oughtoni* in its ovoid shell, duller luster, and presence of a moderate depression over the palatal lamellae.

Ecology

Base-rich mires, fens, and other spring-fed wetlands.

Biogeography

Europe – British Isles and Scandinavia east to western Russia. Reports of this species by Meng (2008) from southern Siberia and White et al. (2008) from the Lake Baikal region are based on *V. kushiroensis botanicorum*.

Vertigo (*Vertigo*) *oughtoni*

Pilsbry, 1948

Figs. 3 (bottom row), 8K

Vertigo alpestris oughtoni Pilsbry, 1948: 968, text fig. 519.

Type Locality: Lake Harbor, Baffin Island, Northwest Territory, Canada.

Phylogenetics

This species was defined by a very highly supported (98–100) clade in ITS1 + ITS2 across all reconstruction methods and a moderately to highly supported (85–100) clade across all reconstruction methods in CytB + 16S.

Conchology

This species is closest in the subgenus to *V. geyeri*, with both possessing a glassy shell luster and at least three apertural lamellae. It differs by its more columnar shell and lack of any depression over the palatal lamellae.

Ecology

Largely restricted to open, calcareous tundra wetlands.

Biogeography

North America – Arctic Alaska and Baffin Island to the south shore of Hudson's Bay and Anticosti Island. Full glacial fossils are known as far south as central Illinois and southern Ohio.

Vertigo (*Vertigo*) *microsphaera*

Schileyko, 1984

Figs. 3 (bottom row), 4H

Vertigo (*Isthmia*) *microsphaera* Schileyko, 1984: 210.

Type Locality: Podutesnaya Bay, Bering Island, Russia.

Phylogenetics

This species existed as a very strongly supported monophyletic clade (99–100) across all reconstruction methods in CytB + 16S, however, three distinct, non–coalescing branches that differed on average by 4–12 bases were apparent in ITS1 + ITS2. One spans the species biogeographic range; the others have so far only been detected from Hokkaidō, where they may be sympatric within the same population. All were part of the same highly supported (97) Bayesian clade as ***V. genesioides***.

Conchology

Within the subgenus, this species appears closest to *V. substriata* with which it shares an ovate, dull, and strongly striate shell. It differs from that species by lack of an angular lamella, possession of only a weak apertural crest, and presence of a moderately strong sinulus.

Ecology

Humid hemiboreal and riparian forest; also wooded and open wetlands. It is often found in sites possessing considerable graminoid ground cover.

Biogeography

Alaska to Central Asia – Anchorage, Alaska west to Hokkaidō and the northern foothills of the Altai in central Asia.

Vertigo (*Vertigo*) *substriata*

(Jeffreys, 1833)

Fig. 3 (fourth row)

Alaea substriata Jeffreys, 1833: 515.

Type Locality: Rawleigh House, Barnstaple, England.

Phylogenetics

This species was defined by a moderately to highly supported monophyletic clade (82–100) across all reconstruction methods in ITS1 + ITS2 and by a very strongly supported monophyletic clade (99–100) across all reconstruction methods in CytB + 16S. Bayesian analysis of CytB + 16S suggested with moderate support (74) that it may be sister to *V. microsphaera*. However, the inclusion of *V.*

substriata in the *Vertigo genesii* group is much more poorly supported (15–24 in NJ, ME & ML; 79 in Bayesian).

Conchology

Vertigo substriata is most similar within the subgenus to *V. inserta* and some shell forms of *V. nitidula* and *V. arthuri* that possess strong striae and six apertural lamellae: It differs from these in its ovate shape. It is also close to *V. microsphaera*, from which it differs in its strong apertural crest and angular lamella, and lack of a sinulus.

Ecology

Largely limited to humid forest and wetland habitats.

Biogeography

Western Eurasia – British Isles and Scandinavia east to south-central Siberia.

VERTIGO S. STR. DISCUSSION

It is clear that additional taxonomic work is required to resolve several issues, including: How many species-level entities are present within ***V. chiricahuensis*** *s. lat.*? What is the correct taxonomic status for the Yakutian material here referred to ***V. genesioides***? These issues can only be addressed with DNA sequence and conchological data from individuals sourced from additional sites.

We suspect that the poor resolution of *V. genesii*, ***V. genesioides***, *V. geyeri* and *V. oughtoni* in CytB + 16S in combination with frequent occurrence of ITS1 + ITS2 sequence atypical for ***V. genesioides*** indicates that these species have relatively recently diverged, with their genetics having not yet become stabilized.

The existence of deep but consistent variability within ITS1 + ITS2 copies (i.e., the “normal” and “divergent” clades) begs an explanation. We note that topology in the divergent clade is similar to that of the normal clade, but with longer branch lengths. From this we hypothesize that both the normal and divergent clades have been subject to similar neutral evolutionary processes, but with the divergent clade being older. Although we cannot test this hypothesis using the current data, it seems possible that the divergent clade represents relict sequence dating to contiguous northern hemisphere temperate/semitropical forest of the mid-Tertiary.

Finally, transcontinental biogeographic ranges are common in *Vertigo s. str.* for both species (e.g., ***V. beringiana***, ***V. genesioides*** and *V. microsphaera*) and also within each of the four species groups. While extensive passive dispersal and long-term persistence appears to be the rule for much of the subgenus, this pattern is not universal, as indicated by the marked contrast of *V. arizonensis* group members which are all limited to geographic extents < 1,000 km. ***Vertigo chiricahuensis***, and *V.* cf. *utahensis* may in fact be local endemics. It is unclear whether these localized distributions are due to a higher degree of geographic isolation per unit distance or to more limited sampling of Maderan Sky Island forest habitats, especially in northern Mexico.

SUBGENUS ***BOREOVERTIGO***, n. subgen.

Analysis of the subgenus ***Boreovertigo*** is based on 81 specimens for CytB + 16S and 73 for ITS1 + ITS2. The CytB segment was 367 bases and the 16S segment 441–445 bases, with a total of 160 variable sites along the entire CytB + 16S construct. The analyzed ITS1 segment was 609–630 bases, the analyzed ITS2 segment was 673–675 bases, with a total of 97 variable sites along the entire ITS1 + ITS2 construct. Support values tended to be higher in CytB + 16S than ITS1 + ITS2, although high support (> 90) was achieved in Bayesian reconstructions for most species-level clades for both sets of data.

In combination with conchology and ecological preferences, these phylogenetic analyses establish 13 or 14 valid species-level and two subspecies-level entities within the subgenus (Tables 5, 6, Figs. 9, 10): *V. arctica*, *V. circumlabiata*, *V. coloradensis*, *V. columbiana*, *V. cristata*, *V. extima*, *V. hoppii*, *V. modesta*, *V. modesta castanea*, *V. modesta concinnula*, *V. parcedentata*, *V. pseudosubstriata*, *V. ronnebyensis*, *V. ultima* and possibly *V. ultimathule*. ***Vertigo pisewensis*** n. sp. is formally described below.

Mean within-species variability ranged in ITS1 + ITS2 from none in *V. extima*, *V. ultima* and *V. parcedentata* to 7.0 bases in *V. ultimathule*. In CytB + 16S observed within-species variability ranged from 1.0 (***V. pisewensis***) to 20.4 (*V. coloradensis*) bases. Mean pairwise variation between species ranged in ITS1 + ITS2 from 3 (*V. extima* vs. *V. ultima*) to

24.6 (*V. columbiana* vs. *V. ultimathule*) bases and in CytB + 16S from 4.1 (*V. ronnebyensis* vs. *V. ultimathule*) to 52.3 (*V. coloradensis* vs. *V. modesta concinnula*) bases (Table 5). The central Asian clade (consisting of *V. parcedentata* and *V. pseudosubstriata*) differed from the other taxa in the subgenus by 18.8–29.8 bases in ITS1 + ITS2 and 43.0–66.4 bases in CytB + 16S. The three *V. modesta* subspecies varied by 2.2–3.2 bases in ITS1 + ITS2 and 9.4–14.8 bases in CytB + 16S.

Groupings below the subgenus level are poorly defined within ***Boreovertigo***, being limited in ITS1 + ITS2 to the association between *V. parcedentata* and *V. pseudosubstriata* (support = 99–100), *V. arctica* and *V. columbiana* (47–100) and *V. modesta*, *V. extima*, and *V. ultima* (39–55). However, two additional groups are readily apparent based on conchology: The *V. modesta* group possess shells with a tendency to have weaker, blunter, and more irregular striae and often a shiny shell luster compared with the *V. ronnebyensis* group that have a tendency for strong and sharp striae covering the shell surface and often a dull luster. Bayesian CytB + 16S reconstruction provided high support (96–100) for these two groups, although with *V. cristata* and the British Columbia *V. coloradensis* representing a third highly supported (100) clade.

VERTIGO MODESTA GROUP

Vertigo (***Boreovertigo***) *arctica*
(Wallenberg, 1858)
Fig. 10 (third row)

Pupa arctica Wallenberg, 1858: 32.

Type Locality: Kvikkjokk (“Quickjock”), Lule Lappmark, Sweden.

Phylogenetics

This species was strongly supported (94–100) across all reconstruction methods in both datasets. Additionally, all reconstruction methods in ITS1 + ITS2 suggested weak to strong (47–100) membership in a clade containing *Vertigo columbiana*.

Conchology

Within the subgenus this species is closest to *V*. cf. *hoppii* and forms of *V. modesta* with weakly developed lamellae, all of which have an ovate to ovate-conic shell, normal suture depth, silky-shiny luster, red-brown color, presence of weak parietal and columellar lamellae and lack of palatal lamellae. It differs from *V.* cf. *hoppii* in its larger size, sharper striae, and occasional presence of a weak crest and sinulus. It differs from *V. modesta* in its sharper and more numerous striae, more conical shape, weaker crest, shorter parietal lamella and the palatal lamellae being absent or very weakly developed. *Vertigo arctica* also resembles some ***V. genesioides*** that possess weak columellar and parietal lamellae. It differs, however, in its larger size and sharper striae.

Ecology

Willow/birch scrub, moist tundra and fens.

Biogeography

Europe – Iceland east through Scotland and Scandinavia south to the Tatra Mountains in Slovakia and the Austrian Alps.

Nomenclature

Greenland *V*. *hoppii* (e.g., ANSP 139922) populations could conceivably represent small shells of *V*. *arctica*. Should this be proven, *Vertigo hoppii* would have precedence over *V. arctica* (see below). Material suitable for DNA extraction is not currently available to evaluate this hypothesis.

Vertigo (***Boreovertigo***) *circumlabiata*
Schileyko, 1984: 208, fig. 129.
Fig. 10 (third row)

Type Locality: Kunashir Island, vicinities of Sernovodsk City (South Kuril Islands), Russia.

Phylogenetics

This species existed as a highly supported (99–100) clade across all reconstruction methods in CytB + 16S, and as a poorly supported clade (35–50) clade in NJ, ME, and ML reconstruction methods of ITS1 + ITS2. Bayesian reconstruction identified three non-coalescing short branches. All reconstruction methods in CytB + 16S included this species in a poorly to highly supported (58–100) clade with *V. modesta*, *V. extima*, and *V. ultima*.

Conchology

This species is closest in appearance to *V. modesta modesta*, with which it shares a large shell size (> 2.2 mm), blunt and irregular striae, shiny-silky luster, and presence of 4 apertural lamellae. It differs from that species in its more conic shape, shallower suture, and presence of a depression over the palatal lamellae.

Ecology

Occurs in a range of habitats from upland birch-alder forest to wooded seeps and open wetlands.

Biogeography

Boreal-Arctic Pacific Coast – central and eastern Hokkaidō north and east through the Kuril Islands to Anchorage, Alaska.

Nomenclature

The earliest name proposed for east-Asian relatives of *V. modesta* is *V. borealis* (Morelet, 1858). This was subsumed under *V. modesta* by Pilsbry (1948) on the false assumption that *V. modesta* was of Holarctic distribution. The *V. borealis* holotype no longer exists, with the only potential remaining type material being a claimed topotype lot from the Binney Collection (USNM 39134). This lot appears to not only be of mixed species but also shell condition is such that none can be unequivocally identified. Reanalysis of *Vertigo* collected in the 1990s from the Kuril Islands (Pearce et al., 2002) showed that *V. modesta* is absent from the archipelago, with *V. circumlabiata* representing the only large *Vertigo*. It seems probable that a revisit to the *V. borealis* type location on the Kamchatka Peninsula would also only document the presence of *V. circumlabiata*.

TABLE 5. Mean pairwise distances between *Vertigo* (***Boreovertigo***) species for the analyzed nDNA and mtDNA constructs, reported as nucleotide bases/construct. The lower half of the matrix represents distances in the ITS1 + ITS2 construct and the upper half (demarcated by *italic font*) represents distances in the CytB + 16S construct.

	modesta	*m. castanea*	*m. concinnula*	*circumlabiata*	*coloradensis*	*ultima*	*extima*	***pisewensis***	*ronnebyensis*	cf. *hoppii*	*columbiana*	*arctica*	*cristata*	*ultimathule*	*parcedentata*	*pseudosubstriata*
modesta		*10.0*	*14.8*	*36.3*	*46.5*	*12.5*	*24.3*	*44.8*	*37.2*	*40.4*	*41.2*	*39.0*	*48.3*	*36.1*	*60.7*	*64.8*
m. castanea	2.2		*9.4*	*36.5*	*48.0*	*16.2*	*21.1*	*46.1*	*38.3*	*41.8*	*41.3*	*43.9*	*47.5*	*37.4*	*59.0*	*62.9*
m. concinnula	3.0	3.2		*38.2*	*52.3*	*21.0*	*24.4*	*51.2*	*41.7*	*45.4*	*45.0*	*43.4*	*51.2*	*40.9*	*63.0*	*66.4*
circumlabiata	8.0	8.1	8.1		*45.7*	*36.4*	*38.1*	*43.5*	*37.0*	*40.7*	*40.4*	*34.0*	*46.8*	*35.3*	*52.8*	*61.9*
coloradensis	8.8	9.0	8.5	4.8		*44.3*	*43.5*	*13.3*	*24.4*	*27.9*	*40.3*	*42.1*	*31.5*	*22.6*	*51.0*	*51.7*
ultima	9.0	9.2	8.0	9.0	6.8		*19.5*	*43.2*	*36.4*	*39.1*	*42.3*	*38.8*	*47.3*	*35.3*	*59.3*	*63.3*
extima	10.0	10.2	9.0	9.0	6.8	3.0		*42.0*	*36.3*	*38.6*	*43.3*	*43.5*	*47.1*	*35.1*	*55.5*	*58.7*
pisewensis	10.5	10.7	10.2	6.5	4.5	8.5	8.5		*21.7*	*24.8*	*40.1*	*41.8*	*30.8*	*20.0*	*49.0*	*51.2*
ronnebyensis	10.6	10.9	10.5	6.7	5.4	9.7	9.7	6.6		*10.1*	*31.3*	*35.6*	*27.6*	*4.1*	*45.2*	*47.9*
cf. *hoppii*	11.3	11.5	11.3	7.3	7.1	11.3	11.3	8.8	8.8		*34.1*	*36.9*	*31.1*	*9.3*	*48.0*	*52.0*
columbiana	12.9	13.1	13.0	12.9	11.7	13.9	14.9	13.4	13.5	15.2		*32.5*	*39.3*	*30.4*	*52.0*	*55.8*
arctica	14.3	14.5	14.0	10.3	8.7	12.8	12.8	10.8	10.7	12.6	9.4		*42.6*	*33.8*	*49.8*	*56.4*
cristata	15.0	15.2	14.9	11.0	9.4	14.0	14.0	9.5	11.6	12.7	17.9	15.3		*25.5*	*52.6*	*56.3*
ultimathule	22.5	22.7	22.5	19.5	17.3	22.5	22.5	19.0	19.4	20.5	24.6	19.8	23.5		*43.0*	*45.7*
parcedentata	24.0	24.0	24.0	19.8	18.8	24.0	24.0	21.5	21.1	22.7	22.1	19.3	26.0	26.5		*11.9*
pseudosubstriata	27.3	27.3	27.3	23.1	21.9	27.3	27.3	24.8	24.4	26.0	25.5	22.6	29.3	29.8	3.3	

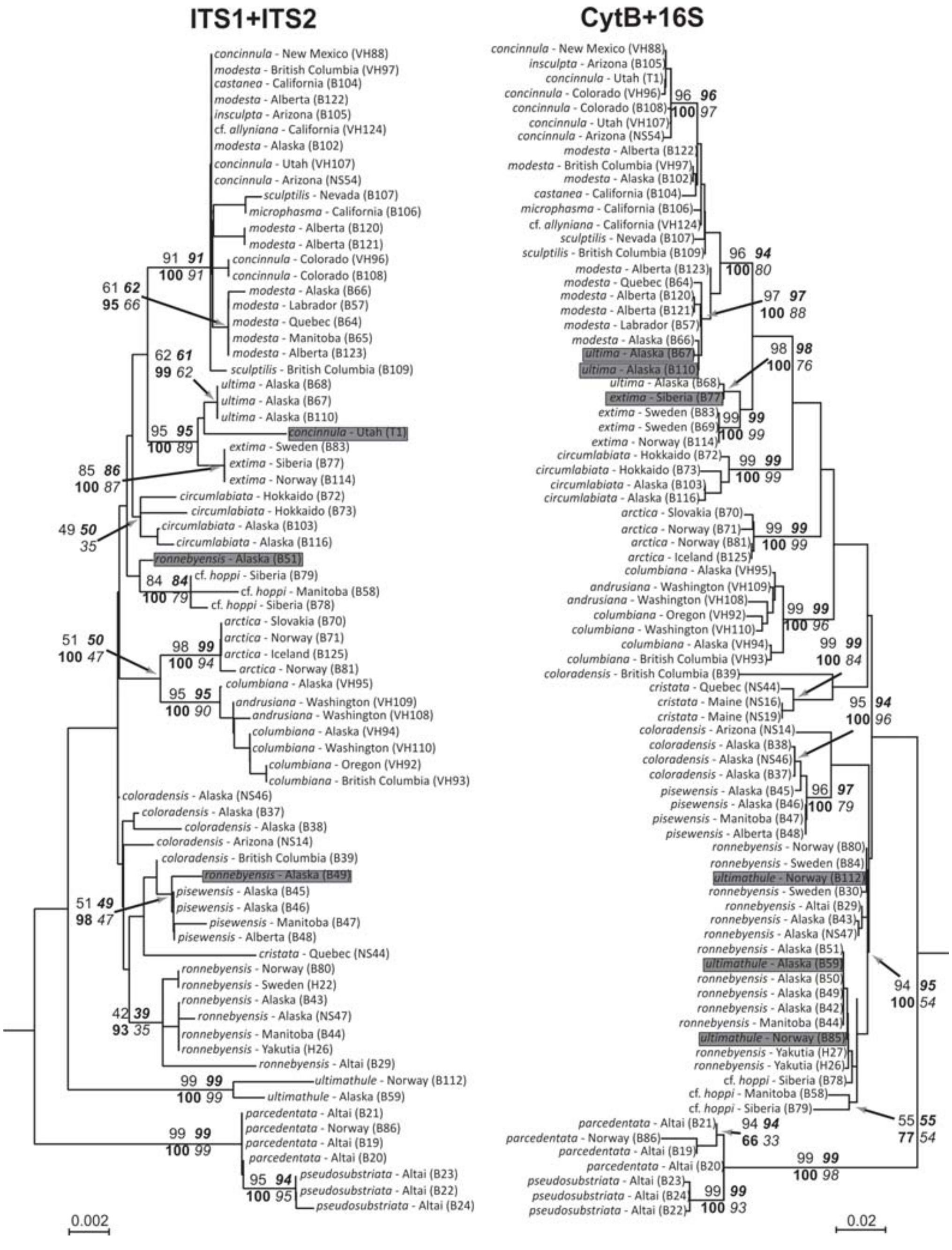


FIG. 9. Maximum-likelihood phylogenetic tree reconstructions in *Vertigo* (***Boreovertigo***) based on separate analyses of concatenated ITS1 + ITS2 and CytB + 16S data. Nodes with strong to moderate support have been labeled by four values: The upper left (normal font) is for Neighbor Joining. The upper right (***bold italic font***) is for Minimum Evolution. The lower left (bold font) is for Bayesian. The lower right (*italic font*) is for Maximum Likelihood. A grey box demarcates specimens that show incongruence in topologic location between the ITS1 + ITS2 and CytB + 16S trees, and likely represent examples of genetic introgression or incomplete sorting.

If true, *V. borealis* would have nomenclatural precedence. However, until such topotype DNA sequence is available we maintain the *status quo* and use *V. circumlabiata*.

Vertigo (***Boreovertigo***) *columbiana*

Sterki, 1892: 5

Fig. 10 (second row)

Type Locality: Vancouver Island, British Columbia, Canada.

Synonym: *Vertigo andrusiana* Pilsbry, 1899: 315, fig. 3; type locality: Douglas County, Oregon, U.S.A.

Phylogenetics

This species was highly supported (90–100) across all reconstruction methods in both datasets. Individuals with shells appearing identical to the *V. andrusiana* holotype (ANSP 76380) and material illustrated in Pilsbry (1948: fig. 517: 9–11) occurred within the same highly supported ITS1 + ITS2 and CytB + 16S clades as the rest of the species, and did not cluster with each other. Thus, *V. andrusiana* simply represents the wet woodland ecophenotype of *V. columbiana*. In ITS1 + ITS2 all methods placed *V. columbiana* in a moderately to highly supported (47–100) clade containing *V. arctica*. This relationship was not evident in CytB + 16S.

Conchology

By possessing an ovate-cylindrical shell this species is perhaps most similar in the subgenus to ***V. pisewensis*** and other species in the *V. ronnebyensis* group. Its shell surface differs from all these in its scattered blunt or obsolete striae, more reflective luster, and the flaring of the bottom aperture margin, which makes the aperture taller than wide. Shells are normally straw-colored, but the *andrusiana* form is more strongly red-brown in color with larger and fewer striae.

Ecology

Ranges across the moisture gradient in forest and rock outcrop habitats, with the *andrusiana* form being limited to swamp forest and willow-dominated wetlands.

Biogeography

North America – Largely confined to temperate rain forest in the Pacific Northwest from northern California to Anchorage, Alaska, and interior to southeastern British Columbia and northern Idaho.

Vertigo (***Boreovertigo***) *extima*

(Westerlund, 1877)

Fig. 10 (bottom row)

Pupa (*Vertigo*) *arctica* var. *extima* Westerlund, 1877: 99.

Type Locality: Baklanowskij, Yenisej region, Siberia, Russia.

Phylogenetics

This species existed as a well to highly supported (85–100) clade across all reconstruction methods in both datasets. The Siberian specimen was found to have CytB + 16S characteristic of *V. ultima*. Across all reconstruction methods *V. extima* and *V. ultima* belonged to the same moderately to highly supported clade in ITS1 + ITS2 (89–100) and CytB + 16S (87–100).

Conchology

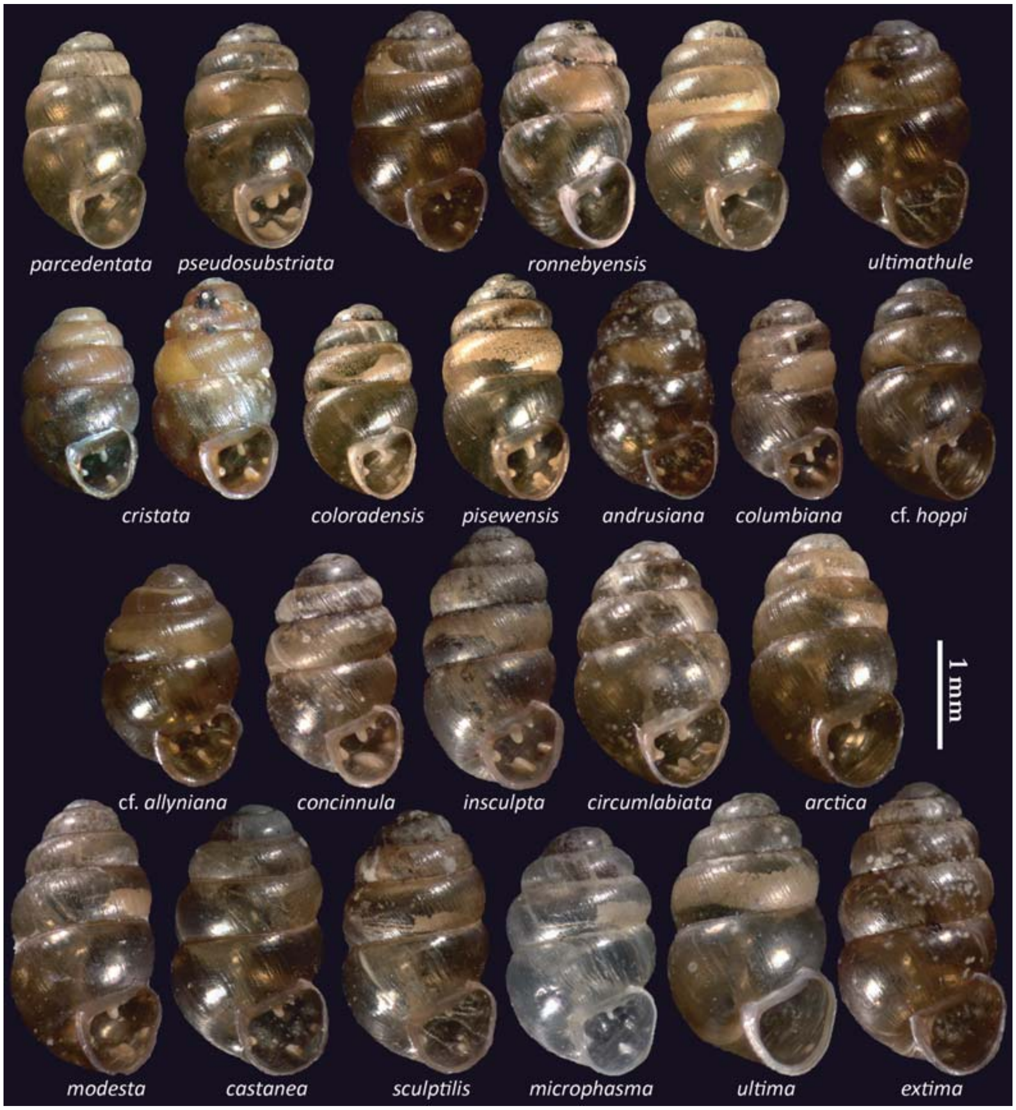
This species has a shell very similar to *V. ultima*, sharing its large size (up to 2.8 mm tall), absence of palatal lamellae and parietal and columellar lamellae absent or developed as small dot-like structures. It may be differentiated from *V. ultima* by its more cylindrical shape with a more shining surface luster and weaker apertural crest.

Ecology

A denizen of various willow-dominated wetlands in a tundra and northern taiga matrix.

Biogeography

Central and Western Eurasian Arctic – northern Scandinavia east to north-central Siberia. It is unknown if it is sympatric with *V. ultima* in eastern Siberia.



Vertigo (***Boreovertigo***) cf. *hoppii*
(Möller, 1842)
Fig. 10 (second row)

Pupa hoppii Möller, 1842: 4.

Type Locality: Greenland.

Phylogenetics

This species existed as a moderately to highly supported monophyletic clade (79–100) in ITS1 + ITS2 across all reconstruction methods. In CytB + 16S across all reconstruction methods two of the three analyzed specimens comprised a more poorly supported (54–77) clade with the third being a member of the *V. ronnebyensis* clade.

Conchology

Within the subgenus, this species is closest to *V. arctica*, *V. ronnebyensis* and *V. ultimathule* which also may lack palatal lamellae. It differs from *V. arctica* by its smaller size (< 2.2 mm), more conic shape, and blunter and less numerous striae. It differs from *V. ronnebyensis* in its more ovate shape and red-brown color, less

FIG. 10. Shells of *Vertigo* (***Boreovertigo***). Bracketed DNA specimen codes precede each entry. Top row (left to right): *Vertigo parcedentata*, [B19] Camp Zhuma-ly 2, Altai, Russia (49.5211°N, 88.0164°E). *Vertigo pseudosubstriata*, [B23] Seminski Pass, Altai, Russia (50.9855°N, 85.6817°E). *Vertigo ronnebyensis*, [B80] Signaldalen, Storfjord, Norway (69.1911°N, 19.9873°E); [B29] Camp Ilbegem 2, Altai, Russia (49.6281°N, 87.6574°E); [B44] Churchill, Manitoba, Canada (58.7709°N, 94.1640°W). *Vertigo ultimathule*, [B112] Basecakka, Finnmark, Norway (69.6612°N, 25.8886°E). Second row (left to right): *Vertigo cristata*, [NS17] Sugar Camp Bog, Wisconsin, U.S.A. (45.8499°N, 89.2958°W); [NS44] Sunny Mountain, Québec, Canada (55.0647°N, 67.2348°W). *Vertigo coloradensis*, [B39] Duncan Lake, British Columbia, Canada (50.6280°N, 117.0356°W). ***Vertigo pisewensis***, [B47] Pisew Falls Park, Manitoba, Canada (55.1982°N, 98.3918°W). *Vertigo columbiana* form *andrusiana*, [VH108] Ocean Shores, Washington, U.S.A. (47.0167°N, 124.1656°W). *Vertigo columbiana* form *columbiana*, [VH92] Manhattan Beach Park, Oregon, U.S.A. (45.6413°N, 123.9410°W). *Vertigo* cf. *hoppii*, [B58] Churchill, Manitoba, Canada (58.7333°N, 93.8069°W). Third row (left to right): *Vertigo* cf. *allyniana*, [VH124] Little Pothole Lake, California, U.S.A. (36.7693°N, 118.3518°W). *Vertigo concinnula*, [VH96] Tincup, Colorado, U.S.A. (38.7171°N, 106.4987°W). *Vertigo modesta* form *insculpta*, [B105] Mt. Lemmon, Arizona, U.S.A. (32.4413°N, 110.7848°W). *Vertigo circumlabiata*, [B73] Shibetsu Pass, Hokkaidō, Japan (43.7527°N, 144.8426°E). *Vertigo arctica*, [B71] Kongsvall, Norway (62.3005°N, 9.6063°E). Bottom row (left to right): *Vertigo modesta*, [B64] La Grande Pointe, Québec, Canada (50.2017°N, 63.4013°W). *Vertigo modesta castanea*, [B104] Luther Pass, California, U.S.A. (38.7900°N, 120.0093°W). *Vertigo modesta castanea* form *sculptilis*, [B107] Bear Creek Summit, Nevada, U.S.A. (41.7903°N, 115.4575°W). *Vertigo modesta castanea* form *microphasma*, [B106] Osita Camp, California, U.S.A. (34.2240°N, 116.9251°W). *Vertigo ultima*, [B68] Anchorage, Alaska, U.S.A. (61.1997°N, 149.9667°W). *Vertigo extima*, [B114] Basecakka, Finnmark, Norway (69.6612°N, 25.8886°E).

←

numerous and blunter striae, weaker parietal lamellae and shinier luster. It differs from *V. ultimathule* in its more ovate shape, red-brown color, blunt striae and shinier luster. It also resembles some ***V. genesioides*** (in *Vertigo s. str.*) that possess a weakly developed parietal lamella, but differs in its more ovate shell with a shallower suture. Even given these trends, demarcation based upon shell features alone may not be possible and DNA sequence data may be required to confirm identity.

Ecology

Appears restricted to acid, *Sphagnum*-dominated tundra peatlands.

Biogeography

Asian and North American Arctic – material confirmed through DNA analysis ranges from the southern shore of Hudson's Bay in Manitoba west to north-central Siberia.

Nomenclature

The *V. hoppii* from Greenland that we have critically observed (ANSP 139922) appear largely identical to the Manitoba and Siberian material. We have thus provisionally assigned this genetic race to *V. hoppii*. However, it is also possible that the Greenland material represents small *V. arctica*. If this is the case, *V. hoppii* would have precedence over *V. arctica* as the name for the European species and the Manitoba-Siberia material would require a new name.

Vertigo (***Boreovertigo***) *modesta*

(Say, 1824)

Fig. 10 (bottom row)

Pupa modesta Say, 1824: 259, pl. 15, fig. 5.

Type Locality: Northwest Territory [of the U.S.A.], "somewhere near or west of the western end of Lake Superior" (Pilsbry, 1919).

Phylogenetics

This species existed as a moderately to highly supported clade across all reconstruction methods in ITS1 + ITS2 (91–100) and CytB + 16S (80–100). Little partitioning is present within ITS1 + ITS2, although typical tundra/taiga *V. modesta* forms a moderately to highly supported subclade (61–95) across all four methods. Stronger subdivision was present in CytB + 16S with typical *V. modesta* forming a moderately to highly supported clade (88–100) distinct from its two other subspecies across all reconstruction methods. Two specimens placed in this clade had ITS1 + ITS2 and shells typical of *V. ultima*.

Conchology

The typical form of this species is distinguished from others in the subgenus by its large (2.3–2.7 mm tall) shell with scattered, blunt and irregular striae, a blunt apertural crest, and (typically) 4–5 apertural lamellae. It is most similar to the large morph of *V. cristata*, but differs in its slightly larger shell and less distinct and more irregular striae. Most *V. modesta* populations have shells with two strong palatal lamellae but forms lacking one or both palatals have been seen in Labrador and Alberta. Typical *V. modesta* differs from *V. modesta castanea* by its more tapered apex and often stronger palatal lamellae and from *V. modesta concinnula* by its scattered, blunt and irregular striae and shiny luster.

Ecology

Typical *V. modesta* is characteristic of tundra/taiga wetlands and seeps. It reaches its greatest population densities in areas supporting dense willow growth.

Biogeography

North America – Newfoundland, Labrador, and Baffin Island west to interior Alaska and south to northeastern Minnesota, northern Michigan, and southern Québec.

Vertigo (***Boreovertigo***) *modesta castanea*
Pilsbry & Vanatta, 1900: 602
Fig. 10 (bottom row)

Type Locality: Fish Camp, Fresno County, California, U.S.A.

Synonyms: *V. allyniana* Berry, 1919: 376, type locality: Donner Lake, California, U.S.A.; *V. modesta microphasma* Berry, 1919: 374, type locality: cienaga near Bluff Lake, San Bernardino Mountains, California, U.S.A., 7,550 feet altitude; *V. modesta sculptilis* Pilsbry, 1934: 100, pl. 24, figs. 2–4, type locality: 2–10 miles up Rock Creek NE of Garrison, Montana, U.S.A.

Phylogenetics

While not differentiated in ITS1 + ITS2, this subspecies was represented by a moderately to highly supported (71–96) clade across all reconstruction methods in CytB + 16S.

Conchology

This subspecies differs from typical *V. modesta* in its tendency to have a more domed apex and poorly developed apertural lamellae. The form *allyniana* represents smaller shells with more strongly developed apertural lamellae. The form *microphasma* represents albinistic individuals. The form *sculptilis* tends to have sharper and more regular striae on the initial whorls.

Ecology

High elevation wetlands, seeps, fens and riparian forests.

Biogeography

North America – San Bernardino and Sierra Nevada ranges in California east to northern Utah and southeastern British Columbia.

Nomenclature

The earliest name applied to western North American mountain *V. modesta* populations was *V. corpulenta* (Morse, 1865), which was subsequently relegated to a *V. modesta* subspecies (Pilsbry 1948). Unfortunately, this taxon is so poorly defined (see above) that we have been unable to locate any extant populations. If DNA sequence should indicate that *V. m. castanea* and *V. m. corpulenta* are the same, *corpulenta* would have precedence. We were unable to locate *V. allyniana* from its type location at Donner Lake, but did find material 300 km to the southeast. Nevertheless, these shells are only provisionally referred to *V. allyniana* until topotype material can be analyzed.

Vertigo (***Boreovertigo***) *modesta concinnula*
Cockerell, 1897: 135
Fig. 10 (third row)

Type Locality: Animas Valley, Colorado and Timberline NE of Antelope Peak, Colorado, U.S.A.

Synonym: *Vertigo modesta insculpta* Pilsbry, 1919: 131, type locality: Mt. Lemon, Santa Catalina Mountains, Arizona, U.S.A.

Phylogenetics

This subspecies was represented by a strongly supported (96–100) clade across all reconstruction methods in CytB + 16S but not differentiated in ITS1 + ITS2. Topotype *Vertigo m. insculpta* was found to have CytB + 16S sequence characteristic of *V. m. concinnula*. One of the Utah specimens had divergent ITS1 + ITS2 distantly related to *V. ultima*. This specimen, however, expressed typical CytB + 16S sequence, shell features, and ecological preferences for *V. m. concinnula*.

Conchology

This subspecies is differentiated from typical *V. modesta* and *V. m. castanea* by its numerous sharp and strong striae, dull shell luster and massive apertural crest. *Vertigo m. insculpta* simply represents the upper end of shell size for the subspecies and does not even warrant shell form status. Some *V. m. concinnula* from high elevation, acid sites in Colorado and Utah possess degenerate palatal lamellae. Material from the Capitan, Sierra Blanco, and Sacramento ranges in southeastern New Mexico are distinguished by their smaller shell size, less prominent striae and frequent presence of a basal lamella. However, these populations were genetically indistinguishable from the rest of the subspecies.

Ecology

Mesic to dry upland high-elevation forest. Unlike the rest of *V. modesta* group, it is not strongly associated with seepage or wetland habitats.

Biogeography

North America – Southern Rocky Mountains in Arizona, Utah, Colorado, and New Mexico.

Vertigo (***Boreovertigo***) *ultima*
Pilsbry, 1919
Fig. 10 (bottom row)

Vertigo modesta ultima Pilsbry, 1919: 128, text fig. 4, 4a.

Type Locality: North shore of Norton Sound, Alaska, U.S.A.

Phylogenetics

This species was represented by a moderately to highly supported clade across all reconstruction methods in ITS1 + ITS2 (61–100) and CytB + 16S (76–100). Incomplete sorting or mitochondrial introgression was apparent, with a majority of analyzed specimens having CytB + 16S characteristic of *V. modesta*. Across all reconstruction methods *V. ultima* and *V. extima* were identified as belonging to the same highly supported clade (89–100) in ITS1 + ITS2 and CytB + 16S (87–100).

Conchology

This species is very similar to *V. extima* in possessing a very large shell (up to 2.8 mm tall), no palatal and absent to reduced parietal and columellar lamellae. It may be differentiated from *V. extima* by its more ovate shape, duller surface luster and stronger apertural crest.

Ecology

Tundra and taiga willow-sedge wetlands.

Biogeography

North America – Alaska. Empty shells similar to *V. ultima* have also been collected in Labrador (Nekola & Coles, 2010) but in the absence of DNA sequence data it is not possible to empirically verify that these represent *V. ultima* rather than large *V. modesta* with degenerate apertural lamellae.

VERTIGO RONNEBYENSIS GROUP

Analysis of species-level taxonomy and phylogenetics within this group was hampered by the presence of considerable insertion-deletion variation between ITS1 copies, most commonly (but not solely) the number of A repeats 59–69 bases downstream of the 18srDNA primer and the number of C repeats 62–70 bases upstream of the LSU1rc primer. Thus, intervening sequence calls were frequently ambiguous or undecipherable. In consequence, the reliability of ITS1 + ITS2 data is poor for *V. coloradensis*, *V. cristata*, *V. ronnebyensis* and *V. ultimathule*; ***Vertigo pisewensis*** did not have this problem, and its sequence was unambiguous. While ITS2 did not exhibit these problems, its level of variation was too low to identify species-level groups. Of necessity, phylogeny in this group is thus primarily based on CytB + 16S data.

Vertigo (***Boreovertigo***) *coloradensis*
(Cockerell, 1891)
Figs. 7O, 10 (second row), 11K–M

Pupa coloradensis Cockerell, 1891: 100.

Type Locality: near Swift Creek, Custer County, Colorado, U.S.A.

Phylogenetics

The three Alaskan individuals were defined by a highly supported (94–100) clade across all reconstruction methods in CytB + 16S. The Arizona individual and ***V. pisewensis*** were associated with this material via a moderately to highly supported (85–100) clade across all reconstruction methods. The British Columbia individual moderately to highly clustered (81–100) across all reconstruction methods with *V. cristata*. In ITS1 + ITS2 the limited available data suggested that this species was represented by 4–5 separate, non-coalescing branches.

Conchology

Vertigo coloradensis and *V. cristata* have in common a narrowly defined suite of shell features consisting of a cylindrical-ovate shell with numerous sharp, regular striae, a dull shell surface, modest to strong crest, and four apertural lamellae. *Vertigo coloradensis* differs by possessing a slightly more cylindrical shell and a blunter crest, but distinguishing these two species based on shells alone is too unreliable to be practicable.

Ecology

Upland taiga and high elevation forests.

Biogeography

North America – Alaska south along the Rocky Mountains to southeastern Arizona. It likely ranges east in the Canadian taiga but due to lack of corroborating DNA sequence data, this premise cannot currently be tested.

Vertigo (***Boreovertigo***) *cristata*
Sterki, in Pilsbry, 1919
Figs. 10 (second row), 11N, O

Vertigo gouldii cristata Sterki, in Pilsbry, 1919: 100, pl. 12, figs. 4, 5.

Type Locality: Québec, Canada.

Phylogenetics

This species existed as a moderately to highly supported (84–100) clade across all reconstruction methods in CytB + 16S. Only a single ITS1 sequence of poor quality has been recovered. The ITS1 + ITS2 construct from this individual was a long-branch member of the same poorly to moderately supported (43–80) clade identified across all reconstruction methods that also contained ***V. pisewensis*** and the British Columbia *V. coloradensis*.

Conchology

Almost indistinguishable from *V. coloradensis* (see above) although perhaps possessing a slightly more ovate shell and a sharper crest. *Vertigo cristata* exhibits a bimodal shell size distribution, one form ranging from 1.7–1.9 mm and the other from 2.0–2.2 mm tall. No DNA sequence differences between these have been noted (Nekola et al., 2009). The larger morph has been commonly confused with *V. modesta*, and can be most easily distinguished by its slightly smaller size and sharper and more regular striae.

Ecology

While occurring in a wide range of taiga habitats, it is most common in acid upland conifer forest and heath scrub of *Sphagnum*-dominated peatlands.

Biogeography

North America – Newfoundland (where it was called *V. alpestris* by Brooks & Brooks, 1940) and Labrador west though northern New England and the Great Lakes region to northwestern Minnesota and western Ontario. Due to lack of DNA sequence data, it is not known how far west this species extends into the central Canadian taiga or whether its range overlaps with that of *V. coloradensis*.

Vertigo* (*Boreovertigo*) *pisewensis, n. sp.
Figs. 10 (second row), 11A–J, Table 6

GenBank Accessions: KY217266-9; KY216865-8; KY217663-6; KY216518-21.

Diagnosis

Shell small, columnar-ovate, most similar to *V. cristata*, *V. coloradensis*, and *V. modesta* of the North American taiga, differing by its upper palatal lamella which diverges from (is not parallel with) and is inserted more closely to the apertural margin than the lower palatal lamella, making long face of the upper palatal visible in apertural view; the radial striae are also less

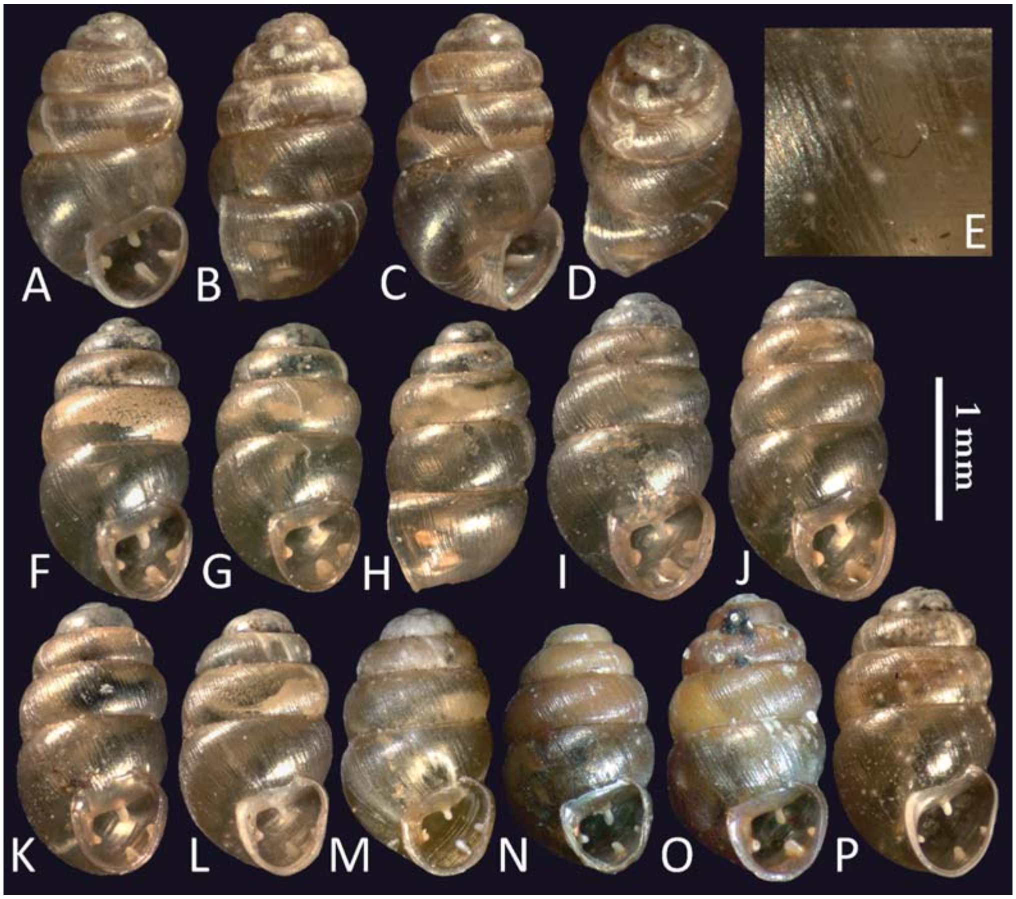


FIG. 11. ***Vertigo pisewensis*** n. sp. A–E: Holotype, ANSP 467360, Rich, wooded north-facing igneous bedrock outcrops, Pisew Falls Provincial Park, Manitoba, Canada (55.1982°N, 98.3918°W); F: [B47] Rich, wooded north-facing igneous bedrock outcrops, Pisew Falls Provincial Park, Manitoba, Canada (55.1982°N, 98.3918°W); G, H: [B46] Xeric upland aspen-spruce forest, Clearwater State Recreation Area, Southeast Fairbanks Census Area, Alaska, U.S.A. (64.0530°N, 145.4332°W); I: [B45] Mesic spruce-birch forest, Coldfoot, Yukon-Koyukuk Census Area, Alaska, U.S.A. (67.2744°N, 150.1688°W); J: [B48] Aspen-spruce woodland, Highway 40 at Rabbit Hill Road west of Cochrane, Big Horn County, Alberta, Canada (51.2642°N, 114.7326°W); *Vertigo coloradensis.* K: [B38] Xeric upland aspen-spruce forest, Clearwater State Recreation Area, Southeast Fairbanks Census Area, Alaska, U.S.A. (64.0530°N, 145.4332°W); L: [B39] Duncan Lake, British Columbia, Canada (50.6280°N, 117.0356°W); M: [NS14] Mt. Lemmon, Arizona, U.S.A. (32.4413°N, 110.7848°W); *Vertigo cristata.* N: [NS17] Sugar Camp Bog, Wisconsin, U.S.A. (45.8499°N, 89.2958°W); O: [NS44] Sunny Mountain, Québec, Canada (55.0647°N, 67.2348°W); P: *Vertigo ronnebyensis* [B30] Kiruna, Sweden (67.8660°N, 20.2478°E). When applicable, bracketed DNA specimen codes precede each entry.

sharp and distinct compared to *V. cristata* and *V. coloradensis*, giving the shell a more reflective surface.

Description

Shell: 1.9–2.3 mm tall x 1.0–1.2 mm wide (Holotype 2.1 x 1.1 mm), translucent, yellowish-brown; approximately 5 whorls; ovoid-columnar; suture of average depth (Fig. 11A–D, F–H); shiny luster with irregular, and relatively indistinct radial striae, especially on the body whorl (Fig. 11E); aperture $^1/_4$–$^1/_3$ of shell height, being as wide to wider than tall (Fig. 11A, F–H), in profile ascending onto body whorl (Fig. 11B); umbilicus closed by preceding whorls (Fig. 11C); peristome interrupted by body whorl, apertural lip only indistinctly flared (Fig. 11A–D, F–H); a typically strong crest is present behind the apertural margin (Fig. 11B, D); four to five apertural lamellae, including a peg-shaped columellar, a blade-shaped parietal, two blade-shaped palatals, and occasionally a weak angular or basal (Fig. 11A, F–H), no depressions are present on the shell surface over the palatal wall (Fig. 11D). In some populations, the upper palatal lamella extends to the margin of the lip where it forms a callus.

Holotype (Fig. 11A–E): ANSP 467360, Pisew Falls Provincial Park, Manitoba, Canada; Rich, wooded north-facing igneous bedrock outcrops; 55°11'56''N, 98°24'4''W; August 17, 2003.

Paratypes: ANSP 467361, collected with holotype: 10 shells; NMW.Z.2005.011.02262, as above: ~300 shells. ANSP 467362, highway 40 at Rabbit Hill Road, west of Cochrane, Big Horn County, Alberta, Canada; aspen-spruce woodland; 51°15'51''N, 114°43'57''W; August 25, 2011: 5 shells; NMW.Z.2015.009.00020, as above: ~45 shells. ANSP 467363, Clearwater State Recreation Area, Southeast Fairbanks Census Area, Alaska, U.S.A.; Xeric upland aspen-spruce forest; 64°03'10''N, 145°25'29''W; August 11, 2007: 10 shells. ANSP 467364, Coldfoot, Yukon-Koyukuk Census Area, Alaska, U.S.A.; mesic spruce-birch forest; 67°16'27''N, 150°10'07''W; August 7, 2007: 10 shells.

Other, Non-Type Material Examined: NMW.Z.2005.011.01515, 01617, 01741, 01763, 01810, 02279, 02338: ~700 shells from Alaska; NMW.Z.2015.009.00021-00032: approximately 1000 shells from Alberta and Manitoba, Canada and Alaska, U.S.A.; 15 lots representing 1562 individuals from Manitoba, Canada and Alaska, U.S.A. in the Nekola collection.

Etymology

The specific epithet refers to the initial site of discovery and type location at Pisew Falls Provincial Park in central Manitoba.

Phylogenetics

This species was defined by a poorly to highly supported clade across all reconstructions in both CytB + 16S (69–100) and ITS1 + ITS2 (47–98). In CytB + 16S, the Alaskan *V. coloradensis* formed a highly supported subclade within this group. One Alaskan *V. ronnebyensis* with typical shells and CytB + 16S possessed ITS1 + ITS2 of ***V. pisewensis***.

Comparisons with Other Species

Shells are most closely reminiscent of *V. cristata* and *V. coloradensis*, but differ in the strongly angled upper palatal lamella that is inserted forward of the lower palatal, the less distinct radial striae on the body whorl, and the more yellowish shell color. The position of the upper palatal also demarcates this species from *V. modesta*, which is also differentiated by its larger and darker shell with less distinct radial striae and preference for wetland habitats vs. the mesic to dry upland sites favored by ***V. pisewensis***.

Geographic Distribution

North America – Central Manitoba to northern Alaska and the foothills of the Canadian Rockies in southern Alberta.

Ecology

Occurs in wet-mesic to dry upland taiga, becoming most abundant in dry-mesic or xeric sites dominated by white spruce, birch and aspen.

Vertigo (***Boreovertigo***) *ronnebyensis*
(Westerlund, 1871)
Figs. 10 (top row), 11P

Pupa ronnebyensis Westerlund, 1871: 94.

Type Locality: Persborg, near Ronneby, Blekinge, Sweden.

Phylogenetics

This species was defined by a poorly to strongly supported (54–100) clade across all reconstruction methods in CytB + 16S. Although the node for this clade was difficult to distinguish in the illustrated ML reconstruction (Fig. 9), it is more readily apparent in the NJ, ME and Bayesian trees. It was also defined by a less-well supported (35–93) clade across all reconstruction methods in ITS1 + ITS2. Two of the analyzed Alaskan specimens possessed divergent ITS1 + ITS2 sequence, falling into the *V.* cf. *hoppii* and ***V. pisewensis*** clades, respectively, even though these individuals all possessed typical *V. ronnebyensis* shells and CytB + 16S sequence.

Conchology

This species shares with *V. coloradensis*, *V. cristata* and *V. ultimathule* a shell < 2.4 mm tall with sharp striae. It differs from *V. coloradensis* and *V. cristata* in its much weaker (often absent) crest and more reflective shell luster. It differs from *V. ultimathule* by possessing more numerous and regular striae and a more ovate shell. While most illustrations of *V. ronnebyensis* show two strong palatal lamellae (e.g., Kerney & Cameron, 1979), fully $^2/_3$ of observed Scandinavian shells lacked an upper palatal. Shells from the Altai east to Hudson's Bay never possess palatal lamellae.

Ecology

Acid upland taiga, with *Vaccinium* leaf litter being especially favored. In North America, it is also frequent in base-rich forest and extends into tundra.

Biogeography

Boreal Eurasia to North America – Scandinavia east through the Czech Republic to the Altai in southern Siberia, Yakutia in eastern Siberia, interior Alaska, and the south shore of Hudson's Bay at Churchill, Manitoba.

Vertigo (***Boreovertigo***) *ultimathule*

Proschwitz, 2007: 73
Fig. 10 (top row)

Type Locality: 1.2 km SSE of Pältsa cottage, Gobmevarri, Mount Pältsan, Karesuando, Torne Lappmark, Sweden.

Phylogenetics

This taxon is questionably distinct. All three analyzed specimens had CytB + 16S falling within the highly supported clade defining *V. ronnebyensis*. One specimen had ITS2 identical to *V. ronnebyensis* (its ITS1 sequence was not readable); the others possessed distinct ITS1 + ITS2 representing a highly supported (99–100) clade across all reconstruction methods. It is for this reason that we have provisionally considered this a species-level taxon. While this situation is reminiscent of the taxonomically uninformative divergent clade seen in *Vertigo s. str.*, we are unwilling to designate *V. ultimathule* as a shell form within *V. ronnebyensis* until sequence has been analyzed from a larger sample of individuals across its range.

Conchology

If valid, this species is very similar to *V. ronnebyensis*, with which it shares a sharply striate shell that often lacks palatal lamellae. According to Proschwitz (2007), *V. ultimathule* is differentiated by a more cylindrical shell with less numerous and regular striae, a glossier luster, a lighter brown color, and absence of a columellar lamella.

Ecology

In northern Scandinavia this putative species is limited to somewhat acidic birch and willow forest. In Alaska it was found in acidic upland tundra.

Biogeography

If a valid species-level taxon, genetically identified populations are known from northern Scandinavia to northern Alaska.

VERTIGO PARCEDENTATA GROUP

Vertigo (***Boreovertigo***) *parcedentata*

(Braun, 1847)
Fig. 10 (top row)

Pupa parcedentata Braun, 1847: 51.

Type Locality: Hessen, near Wiesbaden, Germany (fossil).

Phylogenetics

Both this species and *V. pseudosubstriata* occurred in a highly supported (98–100) clade across all reconstruction methods in both datasets. In ITS1 + ITS2, *V. parcedentata* represented the basal member of the clade, with *V. pseudosubstriata* being a distinct subclade of high support (94–100). In CytB + 16S, *V. parcedentata* existed as a poorly to highly supported (33–94) clade across all reconstruction methods.

TABLE 6. Conchological traits for *Vertigo* (***Boreovertigo***) members.

Species	Height (mm)	Width (mm)	Shell Shape	Suture Depth	Striae	Luster	Color	Crest	Callus	Sinulus	Angular	Parietal	Columellar	Basal	Palatal	Palatal Depression	Other
arctica	2.2–2.7	1.3–1.4	Ovate – conic	Moderate to deep	Numerous, sharp, irregular	Silky to shiny	Red-brown	None to weak	None	None to weak	None	Short	Peg	None	Absent to 1–2 weak	None	
circumlabiata	2.2–2.6	1.3–1.5	Conic	Shallow	Scattered, blunt, irregular	Silky to shiny	Brown	Modest to strong	None	None to weak	None to weak	Long	Peg	None	2	Deep	
coloradensis	1.6–1.9	0.9–1.1	Cylindrical – ovate	Moderate to deep	Numerous, sharp, regular	Dull	Brown	Modest to strong	None	Weak to none	None	Long	Peg	None	2	Weak to modest	Palatals sub-parallel
columbiana	1.7–2.4	0.9–1.3	Ovate – cylindrical	Shallow	Absent to scattered, blunt, irregular	Shiny to glassy	Straw-yellow to red-brown	Weak to strong	None to weak	Weak to none	None to weak	Long	Peg	None to weak	2 long to short	Weak to modest	Flared aperture bottom
cristata	1.7–2.1	0.9–1.1	Ovate – cylindrical	Moderate	Numerous, sharp, regular	Dull	Brown	Modest to strong; sharp	None	Weak to none	None	Long	Peg	None	2	Weak to none	Palatals sub-parallel
extima	2.6–2.8	1.5-1.6	Ovate – cylindrical	Moderate	Sparse, blunt, irregular	Shiny to glassy	Brown	Weak	None	None to weak	None	None	None to peg	None	None	None	
cf. *hoppii*	1.9–2.2	1.0–1.2	Ovate	Moderate to deep	Scattered, blunt, irregular	Silky to shiny	Red brown	None	None	None	None	Short	Weak	None	None	None	
modesta	2.3–2.7	1.2–1.5	Ovate – cylindrical	Moderate	Scattered, blunt, irregular	Shiny to silky	Red brown	Modest, blunt	None	Weak to none	Weak to none	Long	Peg	None	0–2 short	None	

(continues)

(continued)

Species	Height (mm)	Width (mm)	Shell Shape	Suture Depth	Striae	Luster	Color	Crest	Callus	Sinulus	Angular	Parietal	Columellar	Basal	Palatal	Palatal Depression	Other
modesta castanea	2.0–2.8	1.3–1.6	Ovate – cylindrical	Moderate	Scattered, blunt to sharp, irregular	Shiny to silky	Red to yellow-brown	Modest, blunt	None	Weak to none	Weak to none	Long	Peg	None	0–2 short	None	
modesta concinnula	2.1–2.6	1.2–1.4	Cylindrical – ovate	Moderate	Numerous, sharp, irregular	Dull to silky	Red-brown	Strong to modest	None to weak	Weak to none	Strong	Long	Peg	None to modest	2 long	None to weak	
parcedentata	1.9–2.1	1.0–1.1	Cylindrical	Moderate	Scattered, blunt irregular	Silky to shiny	Red-brown	Weak to none	None	Weak to none	None	Short	Weak to none	None	1–2 short	None	
pisewensis	1.9–2.3	1.0–1.2	Cylindrical – ovate	Moderate	Numerous, blunt, irregular	Silky	Yellow-brown	Modest to strong	None to weak	None to weak	None to modest	Long	Peg	None to weak	2 long	None to weak	Upper palatal inserted less deeply and at angle to lower
pseudo-substriata	1.9–2.3	0.9–1.2	Ovate – cylindrical	Moderate	Sparse, blunt, irregular	Shiny	Brown	None to weak	None	Modest to strong	Strong	Long	Long	None	2 very long	Weak	
ronnebyensis	2.0–2.4	1.1–1.4	Ovate – cylindrical	Moderate	Numerous, sharp, regular	Silky to dull	Brown	Weak to none	None	Weak	None	Long	Peg	None	0–2 short	Weak to none	
ultima	2.4–2.8	1.5–1.6	Ovate – conic	Moderate	Scattered, sharp, irregular	Silky to shiny	Brown	Weak to modest	None	None to weak	None	None	None to peg/ plate	None	None	None	Aperture margin often thick
ultimathule	2.0–2.1	1.3–1.4	Cylindrical – ovate	Moderate	Sparse, sharp, irregular	Silky to shiny	Yellow-brown	None to weak	None	None to weak	None	None or one	None	None	None	None to weak	

Conchology

This species is most similar in ***Boreovertigo*** to *V. modesta*, with which it shares a mostly cylindrical shell with scattered, blunt and irregular striae, a silky-shiny luster, and often 2 palatal lamellae. It differs from that species in its more cylindrical shell, smaller size, weaker crest, shorter parietal lamella, and weaker columellar lamella. It is also similar to *V. oughtoni* in *Vertigo s. str.* but differs from that species in its less reflective shell luster and better developed crest.

Ecology

Willow scrub in arctic-alpine meadows, wetlands, seeps, and riparian forest.

Biogeography

Central Asia and Europe – Altai and Tien Shan mountains, with a disjunct occurrence in the Dovrefjell of Norway. As a Pleistocene fossil, it ranges from Ukraine to the Netherlands and southern Sweden.

Vertigo (***Boreovertigo***) *pseudosubstriata*
Ložek, 1954: 327
Fig. 10 (top row)

Type Locality: Dolni Věstonice near Dyje River, former Czechoslovakia (fossil).

Phylogenetics

This species existed as a highly supported (93–100) clade across all reconstruction methods in both datasets, and was part of a highly supported (98–100) clade containing *V. parcedentata*.

Conchology

This species appears most similar to races of *V. modesta* that possess an angular lamella, ovate-cylindrical red-brown shell, sparse, blunt and irregular striae and two palatal lamellae while lacking a basal lamella. It differs from these in its smaller size, more reflective luster, stronger sinulus and angular lamella, and much longer palatal lamellae. It also bears some resemblance to ***V. chytryi***, *V. inserta*, *V. hannai* and *V. substriata* in *Vertigo s. str.* However, it differs from all of these in its reflective shell surface and lack of a basal lamella.

Ecology

Occurs in subalpine wet meadows, seepages and riparian zones that typically support willow.

Biogeography

Central Asia – Altai, Tien Shan, Pamir and Himalayan mountains. It is also known as a Pleistocene fossil from central Europe.

BOREOVERTIGO DISCUSSION

There appears on average to be poorer genetic sorting between ***Boreovertigo*** species (especially in the *V. ronnebyensis* group) compared to *Vertigo s. str.*, with taxa not always being resolved into highly supported monophyletic clades (e.g., *V. coloradensis*) and with there being multiple cases of ITS1 + ITS2 and CytB + 16S incongruence. Some of this appears to be due to mitochondrial introgression or incomplete sorting (e.g., *V. extima* and *V. ultima*). ***Boreovertigo*** may thus consist of recently evolved races that have undergone considerable mixing due to repeated Pleistocene glaciations, placing their genetics into a state of flux.

Because of copy variability, the ITS1 region cannot resolve these issues even though amplicon cloning techniques could remove some ambiguity. Deducing phylogenetic relationships within the *V. ronnebyensis* group will thus necessitate development of additional nuclear genetic markers. Some of the more important topics to be addressed by such future analyses will be the actual number of supported species within the *V. ronnebyensis* group, whether *V. coloradensis* is monophyletic, and whether it and *V. cristata* are reproductively isolated in areas of potential range overlap in central Canada. Such data will also be required to also determine the actual status of *V. ultimathule*.

Transcontinental biogeographic ranges are again conspicuous for ***Boreovertigo***, ranging from individual species (*V. ronnebyensis*) to two of the three species-groups. Particularly striking is the sister-status of geographically widely separated species, such as *V. arctica* vs. *V. columbiana*, *V. extima* vs. *V. ultima*, and *V. cristata* vs. *V. coloradensis*, ***V. pisewensis*** and *V. ronnebyensis*.

SUBGENUS *VERTILLA*

Analyses of the subgenus *Vertilla* is based on 35 specimens for CytB + 16S and 32 for ITS1 + ITS2. The CytB segment was 367 bases and the 16S segment 441–447 bases, with a total of 229 variable sites along the entire CytB + 16S construct. The analyzed ITS1 segment was 595–613 bases, the analyzed ITS2 segment was 591–675 bases, with a total of 94 variable sites along the entire ITS1 + ITS2 construct.

In combination with conchology and ecological preferences, these analyses suggest ten valid species-level taxa within the subgenus (Tables 7, 8, Figs. 12, 13): *V. alabamensis*, *V. angustior*, *V. clappi*, *V. dedecora*, *V. hebardi*, *V. hinkleyi*, *V. malleata*, *V. marciae*, *V. oscariana* and *V. parvula.*

Mean within-species variability ranged in ITS1 + ITS2 from none in *V. hinkleyi* to 5.3 bases in *V. clappi*. In CytB + 16S, within-species variability ranged from 0 (*V. marciae*) to 39.7 bases (*V. dedecora*). Mean pairwise variation between species ranged in ITS1 + ITS2 from 3.3 (*V. parvula* vs. *V. oscariana*) to 33.0 (*V. malleata* vs. *V. marciae*) and in CytB + 16S from 10.6 (*V. alabamensis* vs. *V. hebardi*) to 88.8 (*V. hinkleyi* vs. *V. parvula*) bases (Table 7).

Two main groups below the subgenus level can be identified: (1) the *V. alabamensis* group is highly supported (99–100) across all four methods in ITS1 + ITS2 and CytB + 16S. We include *V. oscariana* and *V. parvula* because of their consistent linking with moderate support (73–78) in NJ / ME / ML in reconstructions of the ITS1 + ITS2 data, and (2) the *V. angustior* group, including all remaining species, is identified across all reconstruction methods in ITS1 + ITS2 with high support in Bayesian (100). While CytB + 16S did not provide resolution using NJ, ME, and ML, the Bayesian reconstruction identified a highly supported (100) clade consisting of these remaining species plus *V. oscariana* and *V. parvula*.

VERTIGO ALABAMENSIS GROUP

Vertigo (*Vertilla*) *alabamensis*
Clapp, 1915: 137, plate 6, fig. 6
Fig. 13 (top row)

Type Locality: Ravine near junction of North River with Black Warrior, Tuscaloosa County, Alabama, U.S.A.

Synonyms: *V. alabamensis conecuhensis* Clapp, 1915: 137, type locality: Evergreen, Conecuh County, Alabama, U.S.A.; *Vertigo conecuhensis* of Hubricht, 1985.

Phylogenetics

Vertigo alabamensis existed as a moderately to highly supported (62–94) clade across all reconstruction methods in ITS1 + ITS2 and CytB + 16S. Shells referable to *Vertigo conecuhensis* Clapp, 1915, are spread across the clade in all datasets and reconstruction methods. *Vertigo alabamensis* is a member of a highly supported clade (99–100 for all genes and reconstruction methods) containing *V. hebardi* and *V. marciae*.

Conchology

This species shares with a number of other *Vertilla* an upper palatal lamella with its long axis visible in apertural view. It differs from *V. hebardi* in its much larger size and stronger angular and basal lamellae, and from *V. clappi* and *V. hinkleyi* by its larger size, ovate shape and presence of a strong calcified ridge between the aperture margin and the lamellae. The shell form *conecuhensis* simply represents individuals that have matured at an earlier stage of growth, and occur throughout the range of the species, often mixed with typical shells.

Ecology

A strict acidophile limited to mesic pine woods and pine-wiregrass savanna. We have found it abundant in decaying pine needle accumulations caught on small shrubs and vines just off the ground. Populations are being systematically eliminated throughout its range by the overuse of fire management which removes this habitat.

Biogeography

North America – Southeastern coastal plain from North Carolina to Alabama. It appears absent from peninsular Florida.

Vertigo (*Vertilla*) *hebardi*
Vanatta, 1912: 445
Fig. 13 (top row)

Type Locality: Long Key, Florida, U.S.A.

Phylogenetics

This species was characterized by moderately to highly supported clades across all reconstruction methods in ITS1 + ITS2 (70–100) and CytB + 16S (78–98). It occurred as a member of the same highly supported (99–100) clade as *V. alabamensis* and *V. marciae* across all datasets and reconstruction methods.

Conchology

Within the subgenus, this species appears most similar to *V. marciae* by possessing a small shell (< 1.4 mm tall) with four principal apertural lamellae. It differs in its smaller and more ovate shell, sharper striae, weak angular lamella, and upper palatal lamella with its long axis visible in apertural view. It differs from *V. alabamensis* in its smaller shell, weaker lamellae, and absence of a basal lamella.

Ecology

Deep, humid leaf litter accumulations in subtropical woodland. It is absent from microsites immediately adjacent to exposed limestone rock.

Biogeography

North America – Currently known only from the Florida Keys, but likely ranges into the Bahamas and Cuba.

Vertigo (*Vertilla*) *marciae*

Nekola & Rosenberg, 2013: 109, figs. 1–6
Fig. 13 (top row)

Type Locality: John Crow Peak, Blue Mountains, St. Andrew Parish, Jamaica.

Phylogenetics

Because sequence from only a single individual was recovered in ITS1 + ITS2, there was no opportunity to observe a species level clade. However, its defining branch was separated by 9–12 bases from *V. alabamensis* and *V. hebardi*. In CytB + 16S, this species existed as a highly supported clade (100) across all reconstruction methods. It was a member of the same highly supported (99–100) clade as *V. alabamensis* and *V. hebardi* across all reconstruction methods and datasets.

Conchology

Within the subgenus this species most resembles *V. hebardi*, *V. oscariana* and *V.*

TABLE 7. Mean pairwise distances between *Vertigo* (*Vertilla*) species for the analyzed nDNA and mtDNA constructs, reported as nucleotide bases/construct. The lower half of the matrix represents distances in the ITS1 + ITS2 construct and the upper half (demarcated by *italic font*) represents distances in the CytB + 16S construct.

	hebardi	*alabamensis*	*marciae*	*dedecora*	*oscariana*	*parvula*	*hinkleyi*	*malleata*	*angustior*	*clappi*
hebardi		*10.6*	*42.7*	*69.0*	*77.7*	*81.0*	*75.7*	*82.2*	*77.9*	*81.5*
alabamensis	5.2		*44.3*	*73.8*	*79.7*	*82.7*	*78.0*	*85.8*	*80.3*	*83.5*
marciae	12.0	9.2		*70.7*	*73.0*	*77.3*	*77.0*	*80.3*	*76.3*	*76.0*
dedecora	20.1	18.9	22.8		*73.7*	*75.0*	*77.5*	*75.2*	*65.2*	*72.8*
oscariana	22.7	20.5	23.3	16.3		*32.2*	*80.5*	*78.9*	*72.9*	*73.3*
parvula	24.5	23.2	26.0	19.0	3.3		*88.8*	*80.9*	*77.3*	*83.2*
hinkleyi	28.3	26.2	29.0	18.0	21.3	24.0		*83.5*	*73.3*	*53.0*
malleata	29.3	28.2	33.0	16.0	25.3	28.0	24.0		*84.1*	*80.2*
angustior	29.3	27.2	31.0	11.0	25.3	27.0	24.0	25.0		*69.3*
clappi	30.0	27.8	30.7	18.3	21.0	22.7	14.7	24.7	24.0	

parvula with which it shares a small (< 1.8 mm tall) yellow shell with a shiny/silky luster. It differs from *V. hebardi* by its sparse, irregular, and blunt striae, lack of an angular lamella, and having the narrow end of the upper palatal lamella being visible in apertural view. It differs from both *V. oscariana* and *V. parvula* in having an upper palatal lamella and a flared lower aperture margin. Initially mistaken for *V. gouldii*, it differs from that species in its smaller shell, weaker striae, shiny luster, and lack of a basal lamella (Nekola & Rosenberg, 2013).

Ecology

Leaf litter accumulations in tropical and scrub forest with bamboo at elevations of 1,520–1,755 m. Colonies are often adjacent to limestone boulders and outcrops.

Biogeography

Caribbean – Currently known only from the crest of John Crow Peak and its immediate vicinity in eastern Jamaica. It also occurs as a

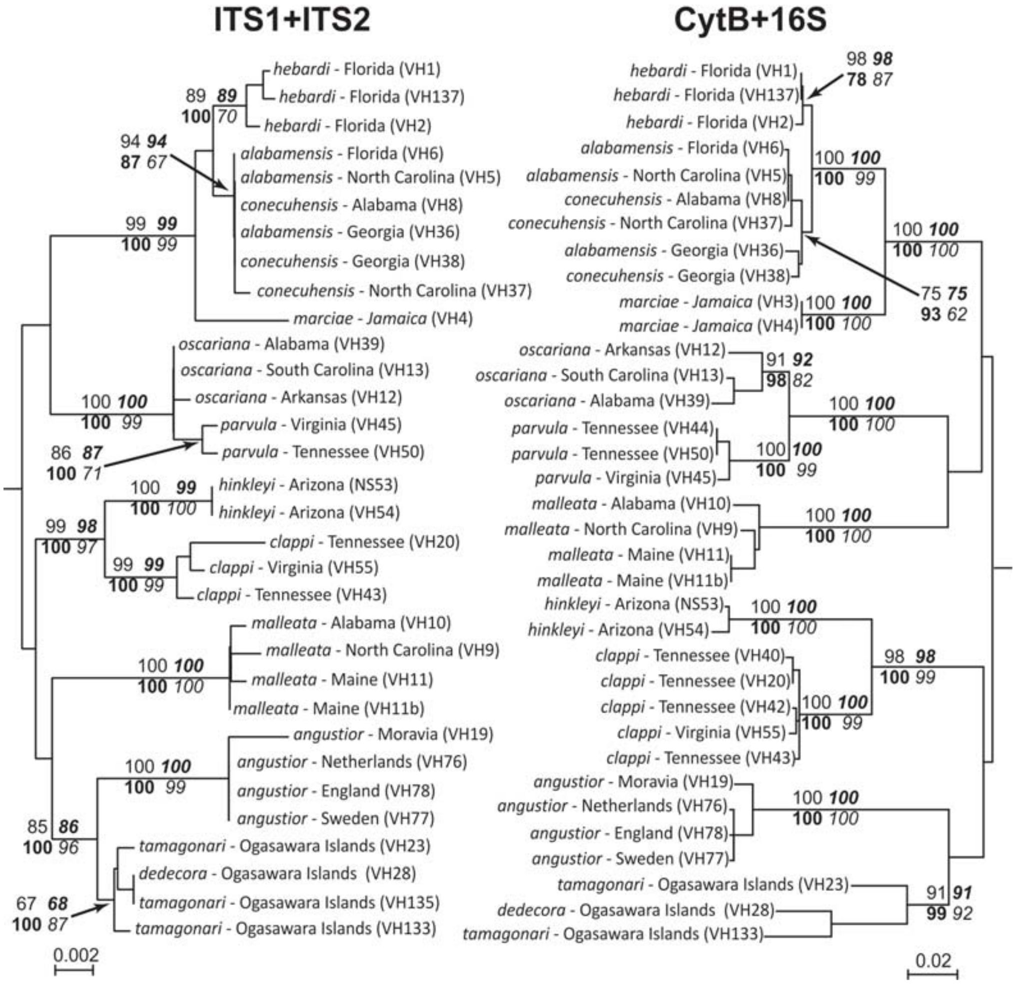


FIG. 12. Maximum-likelihood phylogenetic tree reconstructions in *Vertigo* (*Vertilla*) based on separate analysis of concatenated ITS1 + ITS2 and CytB + 16S data. Nodes with strong to moderate support have been labeled by four values: The upper left (normal font) is for Neighbor Joining. The upper right (***bold italic font***) is for Minimum Evolution. The lower left (**bold font**) is for Bayesian. The lower right (*italic font*) is for Maximum Likelihood.

Pleistocene fossil from Red Hills Road Cave, about 21 km to the west and 1,000 m lower in elevation. It seems likely that the range of *V. marciae* will eventually be found to encompass montane forests in the nearby islands of Dominica and Cuba.

Vertigo (*Vertilla*) *oscariana*
Sterki, 1890: 33
Fig. 13 (top row)

Type Locality: Mosquito Island, Florida, U.S.A.

Phylogenetics

This species was represented by a highly supported clade (99–100) across all reconstruction methods in ITS1 + ITS1, with *V. parvula* existing as a moderately to highly supported subclade (71–100). In CytB + 16S, *V. oscariana* was characterized by a moderate to highly supported clade (82–98). Across all reconstruction methods these data also showed it to be a member of a highly supported clade (100) that included *V. parvula*.

Conchology

Vertigo oscariana has a small, straw-yellow shell with a shiny luster and three apertural lamellae. While *Vertigo parvula* is closely similar, *V. oscariana* differs by its larger strongly ovate shell with a narrower body whorl than penultimate whorl, vertical plate-like columellar lamellae, stronger sinulus, and deep depression over the palatal lamella.

Ecology

A denizen of leaf litter accumulations in upland forest and rock outcrops, where it appears tolerant of acidic soil conditions. Also found on the undersides of fallen palmetto fronds and other large-leaved plants.

Biogeography

North America – Southern Appalachians and southeastern coastal plain from Maryland and West Virginia through all of peninsular Florida to the Hill Country of central Texas.

Vertigo (*Vertilla*) *parvula*
Sterki, 1890: 136
Fig. 13 (top row)

Type Locality: Summit County, Ohio, U.S.A.

Phylogenetics

This species represented a moderately to highly supported clade (71–100) in ITS1 + ITS2 and a highly supported clade (99–100) in CytB + 16S across all reconstruction methods. All reconstruction methods in ITS1 + ITS2 and CytB + 16S also placed this species in a highly supported clade (99–100) with *V. oscariana*.

Conchology

Within the subgenus, this species is most similar to *V. oscariana*, with which it shares a yellow shell, shiny luster and three apertural lamellae. It differs from that species in its smaller cylindrical-ovate shell with a weaker sinulus, a peg-shaped columellar lamella, and a weak depression over the palatal lamella. It is also similar to *V. marciae* in its small size, yellow color and shiny luster. It differs from that species in its more tapered apex, lack of a flared apertural base and absence of an upper palatal lamella. Outside of *Vertilla* it is closest to *V. tridentata* (in *Isthmia*), with which it shares a similar shell shape, color and apertural lamellae. It differs, however, in its much smaller size, shinier luster, and lack of a callus and upper palatal lamella.

Ecology

Leaf litter accumulations associated with cove hardwood forest and rock outcrops.

Biogeography

North America – The main range extends from eastern Tennessee and western North Carolina to northern Virginia. The type locality, however, is from northeastern Ohio.

VERTIGO ANGUSTIOR GROUP

Vertigo (*Vertilla*) *angustior*
Jeffreys, 1830: 361
Fig. 13 (bottom row)

Type Locality: Small stream at Marino, near Swansea, Wales.

Phylogenetics

This species existed across all reconstruction methods as a highly supported clade (99–100) in ITS1 + ITS2 and CytB + 16S. All reconstruction methods across both datasets placed it as a member of a moderately to highly supported clade (85–100) with *V. dedecora*.

Conchology

The shell is distinct, being sinistral, red-brown in color, and strongly striate with a callus pad in place of a lower palatal lamella, a columellar lamella shaped like a vertical plate, and with a very long upper palatal lamella that is hooked at the distal end. Within the subgenus only *V. dedecora* shares such strong and sharp striae.

Ecology

Leaf litter accumulations across a wide variety of moist, calcareous habitats, ranging from fens and limestone pavements to dunes and dune slacks, grasslands, lake margins, brushlands, wet boulder slopes and upland forests.

Biogeography

Western Eurasia – Ireland, Spain and Scandinavia east through the Mediterranean, Caspian Sea shore in Iran and south-central Siberia to the east of Novosibirsk.

Vertigo (*Vertilla*) *clappi*
Brooks & Hunt, 1936: 121, text fig. 1
Fig. 13 (bottom row)

Type Locality: Renick, Greenbrier County, West Virginia, U.S.A.

FIG. 13. Shells of *Vertigo* (*Vertilla*). Bracketed DNA specimen codes precede each entry. Top row (left to right): *Vertigo alabamensis*: [VH36] Dickinson Memorial State Forest, Georgia, U.S.A. (31.1698°N, 82.2243°W). *Vertigo alabamensis* form *conecuhensis*, [VH38] Rayonier forest lands, Georgia, U.S.A. (31.3462°N, 81.8244°W). *Vertigo hebardi*, [VH1] Long Key, Florida, U.S.A. (24.8146°N, 80.8211°W). *Vertigo marciae*, [VH4] John Crow Peak, Jamaica (18.1132°N, 76.6685°W). *Vertigo oscariana*, [VH39] Chewacla State Park, Alabama, U.S.A. (32.5481°N, 85.4855°W). *Vertigo parvula*, [VH45] Fortney Branch, Virginia, U.S.A. (37.9272°N, 79.9861°W). Bottom row (left to right): *Vertigo malleata*, [VH11] Saco Heath, Maine, U.S.A. (43.5477°N, 70.4586°W). *Vertigo clappi*, [VH55] Back Creek Trail, Virginia, U.S.A. (38.0631°N, 79.8885°W). *Vertigo hinkleyi*, [VH54] Cave Creek Canyon, Arizona, U.S.A. (31.8670°N, 109.1889°W). *Vertigo angustior*, [VH78] Gait Barrows, Lancashire, England (54.1901°N, 2.7977°W). *Vertigo dedecora tamagonari*, [28] Hahajima Island, Japan (26.6537°N, 142.1536°E). *Vertigo dedecora*, [VH23] Chichijima Island, Japan (27.0948°N, 142.2166°E).

TABLE 8. Conchological traits for *Vertigo* (*Vertilla*) members.

Species	Height (mm)	Width (mm)	Shell Shape	Suture Depth	Striae	Luster	Color	Crest	Callus	Sinulus	Angular	Parietal	Columellar	Basal	Palatal	Palatal Depression	Other
alabamensis	1.4–1.9	0.9–1.1	Ovate to ovate – cylindrical	Shallow	Apex: sharp; elsewhere: sparse, blunt, irregular	Dull-silky; surface weakly pustulate	Yellow-brown	Modest to strong	Weak to strong; near aperture margin	Modest to strong	Strong	Long	Long	Strong; blunt	2 long blades	Deep	Upper palatal long axis faces aperture margin
angustior	1.4–1.8	0.9–1.0	Sinistral; ovate	Moderate	Strong, regular	Dull	Red-brown	Strong	Strong on lower palatal wall	Very strong	Strong	Long	Vertical blade	None	Upper: very long Lower: weak to absent	Deep channel	Upper palatal hooked at distal end
clappi	1.4–1.8	0.7–0.8	Elongate conic	Moderate	Irregular, blunt	Dull-silky	Pale straw-yellow	Very strong	Absent	Very strong	Strong (rarely absent)	Long	Long	Strong; peg	Upper: curved; Lower: blade	Weak	Upper palatal long axis faces aperture margin
dedecora	1.2–1.6	0.7–1.0	Ovate – cylindrical to broadly ovate	Shallow-moderate	Strong, regular	Dull	Red-brown	Very strong	Strong, near aperture margin	Modest to strong	Strong	Long	Short	Strong	2 blades	Deep to weak channel	Upper palatal reaches aperture margin
hebardi	1.1–1.4	0.8–0.9	Cylindrical – ovate	Shallow	Sharp, irregular	Silky	Yellow-brown	None to weak	None	Weak to modest	Weak	Long	Short	None	2 short	Weak	Upper palatal long axis faces aperture margin

(continues)

(continued)

Species	Height (mm)	Width (mm)	Shell Shape	Suture Depth	Striae	Luster	Color	Crest	Callus	Sinulus	Angular	Parietal	Columellar	Basal	Palatal	Palatal Depression	Other
hinkleyi	1.4–1.8	0.7–0.8	Cylindrical	Shallow	Sparse, irregular, blunt	Silky	Yellow-brown	None	None	Very strong	None	Long	Long	Peg	2 long	Deep channel	Lower palatal more deeply inserted than upper
malleata	1.8–2.1	1.2–1.4	Broadly conical – ovate	Moderate	Numerous sharp, regular	Dull; body whorl strongly pustulate	Brown	None to weak	None	Modest to strong	None; infra-parietal present	Long	Long	Peg	2 short	Modest	Lower aperture margin flared
marciae	1.4–1.6	0.8–1.0	Cylindrical – ovate	Shallow	Sparse, irregular, blunt	Shiny	Yellow	None	None	Modest to weak	None	Long	Short	None	2	Weak	Aperture bottom flared
oscariana	1.4–1.8	0.9–1.0	Narrowly – ovate	Shallow	Very sparse, irregular, blunt	Shiny-silky	Yellow	None	None-weak	Strong	None	Long	Vertical plate	None	Lower only	Deep	Body whorl narrower than penultimate
parvula	1.3–1.6	0.7–0.9	Cylindrical – ovate	Shallow	Very sparse, weak, irregular	Shiny	Yellow	None to very weak	Weak to none; at aperture margin	Modest	None	Long	Peg	None	Lower only	Weak	

Phylogenetics

This species existed as a strongly supported clade (99–100) across all reconstruction methods in ITS1 + ITS2 and CytB + 16S. All reconstructions in both datasets identified it as a member of the same highly supported clade (97–100) as *V. hinkleyi*.

Conchology

This species is unique in the subgenus with its small, elongated-conic, pale straw-yellow shell with a deep suture, dull luster and six apertural lamellae. While the long axis of the upper palatal lamella is visible in apertural view and reminiscent of *V. alabamensis*, their shells share little else in common.

Ecology

Humid leaf litter accumulations and debris associated with wooded rock outcrops.

Biogeography

North America – Narrow band along the Appalachians from southern and central Tennessee to the northern shore of Lake Ontario.

Vertigo (*Vertilla*) *dedecora*
(Pilsbry, 1902)
Fig. 13 (bottom row)

Nesopupa dedecora Pilsbry, 1902: 31.

Type Locality: Hahajima, Ogasawara-jima, Japan – in error (see below).

Synonym: *Nesopupa tamagonari* Pilsbry & Hirase, 1904: 118, type locality: Chichijima, Ogasawara Islands, Japan – in error (see below).

Phylogenetics

This species existed as a moderately to highly supported clade (67–100) in ITS1 + ITS2 and a highly supported clade (91–99) in CytB + 16S across all reconstruction methods. Although only limited nDNA sequence variation existed between populations (2 bases between Hahajima and Chichijima in ITS1 + ITS2), deep mtDNA divergence was found: 44 bases in CytB + 16S between Hahajima and Chichijima, and 32 bases between different populations on Chichijima. Preliminary analyses indicated similar levels of divergence with the population on Minami-daitojima. This species was found to exist in the same moderately to highly supported clade (85–100) as *V. angustior* across all reconstruction methods in ITS1 + ITS2.

Conchology

Within the subgenus, this species shares with *V. angustior* a strongly striate shell with a red-brown color and dull luster. It differs from that species in its dextral coiling, possession of a peg-shaped columellar lamella, a strong lower palatal lamella of equal length as the upper palatal, and the presence of a strong basal lamella. Pilsbry (1919) demarcated the subspecies *V. d. tamagonari* by its possession of a slightly more globose shell. We have not been able to correlate this characteristic with genetic variation and assume it is not taxonomically relevant.

Ecology

Leaf litter accumulations within upland tropical forest.

Biogeography

Western Pacific Archipelagos – Hahajima and Chichijima in the Ogasawara Islands; Minami-daitojima and Kita-daitojima in the Ryukyu Islands (Azuma & Azuma, 1994); and Sarigan, Alamagan, Pagan, Agrihan, Asuncion and Maug in the northern Mariana Islands (Kurozumi, 1994). The lots reported by Pilsbry (1919) for this species were missassigned, with the nominate subspecies being actually limited to Chichijima and subsp. *tamagonari* being limited to Hahajima.

Nomenclature

Pilsbry (1919) recognized two subspecies, each endemic to a different island; however, our analyses document comparable genetic distance between populations on the same island with little corresponding difference in conchology. It seems prudent at this juncture to recognize only a single taxon possessing a highly variable mtDNA genepool, and to recognize *V. d. tamagonari* – if at all – as a simple shell form.

Vertigo (*Vertilla*) *hinkleyi*
Pilsbry, 1920: 234
Fig. 13 (bottom row)

Type Locality: Cave Canyon, Huachuca Mountains, Arizona, U.S.A.

Phylogenetics

This species was characterized by a highly supported clade (99–100) across all reconstruction methods in ITS1 + ITS2 and CytB + 16S. All four methods and both datasets placed this species in a highly supported clade (97–100) with *V. clappi*.

Conchology

This species is unique in the subgenus for its cylindrical shell and five apertural lamellae, with the lower palatal being inserted far more deeply into the aperture than the upper. It is perhaps most reminiscent of *V. nylanderi* (in *Vertigo s. str.*) which also shares this latter trait along with a deep channel over the lower palatal lamella. However, *V. hinkleyi* differs by possessing sparse, irregular, and blunt striae and a silky luster.

Ecology

Leaf litter accumulations in Maderan sky-island oak forest, often on steep slopes with rock outcrops; also leaf litter caches on the upslope side of prostrate *Agave* stems.

Biogeography

North America – Southeastern Arizona and southwestern New Mexico into northern Chihuahua and Sonora.

Vertigo (*Vertilla*) *malleata*
Coles & Nekola, 2007: 18, figs. 1–15
Fig. 13 (bottom row)

Type Locality: Holly Shelter Game Land, Pender County, North Carolina, U.S.A.

Phylogenetics

This species existed as a highly supported (100) clade across all reconstruction methods in ITS1 + ITS2 and CytB + 16S.

Conchology

This species possesses the largest shells in the subgenus. They also uniquely possess a strongly pustulose body whorl and often a strong infraparietal lamella while lacking an angular lamella. In this respect, it appears unique in the genus.

Ecology

Confined to highly acid, wet pinelands and ombrotrophic bogs, with a preference for accumulations of heath leaf litter.

Biogeography

North America – Atlantic coastal plain from southern Maine to Mobile Bay; absent from peninsular Florida. It is likely present in southern Nova Scotia.

VERTILLA DISCUSSION

The unambiguous genetic differentiation of *Vertilla* species with no cases of incongruence between ITS1 + ITS2 and CytB + 16S and complete correspondence between conchology and DNA-based specific assignment suggests that these species have been stable over much longer evolutionary time periods than for any other subgenus. Its global range (including the Caribbean, southeastern and southwestern North America, Europe, and east Asia), potential existence of pre-Pleistocene fossils from areas that no longer support the subgenus (central Asia), and restriction to mid and low latitudes suggest that *Vertilla* may represent a relatively ancient lineage predating fragmentation of the Arcto-Tertiary forest.

Even though shells are unreliable indicators of phylogenetic relatedness, images of *Nesopupa maasseni* Altena, 1975, from the Guianan highlands (Massemin et al., 2009) illustrate a shell extraordinarily reminiscent of *V. hebardi* and *V. marciae*, and quite unlike any genetically verified nesopupid. It thus seems likely that *Vertilla* will ultimately be found to extend into South America.

SUBGENUS *ALAEA*

Analyses of the subgenus *Alaea* were based on 67 individuals for CytB + 16S and 64 for

ITS1 + ITS2. The CytB segment was 367 bases and the 16S segment 443–448 bases, with a total of 252 variable sites along the entire CytB + 16S construct. The analyzed ITS1 segment was 556–613 bases, the analyzed ITS2 segment was 591–672 bases, with a total of 190 variable sites along the entire ITS1 + ITS2 construct.

In combination with conchology and ecological preference, these analyses suggest eleven species-level entities within the subgenus (Tables 9, 10, Figs. 14, 15): *V. antivertigo*, *V. binneyana*, *V. lilljeborgi*, *V. milium*, *V. morsei*, *V. oralis*, *V. ovata*, *V. rugosula*, *V. teskeyae* and *V. ventricosa*, with ***V. kurilensis*** being described as a new species. Three additional taxa with unique conchological traits (*V. berryi*, *V. perryi*, and *V. occidentalis*) are provisionally recognized as species even though they are not well substantiated by our limited DNA sequence data. One new subspecies (***V. lilljeborgi vinlandica***) is also described.

Mean within-species variability ranged in ITS1 + ITS2 from none in *V. binneyana*, ***V. lilljeborgi vinlandica***, *V. rugosula*, and *V. teskeyae* to 8.7 bases in *V. ovata*, 9.0 in *V. ventricosa*, and 17.2 in *V. milium*. In CytB + 16S within-species variability ranged from 0.7 bases in ***V. lilljeborgi vinlandica***, 1.0 in *V. rugosula*, and 1.3 in *V. morsei* to 28.1 in *V. ovata*, 28.3 in *V. oralis*, and 42.3 in *V. milium*. Mean pairwise variation between species ranged in ITS1 + ITS2 from 3.3 bases (*V. morsei* vs. *V. occidentalis*) to 46.0 (*V. occidentalis* vs. *V. rugosula*) and in CytB + 16S from 7.8 (*V. perryi* vs. *V. ventricosa*) to 95.2 (***V. l. vinlandica*** vs. *V. rugosula*) bases (Table 9).

Two main groups below the subgenus level were apparent (Fig. 14). The *V. milium* group was moderately to highly supported in ITS1 + ITS2 (66–90) for NJ, ME and ML reconstructions, and included *V. binneyana*, ***V. kurilensis***, *V. lilljeborgi*, ***V. l. vinlandica***, *V. milium*, *V. perryi* and *V. ventricosa*. Bayesian reconstruction splits this group into three highly supported (100) unlinked clades consisting of: (1) *V. binneyana* and *V. milium*; (2) ***V. kurilensis***, *V. perryi* and *V. ventricosa*; (3) *V. lilljeborgi* and ***V. l. vinlandica***. The *V. milium* group was not as well supported in CytB + 16S, although tree topologies across all reconstruction methods generally followed the ITS1 + ITS2 Bayesian topology. The *V. antivertigo* group was moderately to highly supported (85–100) in ML and Bayesian reconstructions of the ITS1 + ITS2 data, and included *V. antivertigo*, *V. berryi*, *V. morsei*, *V. occidentalis*, *V. oralis*, *V. ovata*, and *V. teskeyae*; *V. rugosula* is included because of its membership with high support (100) in the Bayesian reconstruction. The *V. antivertigo* group was identified across all reconstruction methods in CytB + 16S with low (36–50 in NJ, ME, ML) to high (100 Bayesian) support.

VERTIGO MILIUM GROUP

Vertigo (*Alaea*) *binneyana*
Sterki, 1890: 33
Fig. 15 (top row)

Type Locality: Helena, Montana, U.S.A., and Winnipeg, Manitoba, Canada

Phylogenetics

This species existed as a highly supported clade (98–100) in ITS1 + ITS2 and CytB + 16S across all reconstruction methods. It was identified as a member of the same clade as *V. milium* in ITS1 + ITS2 across all reconstruction methods with moderate to high support (82–100). In CytB + 16S, it existed as an independent branch.

Conchology

Within the subgenus, this species shares with *V. milium* a shell 2 mm or less in height possessing a silky luster, shallow suture, and narrowly ovate shape. It differs from *V. milium* in its larger size, weaker sinulus, a shorter and uncurved lower palatal lamella, and a deeper depression over the palatals. It is perhaps closest to the southern Great Plains Pliocene fossil *Vertigo hibbardi,* which shares a 1.8–2.0 mm tall shell with a shallow suture and straight lower palatal lamella.

Ecology

Wet-mesic to mesic prairie, often in close association with glacial pothole lakes; also present in adjacent aspen parkland.

Biogeography

North America – Montana and Saskatchewan to South Dakota and Manitoba. Reports from the Rocky Mountains and west (e.g., Pilsbry, 1948) appear to be erroneous.

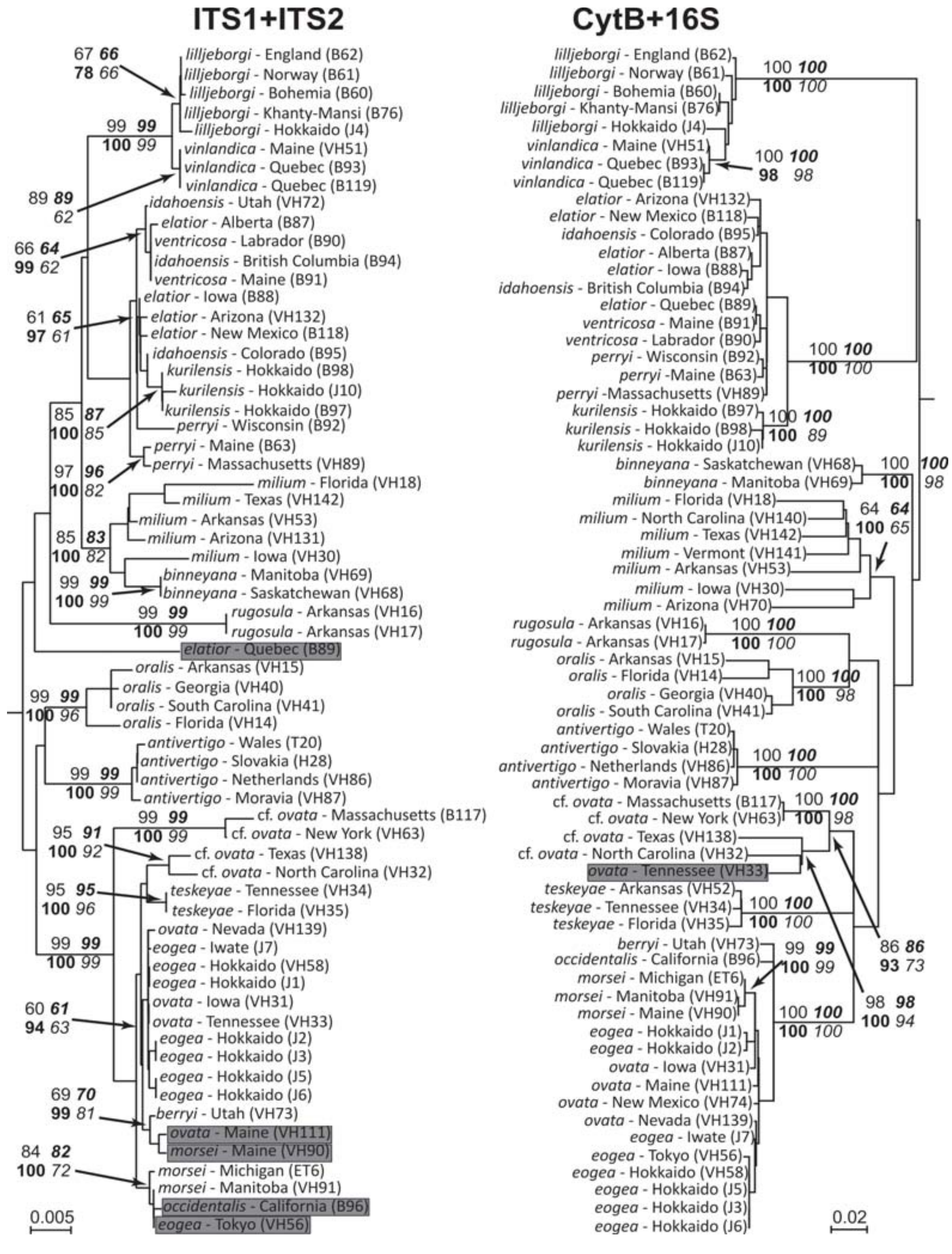


FIG. 14. Maximum-likelihood phylogenetic tree reconstructions in *Vertigo* (*Alaea*) based on separate analysis of concatenated ITS1 + ITS2 and CytB + 16S data. Nodes with strong to moderate support have been labeled by four values: The upper left (normal font) is for Neighbor Joining. The upper right (***bold italic font***) is for Minimum Evolution. The lower left (**bold font**) is for Bayesian. The lower right (*italic font*) is for Maximum Likelihood. A grey box demarcates specimens which show incongruence in topologic location between the ITS1 + ITS2 and CytB + 16S trees, and likely represent examples of genetic introgression or incomplete sorting.

TABLE 9. Mean pairwise distances between *Vertigo* (*Alaea*) species for the analyzed nDNA and mtDNA constructs, reported as nucleotide bases/construct. The lower half of the matrix represents distances in the ITS1 + ITS2 construct and the upper half (demarcated by *italic font*) represents distances in the CytB + 16S construct.

	ventricosa	***kurilensis***	*perryi*	*binneyana*	*lilljeborgi*	***l. vinlandica***	*milium*	*oralis*	*antivertigo*	*berryi*	*morsei*	*occidentalis*	*ovata*	*teskeyae*	*rugosula*
ventricosa		*22.8*	*7.8*	*63.7*	*82.8*	*84.1*	*74.0*	*77.0*	*86.8*	*82.3*	*84.3*	*78.0*	*81.7*	*80.1*	*83.4*
kurilensis	8.6		*25.0*	*64.0*	*84.1*	*86.0*	*72.9*	*73.2*	*83.0*	*81.0*	*81.3*	*80.0*	*79.9*	*79.3*	*78.5*
perryi	9.3	9.0		*63.0*	*79.5*	*81.0*	*72.4*	*75.9*	*83.7*	*81.0*	*80.3*	*74.7*	*78.1*	*77.0*	*80.8*
binneyana	21.8	21.7	22.3		*68.0*	*71.7*	*48.7*	*57.8*	*64.8*	*57.0*	*62.3*	*60.0*	*59.8*	*61.5*	*68.0*
lilljeborgi	23.8	23.7	24.4	25.4		*12.3*	*75.8*	*84.8*	*80.7*	*83.2*	*85.3*	*81.2*	*84.2*	*79.3*	*91.5*
l. vinlandica	24.2	24.3	25.0	24.0	3.2		*79.7*	*86.9*	*84.7*	*86.7*	*87.0*	*84.7*	*87.2*	*82.0*	*95.2*
milium	26.1	26.1	26.2	18.2	29.2	27.8		*64.9*	*64.2*	*59.4*	*64.0*	*60.9*	*62.5*	*74.1*	*71.8*
oralis	29.3	31.2	29.5	32.3	34.7	33.3	32.9		*71.6*	*66.3*	*69.6*	*68.3*	*67.3*	*74.2*	*66.5*
antivertigo	33.7	34.7	34.0	34.5	37.4	36.0	36.0	23.5		*62.5*	*65.1*	*63.5*	*65.5*	*70.4*	*74.3*
berryi	34.0	35.7	34.0	37.0	37.4	37.0	40.2	29.3	29.8		*14.3*	*15.0*	*21.5*	*65.0*	*69.5*
morsei	34.4	36.3	34.7	37.3	38.7	38.0	39.5	28.6	30.4	4.7		*19.3*	*23.2*	*66.3*	*74.8*
occidentalis	34.7	36.7	35.0	38.0	39.4	39.0	40.2	29.3	31.8	6.0	3.3		*25.4*	*63.3*	*67.5*
ovata	36.0	38.4	36.8	39.0	39.5	39.0	41.2	30.5	31.1	6.9	7.8	8.4		*63.1*	*72.0*
teskeyae	36.7	38.7	37.0	38.0	39.4	39.0	40.2	29.3	29.8	6.0	7.3	8.0	8.5		*76.5*
rugosula	40.0	39.7	42.3	36.0	40.4	39.0	40.0	42.3	44.0	44.0	44.0	46.0	44.3	44.0	

→

FIG. 15. Shells of *Vertigo* (*Alaea*). Bracketed DNA specimen codes precede each entry. Top row (left to right): *Vertigo binneyana*: [VH69] Sanford SE, Manitoba, Canada (49.6500°N, 97.4947°W). *Vertigo milium*: [VH30] Rowley North fen, Iowa, U.S.A. (42.3764°N, 91.8507 W°); [VH18] Lake Annie, Florida, U.S.A. (27.2108°N, 81.3490°W); [VH53] Blanchard Springs 2, Arkansas, U.S.A. (35.9582°N, 92.1778°W); [VH131] Blind Canyon, Huachuca Mts., Arizona, U.S.A. (31.3847°N, 110.3136°W). *Vertigo lilljeborgi*: [B61] Sør-Trøndelag, Kongsvoll, Norway (62.3558°N, 9.6832°E). ***Vertigo lilljeborgi vinlandica***: [B119] Lac John, Québec, Canada (54.8138°N, 66.7920°W). Second row (left to right): *Vertigo ventricosa* form *elatior*: [B88] Rowley North fen, Iowa, U.S.A. (42.3764°N, 91.8507°W). *Vertigo ventricosa*: [B91] Salmon Brook Lake, Maine, U.S.A. (46.9004°N, 68.2466°W). *Vertigo ventricosa* form *idahoensis*: [B94] Incomappleux swamp, British Columbia, Canada (50.9227°N, 117.5787°W). ***Vertigo kurilensis***: [J10] Akkeshi North, Hokkaidō, Japan (43.0817°N, 144.8442°E). *Vertigo perryi*: [VH89] Tispaquin Street, Massachusetts, U.S.A. (41.9010°N, 70.8521°W). *Vertigo rugosula*: [VH16] 0.5 miles S L&D #5, Arkansas, U.S.A. (34.4040°N, 92.1020°W). Third row (left to right): *Vertigo oralis*: [VH14] Highlands Hammock State Park, Florida, U.S.A. (27.4726°N, 81.5550°W). *Vertigo antivertigo*: [VH86] Valkenburgse Meer, Katwijk, Netherlands (52.1590°N, 4.4331°E). *Vertigo occidentalis*: [B96] Yellow Post fen, San Bernardino Mts., California, U.S.A. (34.2230°N, 116.9410°W). *Vertigo* aff. *ovata*: [VH32] Sheep Ridge pocosin, North Carolina, U.S.A. (34.9345°N, 77.0100°W); [B117] Tispaquin Street, Massachusetts, U.S.A. (41.9010°N, 70.8521°W). Bottom row (left to right): *Vertigo morsei*: [VH90] Woodland fen, Maine, U.S.A. (46.8795°N, 68.1391°W). *Vertigo berryi*: [VH73] Mystic River seep, Utah, U.S.A. (37.3743°N, 112.5945°W). *Vertigo teskeyae*: [VH34] Lady Finger Bluff trail, Tennessee, U.S.A. (35.6904°N, 88.0207°W). *Vertigo eogea*: [VH56] Renkoji seep, Tōkyō, Japan (35.6325°N, 139.4677°E); *Vertigo ovata*: [VH111] Orient, Maine, U.S.A. (45.8362°N, 67.8482°W).

Vertigo* (*Alaea*) *kurilensis, n. sp.

Figs. 15 (second row), 16A–H, Table 10

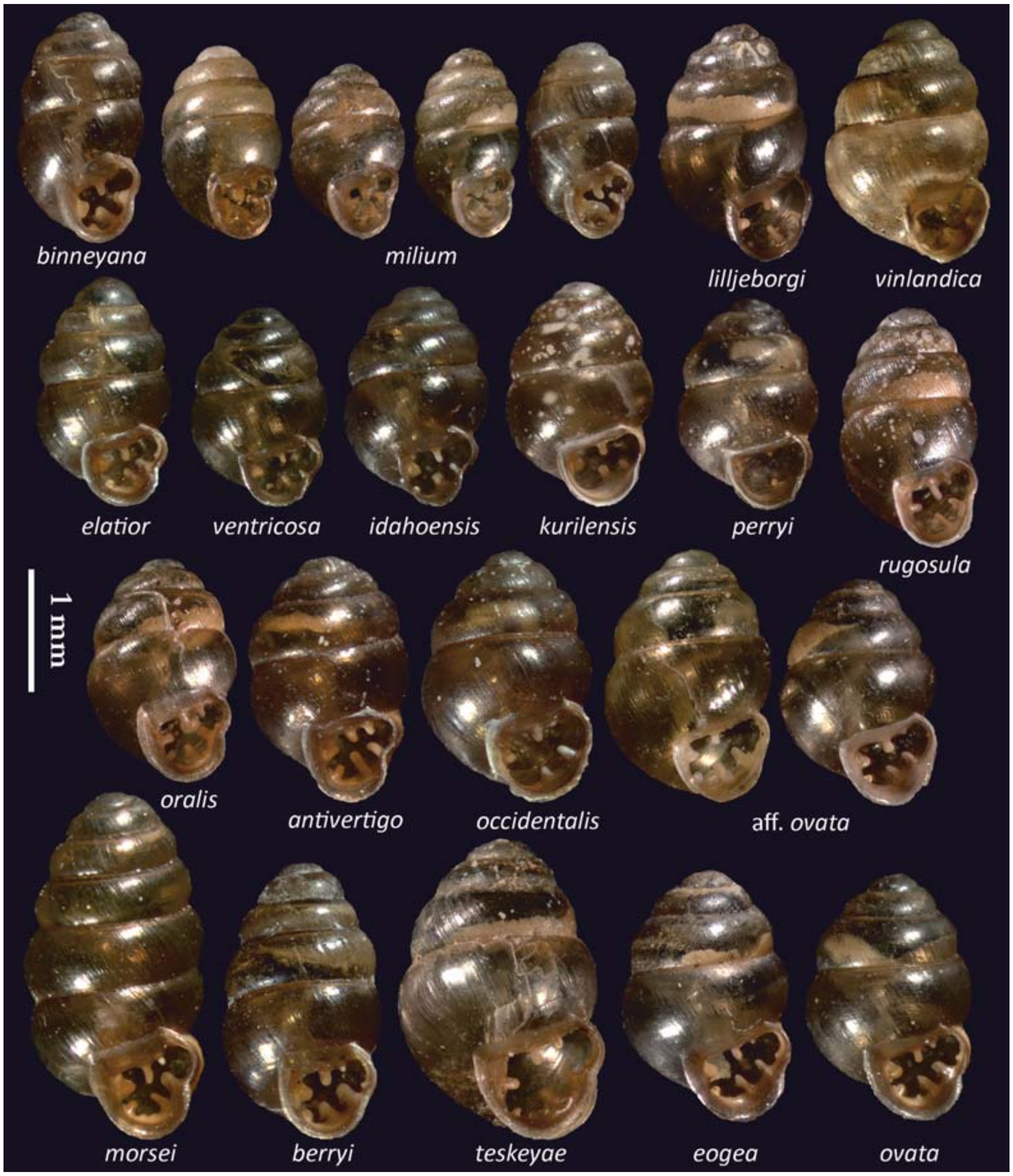
GenBank Accessions: KY217155-7; KY216767-9; KY217558-60; KY216414-6.

Diagnosis

Shell small, broadly ovoid, most similar to *V. ventricosa* and *V. perryi* of boreal North America but differing by its larger aperture with a much more flared lower margin and tendency to have a shallower suture.

Description

Shell: 1.7–2.0 mm tall x 1.1–1.2 mm wide (Holotype 1.9 x 1.2 mm), translucent to transparent, cinnamon-brown; approximately four whorls; broadly ovoid-conical; suture shallow with depressed whorls (Fig. 16A–D, F–H); shiny luster with a few, irregular, weak radial striae and



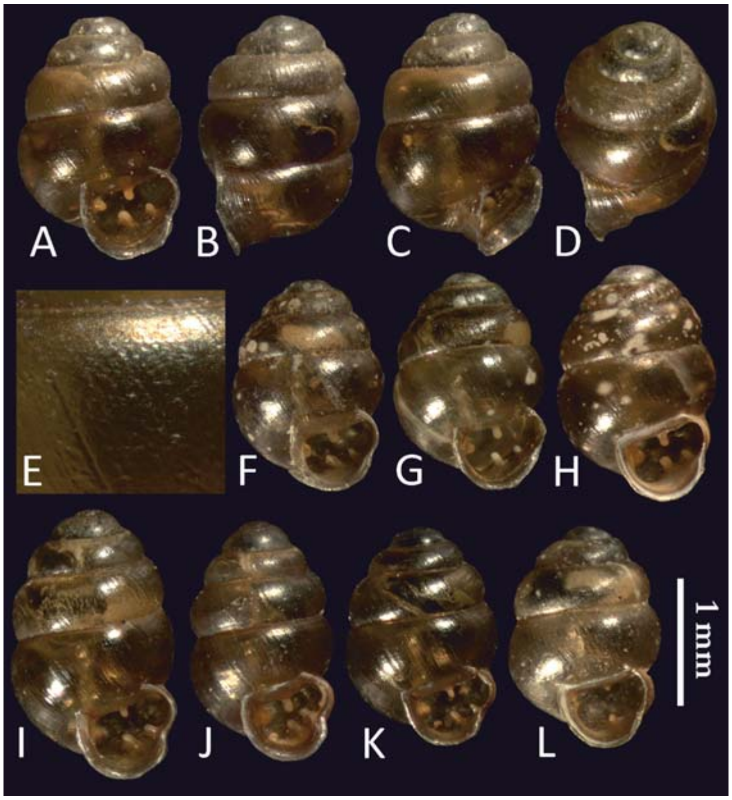


FIG. 16. ***Vertigo kurilensis*** n. sp. A–E: Holotype, ANSP 467366, Rich grassland and pond on dune slack, Sakakimachinishi, Hamanaka, Akkeshi District, Hokkaidō, Japan (43.1108°N, 145.1068°E); F: [B97] Rich grassland and pond on dune slack, Sakakimachinishi, Hamanaka, Akkeshi District, Hokkaidō, Japan (43.1108°N, 145.1068°E); G: [B98] Acid fen dominated by *Myrica, Scirpus, Eriophorum* and *Carex*, Tokotan, Betsukai, Notsuke District, Hokkaidō, Japan; (43.4352°N, 145.2616°E); H: [J10] Alder swamp with *Phragmites, Spiraea*, and *Osmunda* north of Akkeshi, Akkeshi District, Hokkaidō, Japan (43.0817°N, 144.8442°E); I: *Vertigo ventricosa* form *idahoensis* [B95] Sedge turf of streamside fen, Trujillo Meadows, Colorado, U.S.A. (37.0539°N, 106.4626°W); J: *Vertigo ventricosa* form *elatior* [B88] Marl flat and sedge turf, Rowley North fen, Iowa, U.S.A. (42.3764°N, 91.8507°W); K: *Vertigo ventricosa* [B91] Acid Kalmia-Leatherleaf mat, Salmon Brook Lake, Maine, U.S.A. (46.9004°N, 68.2466°W); L: *Vertigo perryi* [VH89] Abandoned cranberry bog, Tispaquin Street, Massachusetts, U.S.A. (41.9010°N, 70.8521°W). When applicable, bracketed DNA specimen codes precede each entry.

indistinct microscopic malleations covering the surface (Fig. 16E); aperture approximately $^1/_3$ of shell height, being approximately as wide as tall (Fig. 16A, F–H), in profile barely ascending onto body whorl (Fig. 16B); umbilicus closed by preceding whorls (Fig. 16C); peristome interrupted by body whorl, apertural lip greatly flared on the bottom (Fig. 16A–D, F–H), in profile appearing thistle-shaped (Fig. 16B–D); no crest, apertural thickenings or callus (Fig. 16B, D); four apertural lamellae, a peg-shaped columellar, a blade-shaped parietal, and two blade-shaped palatals, the palatal lamellae appearing to be inserted into the aperture to a moderate depth because of the flaring of the lower apertural margin (Fig. 16A, F–H), a depression is present on the shell surface over the palatal wall (Fig. 16D).

Holotype (Fig. 16A–E): ANSP 467365, Sakakimachinishi, Hamanaka, Akkeshi District, Hokkaidō, Japan; Rich grassland and pond on dune slack; 43°06'39''N, 145°06'24''E; July 24, 2012.

Paratypes: ANSP 467366, collected with holotype: 10 shells. ANSP 467367, North of Akkeshi, Akkeshi District, Hokkaidō, Japan; Alder swamp with *Phragmites*, *Spirea* and *Osmunda*; 43°04'54''N, 144°50'39''E; July 24, 2012: 2 shells. ANSP 467368, Tokotan, Betsukai, Notsuke District, Hokkaidō, Japan; acid fen dominated by *Myrica*, *Scripus*, *Eriophorum* and *Carex*; 43°26'07''N, 145°15'24''E; July 24, 2012: 1 shell.

Other, Non-Type Material Examined: NMW.Z.2015.009.00017-00019, ~70 shells from Hokkaidō, Japan; in the Nekola collection eight lots representing 100 individuals from Hokkaidō, Japan; in the Delaware Museum six lots collected by Tim Pearce during the mid-1990s expedition to the Kuril Islands from Paramushir, Antsiferov, Makanrushi, Onekotan, Ekarma, and Urup Islands. All of the latter were originally identified as *V. modesta* (Pearce et al., 2002).

Etymology

The specific epithet refers to the geographic range of this species which is centered on the Kuril Islands.

Phylogenetics

This species was defined by a moderately to highly supported clade across all reconstructions in ITS1 + ITS2 (85–100) and CytB + 16S (89–100). In ITS1 + ITS2 and CytB + 16S and all reconstruction methods this species was shown to be a member of a highly supported clade (98–100) that included *V. ventricosa* and *V. perryi*.

Comparisons with Other Species

Shells are most closely reminiscent to North American *V. ventricosa*, but differ by their greatly dilated and flared lower apertural margin, larger and more circular aperture and shallower suture. In addition, *V. ventricosa* form *elatior* usually supports not only a basal lamella but also a strong callus along the palatal wall. ***Vertigo kurilensis*** also bears some resemblance to the northeastern North American *V. perryi* from which it differs in its reddish-brown shell color and well-developed apertural lamellae. East Asian populations of *V. lilljeborgi* differ in their larger size (> 2 mm shell height), possession of an angular lamella, and a strongly calcified callus along the palatal wall.

Geographic Distribution

East Asia – The known range of this species extends over 1,200 km from Paramushir Island in the north to Watenbetsu, Shiranuka District, Hokkaidō in the south. On the basis of field sampling, we suspect that Hokkaidō represents the actual southern range limit. However, the northern limit remains unknown as surveys have yet to be conducted on the Kamchatka Peninsula or the western Aleutian Islands.

Ecology

Acid graminoid (e.g., sedges, *Phragmites*, bamboo), myrtle and alder-dominated wetlands.

Vertigo (*Alaea*) *lilljeborgi*

(Westerlund, 1871)

Fig. 15 (top row), 17I–L

Pupa lilljeborgi Westerlund, 1871: 90.

Type Locality: Southern shore of Lake Tresjön near Ronneby, Blekinge, Sweden.

Phylogenetics

This species existed across ITS1 + ITS2 and CytB + 16S as a highly supported clade (99–100) in all reconstruction methods. It was moderately differentiated from ***V. lilljeborgi vinlandica*** across all reconstruction methods (66–78) in ITS1 + ITS2. Material from the lone Japanese population differed on average by 2.3 bases in ITS1 + ITS2 and 14.8 bases in CytB + 16S from central Asian and European material.

Conchology

Within *Alaea*, this species shares with *V. ventricosa*, *V. occidentalis* and *V. ovata* a broadly ovate, yellow to red-brown shell with reduced surface striation and a shiny luster. It differs from all these in its weakly malleate surface and short parietal lamella. It also differs from *V. ventricosa* in its larger volume and weaker sinulus; from *V. occidentalis* in its smaller aperture, stronger sinulus and crest and longer columellar lamella; and from *V. ovata* in its generally stronger crest and weaker sinulus. It should be noted that shells from the lone observed Japanese population differ from European and central Asian

TABLE 10. Conchological traits for *Vertigo* (*Alaea*) members.

Species	Height (mm)	Width (mm)	Shell Shape	Suture Depth	Striae	Luster	Color	Crest	Callus	Sinulus	Angular	Parietal	Columellar	Basal	Palatal	Palatal Depression	Other
antivertigo	1.8–2.3	1.1–1.3	Ovate – conical	Shallow	Scattered, weak, irregular, blunt	Silky-shiny	Red-brown	Modest to strong	Modest to weak	Strong	Strong	Long	Long	1 strong; weak 2nd sometimes present	2 long 1 short	Modest to strong	Infra-parietal sometimes present
berryi	1.9–2.4	1.2–1.5	Conical – ovate	Moder-ate	Numerous, weak, irregular, blunt	Shiny-silky	Red-brown	Modest to strong	Strong to modest; white	Modest	Modest	Long	Long	Strong; weak 2nd sometimes present	2	Modest to weak	Body whorl < $^1/_2$ of shell height
binneyana	1.6–2.1	0.9–1.1	Cylindrical – ovate	Shallow	Numerous, weak, blunt	Silky-shiny	Red-brown	Strong	Strong-modest; white	Modest	Modest to weak	Long	Short	Long	2	Deep	
kurilensis	1.7–2.0	1.1–1.2	Ovate – conical	Shallow	Scattered, weak, blunt	Shiny; weakly malleate	Red-brown	None	None	Modest	None	Long	Short	None	2 short	Modest	Flared aperture bottom
lilljeborgi	1.7–2.2	1.2–1.4	Broadly ovate	Moder-ate to deep	Scattered, weak, blunt	Silky-shiny; weakly malleate	Yellow to red-brown	Sharp; modest to strong	None to modest	Weak to modest	None	Long	Short	0–1	2 short	None to weak	
lilljeborgi vinlandica	1.8–2.4	1.2–1.5	Broadly conical – ovate	Deep	Scattered, weak, blunt	Silky-dull; malleate	Yellow to red-brown	None to weak	None to modest	Weak to modest	None	Long	Short	None	2 short	None	

(continues)

(continued)

Species	Height (mm)	Width (mm)	Shell Shape	Suture Depth	Striae	Luster	Color	Crest	Callus	Sinulus	Angular	Parietal	Columellar	Basal	Palatal	Palatal Depression	Other
milium	1.3–1.8	0.8–1.0	Ovate – conical	Shallow to moderate	Strong-sharp to weak-blunt	Shiny to silky-dull	Red-brown	Weak to strong	None to modest; white	Strong to very strong	Strong	Long	Large; horizontal and vertical limbs pyramidal	Long	2 long; lower curved; rarely a weak 3rd	Modest	Palatals often grooved
morsei	2.3–3.0	1.2–1.5	Narrowly conical – ovate	Moderate	Scattered, weak blunt	Shiny	Red-brown	Weak to modest	Weak to strong; white	Strong to very strong	Strong	Long; weak infraparietal sometimes present	Long	1 strong; sometimes a weak 2nd	2 long; sometimes a weak 3rd	Modest	Body whorl < $^{1}/_{3}$ of shell height
occidentalis	1.9–2.3	1.2–1.4	Broadly ovate	Moderate	Scattered, weak blunt	Shiny	Red-brown	Weak to modest; sharp	None	None to weak	None to vestigal	Short to vestigal	Short	None	1–2 short to vestigal	Weak to modest	
oralis	1.5–2.0	1.1–1.2	Ovate	Shallow	Numerous, regular, sharp	Silky	Red-brown	Strong	Strong	Very strong	Strong	Long	Long	1 strong; sometimes a weak 2nd and 3rd	2 long; sometimes a weak 3rd	Modest	Flaring aperture lip; palatals grooved
ovata	1.6–2.4	1.0–1.4	Broadly ovate	Moderate	Scattered, weak, blunt	Shiny	Yellow to red - brown	None to modest	None to strong; white	Modest	Strong-absent	Long	Long; infraparietal often present	1 strong; often a weak 2nd	2 long; often a weak 3rd	Weak to modest	Body whorl > $^{1}/_{2}$ shell height; columella wall not visible

(continues)

(continued)

Species	Height (mm)	Width (mm)	Shell Shape	Suture Depth	Striae	Luster	Color	Crest	Callus	Sinulus	Angular	Parietal	Columellar	Basal	Palatal	Palatal Depression	Other
perryi	1.5–1.9	1.0–1.1	Ovate – conical	Shallow	Scattered, irregular, weak. blunt	Silky; weakly malleate; spiral lines present	Yellow/ gray-brown	None to weak	None	None to weak	None	Short	Short	None	1–2 weak	Weak to modest	Aperture margin often dark
rugosula	1.7–2.2	1.0–1.2	Ovate – cylindrical	Shallow to moder-ate	Numerous, regular, sharp, strong	Dull; body whorl somtimes malleate	Red-brown	None to modest	Modest to none	Modest to strong	Strong	Long	Long	Short	2 long; some-times a weak 3rd	None to weak	Upper palatal often bent
teskeyae	2.1–2.9	1.5–1.8	Broadly ovate	Moder-ate to shallow	Scattered, irregular, weak blunt	Silky-dull	Red/ yellow-brown	Weak to modest	Modest to strong	Strong	Strong	Long	Long	Short	2	Weak to modest	Straight columellar wall; aperture flared basally and at columella
ventricosa	1.5–2.2	1.0–1.2	Conical – ovate	Moder-ate to deep	Scattered, irregular, blunt	Shiny	Red/ yellow-brown	None to strong	None to strong	Weak to strong	None	Long	Long	None-strong	2	Weak to strong	

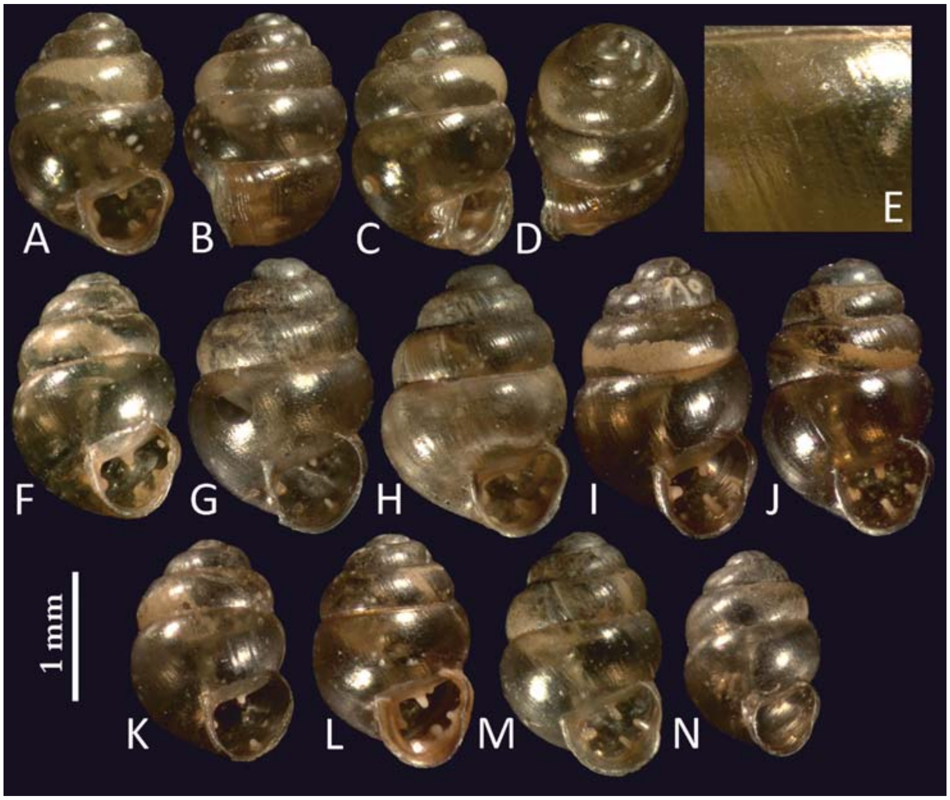


FIG. 17. ***Vertigo lilljeborgi vinlandica*** n. ssp. A–E: Holotype, ANSP 467369, Acid white cedar, ash, red maple swamp forest along inlet stream, Portage Lake, Maine, U.S.A. (46.7850°N, 68.5408°W); F: [VH51] Acid white cedar, ash, red maple swamp forest along inlet stream, Portage Lake, Maine, U.S.A. (46.7850°N, 68.5408°W); G: [B93] Acid sedge-grass turf, Schefferville Airport fen, Québec, Canada (54.8071°N, 66.8036°W); H: [B119] Sedge-willow lake margin Lac John, Schefferville, Québec, Canada (54.8138°N, 66.7920°W); *Vertigo lilljeborgi.* I: [B61] Sør-Trøndelag, Kongsvoll, Norway (62.3558°N, 9.6832°E); J: [B76] Urengoi, Khanty-Mansi, Russia (59.9880°N, 71.2883°E); K: [B62] Acid sedge tussocks, Little Langdale Tarn, Cumbria, England (54.4210°N, 3.0672°W); L: [J4] Alder-sedge margin, Lake Abashiri, Hokkaidō, Japan (43.9200°N, 144.1586°E); M: *Vertigo* cf. *ovata* [B117] Abandoned cranberry bog, Tispaquin Street, Massachusetts, U.S.A. (41.9010°N, 70.8521°W); N: *Vertigo perryi* [B63] Alder-sedge wetland, Clinton SE, Maine, U.S.A. (44.6112°N, 69.4430°W). When applicable, bracketed DNA specimen codes precede each entry.

material in their somewhat more ovate shape, shallower suture, stronger apertural callus, and presence of a weak angular lamella.

Ecology

Open or shrubby acid wetlands. In northwestern Europe, it is typically found on sedge and grass tussocks in lake shore flood zones.

Biogeography

Eurasia – British Isles, Scandinavia, and Baltic Countries east to north-central Asia and Hokkaidō with a few isolated locations in Spain, France, Switzerland, Germany and the Czech Republic. Preliminary MaxEnt climate envelopes based on all known *V. lilljeborgi* populations – including both the Hokkaidō and northeastern North American forms – strongly suggests that this species occurs as three highly disjunct populations: one centered on boreal Eurasia west of the Urals (typical *V. lilljeborgi*); one on the boreal Pacific coast of Alaska and eastern Eurasia (considered here as *V. lilljeborgi*); and one on the boreal eastern Atlantic coast of North America (***V. lilljeborgi vinlandica***, see below).

Nomenclature

If the presence of three disjunct population centers is empirically validated by more thorough field sampling in boreal central and eastern Eurasia and central North America, recognition of the forms restricted to each disjunct region as full species would appear justified. However, until such data is available we choose to not conduct this taxonomic act. Based on the original description, *Vertigo hydrophila* could represent the senior synonym for the boreal eastern Eurasian Pacific coast form of *V. lilljeborgi*.

Vertigo* (*Alaea*) *lilljeborgi vinlandica, n. ssp.

Fig. 15 (top row), 17A–H, Table 10

GenBank Accessions: KY217174-6; KY216786-8; KY217577-9; KY216433-5.

Diagnosis

Shell small, conical-ovate and similar to the boreal Eurasian *V. lilljeborgi*, but differing in its northeastern boreal North American range and distinct mtDNA and nDNA sequence; its shells also tend to have more strongly developed malleation.

Description

Shell: 1.8–2.4 mm tall x 1.2–1.5 mm wide (Holotype 1.9 x 1.3 mm), translucent to transparent, greenish-yellow to cinnamon-brown; approximately four whorls; broadly conical-ovoid; deep suture with tumid whorls (Fig. 17A–D, F–H); surface shiny to somewhat dull dependent upon malleation development (Fig. 17E); aperture $^1/_4$–$^1/_3$ of shell height, somewhat wider than tall and conspicuously small for the shell size (Fig. 17A, F–H), in profile not ascending onto body whorl (Fig. 17B); umbilicus closed by preceding whorls (Fig. 17C); peristome interrupted by body whorl, apertural lip only indistinctly flared (Fig. 17A–D, F–H); a crest may be present in back of the apertural margin with weak to absent apertural thickenings or callus (Fig. 17A–D, F, H); four to five apertural lamellae present including a peg-shaped columellar, a short blade-shaped parietal, two short blade-shaped palatals, and occasionally a weak basal (Fig. 17A, F–H), no depressions are present on the shell surface over the palatal wall (Fig. 17D).

Holotype (Fig. 17A–E): ANSP 467369, Portage Lake, Aroostook County, Maine, U.S.A.; acid white cedar, ash, red maple swamp forest along inlet stream; 46°47'05"N, 68°32'26"W; September 9, 2007.

Paratypes: ANSP 467370, collected with holotype: 5 shells. ANSP 467371, Schefferville Airport fen, Schefferville, Nunavik District, Québec, Canada; acid sedge-grass turf; 54°48'25"N, 66°48'12"W; August 8, 2006: 10 shells. ANSP 467372, Lac John, Schefferville, Nunavik District, Québec, Canada; sedge-willow lake margin; 54°48'49"N, 66°47'31"W; August 10, 2006: 5 shells.

Other, Non-Type Material Examined: NMW.Z.2015.0003-00005, ~200 shells from the above two Québec sites; 4 lots representing 61 individuals from the above sites plus and additional Schefferville, Québec site in the Nekola collection.

Etymology

The specific epithet refers to Vinland, the Viking name for the northeastern North American Atlantic coast which in general summarizes the known range for this subspecies.

Phylogenetics

Across all reconstruction methods in ITS1 + ITS2 this subspecies was part of the same highly supported (99–100) clade as *V. lilljeborgi*, but ***V. l. vinlandica*** was distinguished by a unique moderately supported (62–89) subclade in NJ, ME, and ML. Across all reconstruction methods in CytB + 16S this subspecies represented a highly supported subclade (98–100) within *V. lilljeborgi*.

Comparisons with Other Species

Shells are at best only weakly differentiated from *V. lilljeborgi* of boreal Eurasia, having perhaps a slightly more malleate surface sculpture and proportionally smaller aperture. This entity is much more readily distinguished in its mtDNA and nDNA sequence, and clearly represents a long-term North American isolate. However, because of its similar conchology and our lack of knowledge of range-wide *V. lilljeborgi* genetics, it seems prudent at the moment to identify the North American populations only at the subspecies level. This subspecies is also quite similar to various eastern North American races of *V. ovata*, in particular a distinct New England coastal form similarly restricted to highly acid wetlands. ***Vertigo l. vinlandica*** is most easily distinguished from that entity by its proportionally smaller aperture and much less flared apertural margin. ***Vertigo l. vinlandica*** can also be distinguished from *V. perryi*, which also inhabits highly acidic northeastern North American wetlands, by possessing a considerably larger shell with more prominent lamellae development.

Geographic Distribution

North America – Northern Maine to the central Québec/Labrador border. Given the frequent occurrence of its acid wetland habitat in northeastern maritime boreal North America, we expect that this taxon occurs across eastern Québec, Labrador, Newfoundland, and the maritime provinces of Canada. We suspect that the Ungava Bay record of "*V. ovata*" reported by Pilsbry (1948) actually represents ***V. l. vinlandica***; in our experience *V. ovata* does not occur north of the Gulf of St. Lawrence. Preliminary MaxEnt climate envelopes based on known sites for *V. lilljeborgi* s. lat. suggest that ***V. l. vindlandica*** may be highly disjunct from the nearest *V. lilljeborgi* populations along the boreal north Pacific coast, with boreal North America from Hudson's Bay to central Alaska possessing an inappropriate climate. If this prediction is borne out by additional empirical sampling, elevation of ***V. l. vindlandica*** to species level status may be warranted.

Ecology

Acid wetlands supporting extensive graminoid cover.

Vertigo (*Alaea*) *milium*
(Gould, 1840)
Fig. 15 (top row)

Pupa milium Gould, 1840: 402.

Type Locality: Oak Island, Chelsea, near Boston, Massachusetts, U.S.A.

Phylogenetics

In ITS1 + ITS2 analyzed specimens were part of a moderately to highly supported (82–100) clade across all reconstruction methods that included *V. binneyana*. In CytB + 16S all specimens were members of the same moderately to highly supported (64–100) clade across all reconstruction methods. Deep genetic variation was observed, however, with individuals varying on average by 17.2 bases in ITS1 + ITS2 and 42.3 bases in CytB + 16S. Although this suggests that *V. milium* may represent a species complex, individuals from populations separated by < 1 km in SW Arizona that varied in ITS2 by 8 bases, along with possessing different insertion-deletion patterns, shared similar shells and identical 16S sequence.

Conchology

This species is unique in the genus by possessing a curved lower palatal lamella that deeply enters the shell. However, considerable variability in other features was noted. Shells from northeastern and northcentral North America (and from which the type population was sourced) are cylindrical-ovate and have a very deep sinulus and a shiny shell luster with very weak striation. Shells from Florida and the Gulf Coast are smaller, more ovate, have a shallower sinulus, and possess sharp and regular striae over the first few whorls. Shells from the Ozarks and Arizona are narrowly cylindrical-ovate, have a moderately deep sinulus, and possess a dull-silky luster due to microscopic sculpture.

Ecology

Favors different habitats across its range. In northeastern and northcentral North America and Arizona *V. milum* is typically found in a variety of base-rich wetlands. It also inhabits wetlands along the Atlantic and Gulf Coasts where it appears tolerant of acidic conditions. In the Ozarks *V. milium* is found in upland forested calcareous rock outcrops. Such rock outcrop populations extend northeast into Iowa, Wisconsin and Vermont; Jamaican habitats are similar.

Biogeography

North America and Caribbean – New England states and adjacent southern Canada west to southern Manitoba and southeastern Arizona and south to Jamaica and Tampico, Mexico. While generally common, it is of sparse occurrence in western Tennessee, Kentucky, northern Mississippi and much of west Texas and New Mexico.

Vertigo (*Alaea*) *perryi*
Sterki, 1905: 53
Figs. 15 (second row), 16L

Type Locality: Warwick, Rhode Island, U.S.A.

Phylogenetics

Although differing on average in ITS1 + ITS2 by 9.3 bases from *V. ventricosa* and 9.0 bases from ***V. kurilensis***, and in CytB + 16S by 7.8 bases from *V. ventricosa* and 25.0 from ***V. kurilensis***, none of the four phylogenetic reconstruction methods placed analyzed specimens into a single monophyletic clade. In ITS1 + ITS2 the two New England specimens were shown across all four methods to represent a moderately to highly supported clade (82–100), with the Wisconsin specimen representing an unresolved separate branch. In CytB + 16S across NJ, ME and Bayesian methods all specimens were unresolved separate short branches. In ML the Wisconsin and Maine specimens were grouped into a clade with very poor support (21).

Conchology

Despite its ambiguous phylogenetic status, we consider this to be a species-level entity based on its well-defined and unique conchology*. Vertigo perryi* shares with *V. ventricosa* and ***V. kurilensis*** a small shell with irregular, weak striae and ovate-conical shape. It consistently differs from *V. ventricosa* shells in its more ovate shape, grayer olive-yellow color, silky luster from the presence of weak malleation and fine spiral lines on the shell surface, weaker lamellae development and a dark coloration of the apertural margin. These features remain constant across its range. No intermediate individuals between *V. perryi* and *V. ventricosa* have ever been noted, even in sites of sympatry. It differs from ***V. kurilensis*** in its lack of a flared apertural base, the presence of spiral lines on the shell surface, and its more poorly developed apertural lamellae.

Ecology

Moderately to highly acidic wetlands. It can be abundant in dead leaf accumulations adjacent to sedge tussocks and may also ascend into living vegetation.

Biogeography

North America – Northern Wisconsin to Newfoundland; most commonly encountered in the states bordering the Gulf of Maine.

Vertigo (*Alaea*) *ventricosa*
(Morse, 1865)
Fig. 15 (second row), 16I–K

Isthmia ventricosa Morse, 1865: 207.

Type Locality: Maine, U.S.A.

Synonyms: *Vertigo ventricosa* var. *elatior* Sterki, 1894: 5, type locality: New York, Michigan, Ohio and west to Montana, U.S.A.; *Vertigo idahoensis* Pilsbry, 1934: 100, type locality: Meadows, Adams County, Idaho, U.S.A.; along a creek east and northeast of the old town.

Phylogenetics

Across all reconstruction methods in ITS1 + ITS2 and CytB + 16S, this species existed as a highly supported clade (98–100) with ***V. kurilensis*** and *V. perryi* representing subclades and/or unresolved divergent branches. The Québec *V. ventricosa* form *elatior* specimen demonstrated ITS1 + ITS2 sequence differing by 35 bases, even though its CytB + 16S was part of the same strongly supported clade as the remainder of analyzed specimens. We suspect this may represent a taxonomically uninformative divergence similar to that observed in the subgenus *Vertigo*. Geographic partitioning between eastern U.S.A. and central/western U.S.A. montane populations was evident as moderately to highly supported (61–99) subclades in ITS1 + ITS2 and CytB + 16S across all reconstruction methods. However, specimen assignments to these subclades significantly varied between mtDNA and nDNA. Thus, we do not recognize taiga/boreal and western populations as distinct subspecies.

Conchology

This species is most similar in *Alaea* to *V. perryi*, ***V. kurilensis*** and *V. lilljeborgi* in its ovoid shell with reduced striation and 4–5 apertural lamellae. It differs from these species in its lack of spiral sculpture, malleation, and flared apertural margin. It also differs from *V. lilljeborgi* in its smaller shell volume and stronger sinulus. Considerable variability occurs within *V. ventricosa*: *Vertigo v.* form *elatior* has a larger and more conical, less reflective and transparent shell, typically with strong development of apertural lamellae and apertural callus. In the northeastern part of its range both shell forms (and intermediates) may occur within the same site. We have not seen any consistent traits to demarcate *V. idahoensis* and do not consider it to represent even a valid shell form.

Ecology

A wetland species occurring across a wide range of open to wooded, base-rich to base-poor sites. It appears particularly fond of graminoid leaf litter, and may crawl up into damp living grass and sedge leaves.

Biogeography

North America – Labrador and Newfoundland to the Yukon south to the central Appalachians and in the Rocky Mountains to the Mexican border in southeastern Arizona.

VERTIGO ANTIVERTIGO GROUP

Vertigo (*Alaea*) *antivertigo*
(Draparnaud, 1801)
Fig. 15 (third row)

Pupa anti-vertigo Draparnaud, 1801: 57.

Type Locality: Northern France.

Phylogenetics

This species existed as a highly supported clade (99–100) across all reconstruction methods in ITS1 + ITS2 and CytB + 16S. In ITS1 + ITS2 it was a member of the same poorly (51–59 in NJ, ME, ML) to highly (91 in Bayesian) supported clade that contained *V. oralis*. A similar grouping with poor support (50) was shown in the Bayesian reconstruction of CytB + 16S. This clade also contained *V. rugosula*.

Conchology

Within the subgenus this species shares with *V. oralis* and *V. ovata* an ovate shell with silky or shiny luster and at least six prominent apertural lamellae. It differs from *V. oralis* in its larger shell, weaker striation, weaker callus and unflared apertural lip. It differs from *V. ovata* in its less broadly ovate shape, shallower suture, stronger crest and stronger sinulus.

Ecology

Decaying and live vegetation in wetlands.

Biogeography

Western Eurasia – Iberia, British Isles and southern Scandinavia east to at least the Caucasus and southern Siberia.

Vertigo (*Alaea*) *berryi*
Pilsbry, 1919: 89
Fig. 15 (bottom row)

Type Locality: Mill Creek Canyon at 4,600 feet, San Bernardino Mountains, California, U.S.A.

Phylogenetics

As only a single individual has been sequenced, documentation of a species-level clade was not possible. This specimen existed across all reconstruction methods in ITS1 + ITS2 within a moderately to highly supported (69–99) clade containing single Maine specimens of *V. ovata* and *V. morsei* for which CytB + 16S data and conchology were, respectively, typical for those species. In CytB + 16S, *V. berryi* existed as a distinct branch within the highly supported (100) clade that contained *V. morsei*, *V. occidentalis*, and *V. ovata*. It was found to differ on average from these taxa by 4.7–6.9 bases in ITS1 + ITS2 and by 14.3–21.5 bases in CytB + 16S.

Conchology

We provisionally accept this taxon at the species level because it differs from *V. occidentalis*, *V. ovata* and *V. teskeyae* in its more narrowly conical-ovate shell, and body whorl constituting < 50% of the shell height. It differs from *V. morsei* in its smaller size, more conical shape, smaller aperture/shell size ratio, and in coming to maturity in six rather than seven whorls.

Ecology

Low elevation wetlands in the desert southwest, where it occurs in wet, decaying leaf litter.

Biogeography

North America – Southern Utah west into southern California. Pleistocene fossils exist from southeastern Arizona into the Mojave Desert.

Vertigo (*Alaea*) *morsei*
Sterki, 1894: 89
Fig. 15 (bottom row)

Type Locality: Kent County, Michigan, U.S.A.

Phylogenetics

In CytB + 16S, this species was represented across all reconstruction methods by a highly supported (99–100) clade, which was also a member of a highly supported (100) clade containing *V. berryi*, *V. occidentalis* and *V. ovata*. In ITS1 + ITS2, two of the three analyzed individuals were members of a moderately to highly supported (72–100) clade that contained

V. occidentalis and a single Japanese *V. ovata*. However, CytB + 16S and shells and of these latter two specimens were typical of their respective species. Additionally, in ITS1 + ITS2 the Maine *V. morsei* was a member of the same moderately to highly supported (69–99) clade that contained *V. berryi*.

Conchology

This species has a very distinct narrowly conical-ovate shell with 6–7 whorls at maturity and an aperture making up < $^1/_3$ of the shell height. It is most similar to *V. berryi*, but differs in its larger size, greater number of whorls in adult shells, and proportionally smaller aperture. When *Vertigo morsei* co-occurs with *V. ovata* intermediate individuals have never been observed.

Ecology

Highly calcareous fens and wetlands, where it often is found on decaying leaf litter just above marl flats. It may also be found on herbaceous vegetation, especially rushes.

Biogeography

North America – North shore of the Gulf of St. Lawrence in Québec west to the Rocky Mountain foothills in Alberta, and south to New Jersey, Illinois, Iowa and Minnesota. It is known as a Pleistocene fossil from Illinois.

Vertigo (*Alaea*) *occidentalis*
Sterki, 1907: 90
Fig. 15 (third row)

Type Locality: San Bernardino Mountains, California, U.S.A., at 7,600 feet.

Phylogenetics

As only a single individual has been sequenced, documentation of a species-level clade was impossible. Across all reconstruction methods in ITS1 + ITS2 this specimen existed in a moderately to highly supported (72–100) clade also containing *V. morsei* and a Japanese *V. ovata*. Because the topology of this clade is approximately the same as for *V. morsei* in CytB + 16S, we assume that the occurrence of *V. occidentalis* within it is due to incomplete sorting or introgression. In CytB + 16S it existed as an unresolved branch within the highly supported (100) clade containing *V. berryi*, *V. morsei* and *V. ovata*. It was found to differ on average from these species by 3.3–8.4 bases in ITS1 + ITS2 and by 15.0–25.4 bases in CytB + 16S.

Conchology

We only provisionally accept this taxon as a distinct species because DNA sequence data is not sufficient to evaluate the null hypothesis that it is conspecific with *V. berryi*, *V. morsei* or *V. ovata*. However, its shell differs from *V. berryi* and *V. morsei* by its broadly ovate shape and reduced apertural lamellae development, and from *V. ovata* by its weaker sinulus, absence of an apertural callus, short parietal lamella, and lack of a basal lamella.

Ecology

High elevation seepage wetlands.

Biogeography

North America – Currently known only from the San Bernardino Mountains above Big Bear Lake in southern California. It seems likely that it will eventually be found in other southern California ranges.

Vertigo (*Alaea*) *oralis*
Sterki, in Pilsbry, 1898: 120
Fig. 15 (third row)

Type Locality: Volusia County, Florida, U.S.A.

Synonyms: *Vertigo rugosula* var. *ovulum* Sterki, 1890: 35; *Vertigo rugosula oralis* Sterki of Pilsbry & Vanatta, 1900: 608.

Phylogenetics

This species was represented across all reconstruction methods by highly supported (96–100) clades in ITS1 + ITS2 and CytB + 16S. In ITS1 + ITS2, it was a member of the same poorly (51–59 in NJ, ME, ML) to highly (91 in Bayesian) supported clade that contained *V. antivertigo*. A similar grouping with poor support (50) was shown in Bayesian reconstruction of CytB + 16S. This clade also contained *V. rugosula*.

Conchology

Within the subgenus this species shares with *V. antivertigo* and *V. ovata* an ovate shell with silky or shiny luster and at least six prominent apertural lamellae. It differs from *V. antivertigo* in its slightly smaller size, stronger striation and callus, and flared apertural lip. It differs from *V. ovata* in its less broadly ovate shape, domed apex, shallower suture, and stronger crest.

Ecology

Found in a variety of wooded wetland habitats, ranging from pool margins in oak-sweetgum forest, red maple and cypress swamp to riparian and pocosin scrub. Individuals reside under logs and in broadleaf and graminoid leaf litter accumulations.

Biogeography

North America – North Carolina and Florida to Arkansas and Texas.

Vertigo (*Alaea*) *ovata*

Say, 1822: 375

Figs. 15 (third and bottom rows), 17M

Type Locality: Philadelphia, Pennsylvania, U.S.A.

Synonyms: *Pupa* (*Vertigo*) *hydrophila* Reinhardt, 1877: 323, type locality: Hakodate, Hokkaidō, Japan; *Vertigo eogea* Pilsbry, 1919: 151, type locality: Akkeshi, Kushiro on Hokkaidō, Japan.

Phylogenetics

This species as currently defined displays a complicated and polyphyletic phylogenetic pattern, being distributed among three different branches/clades that diverge on average by 9.3–26.5 bases in ITS1 + ITS2 and 41.8–56.1 bases in CytB + 16S. These branches also maintain the same basic topology across all reconstruction methods and datasets. One is a highly supported (98–100) clade in ITS1 + ITS2 and CytB + 16S that includes two specimens from acid wetlands on Long Island and Cape Cod. Another highly supported (91–100) clade in both datasets includes two specimens from the North Carolina and Texas coastal plain; the corresponding CytB + 16S clade also included a Tennessee *V. ovata* that possessed a typical shell and ITS1 + ITS2 sequence for that species. We assume that its inclusion in the CytB + 16S clade is due to mitochondrial introgression or incomplete sorting. Except for the Maine *V. ovata*, in ITS1 + ITS2 the remainder of specimens constituted a moderately to highly (61–94) supported clade. In CytB + 16S across all reconstruction methods, these specimens were members of the same highly supported (100) clade within which *V. berryi*, *V. morsei* and *V. occidentalis* represented divergent branches or subclades. In ITS1 + ITS2 and CytB + 16S no partitioning was noted between *V. ovata* and *V. eogea*.

Conchology

This species differs from the closely related *V. occidentalis* by its stronger callus and apertural lamellae development, and from *V. berryi* and *V. morsei* in its broadly ovate shell. It may be distinguished from *V. teskeyae* by its smaller volume, stronger apertural lamellae development, and curved columellar wall of the aperture. It is also similar to ***V. lilljeborgi vinlandica***, but may be distinguished by is larger aperture/shell size ratio and absence of surface malleation. We have yet to identify consistent conchological differences between the New England coast and southeastern coast races and typical *V. ovata*, other than these two distinct genetic races tend to have reduced apertural calcification.

Ecology

Wetland habitats, where it often prefers leaf litter from wide-leaved monocots such as *Typha*, *Phragmites* and *Carex*. Specimens from the two divergent coastal clades appear limited to highly acid wooded or *Sphagnum*-dominated wetlands.

Biogeography

North America and Caribbean to eastern Asia – Jamaica and other stations in the Caribbean north to Prince Edward Island and west to Arizona, Alaska, the Aleutian Islands, Japan, Taiwan, and perhaps mainland China (see below).

Nomenclature

Clearly, *V. ovata* is polyphyletic, including at least two additional undescribed species. However, because we have seen so few populations of these, we do not feel comfortable describing them at this time. Preliminary investigation of populations from New Jersey, near to the type location of *V. ovata* at Philadelphia, suggests that Say’s initial description represents the wide-ranging taxon that extends from eastern North America into east Asia, making *V. eogea* and *V. hydrophila* junior synonyms of *V. ovata* (but see comments under *V. lilljeborgi*). Based on its description, it also seems likely that the Chinese *V. teilhardi* is also a junior synonym.

Vertigo (*Alaea*) *rugosula*
Sterki, 1890: 34
Fig. 15 (second row)

Type Locality: Sullivan's Island, South Carolina, U.S.A.

Phylogenetics

This species is represented by a highly supported (99–100) clade across all reconstruction methods in both datasets. NJ, ME, and ML analyses of ITS1 + ITS2 showed it to be a member of the *V. milium* group with moderate to high support (66–90), however Bayesian reconstruction placed it in the *V. antivertigo* group with high support (100). This latter topology was replicated in CytB + 16S with low support (36–50) in NJ, ME, and ML and with high support (100) in Bayesian.

Conchology

This species is unique in the subgenus by possessing an ovate-cylindrical shell with dull luster and strong, sharp, regular striae. It also differs from the similar *V. oralis* in its weaker crest, callus, sinulus, and depression over the palatal lamellae.

Ecology

Unlike all other members of the subgenus, *V. rugosula* is found primarily in upland habitats such as prairie, mown roadsides, yards, riparian forests and rock outcrops. In these sites, it favors graminoid thatch accumulations.

Biogeography

North America and Caribbean – Coastal South Carolina to eastern Texas and Oklahoma. In Cuba, *V. rugosula* has been referred to as *V. torrei* Aguayo & Jaume, 1934.

Vertigo (*Alaea*) *teskeyae*
Hubricht, 1961: 62
Fig. 15 (bottom row)

Type Locality: Bank of canal, west side of Lake Waccamaw, Columbus County, North Carolina, U.S.A.

Phylogenetics

This species existed across all reconstruction methods as a highly supported (95–100) clade in both datasets. All reconstruction methods placed *V. teskeyae* in a highly supported clade (99–100) also containing *V. berryi*, *V. morsei*, *V. occidentalis* and *V. ovata*.

Conchology

This species shares with *V. ovata* a large, broadly ovate shell. It differs in its larger volume, relatively larger aperture, reduced apertural lamellae and a relatively straight vertical wall on the columellar side of the aperture.

Ecology

On open mud and water-saturated logs following water level drawdown in mid to late summer in floodplain and cypress forests and along river, pond and lake shores. It is also occasionally found in leaf or grass litter adjacent to boggy pools and streams.

Biogeography

North America – Chesapeake Bay to the Gulf Coast and west to southern Illinois, Oklahoma and Texas.

Nomenclature

It is remotely possible that material from the type locality could represent the distinct southern-coastal plain acidophile clade currently included in *V. ovata* (see above). If DNA analysis of topotype material supports this hypothesis, then the form here called *V. teskeyae* would require a new name.

ALAEA DISCUSSION

While interspecific genetic distances are generally quite high between most *Alaea* species, there appears to be poor genetic sorting within the clade containing *V. berryi*, *V. morsei*, *V. occidentalis* and some *V. ovata*. Not only are these taxa, in general, differentiated by few base pair changes but there is also frequent incongruency in topologic position between nuclear and mitochondrial data. The true nature of biological species within this group, and their relationships to one another, will require considerable additional sampling and likely analysis of more genetic loci. More sampling and loci will also be required to assess whether *V. perryi* represents a biologically valid species.

Similarly, additional sampling will be necessary to determine if cryptic species are present within *V. ovata* and *V. milium*, with both showing deep within-taxon divergence and topologies in ITS1 + ITS2 and CytB + 16S. Yet the identification of deep ITS2 divergence within the same *V. milium* population that possesses only a single 16S haplotype suggests that the story may not be simply deduced. These issues can only be assessed by analysis of individuals from across the range of both species, with *post hoc* consideration of conchological, ecological and biogeographic factors to see which (if any) demarcate any potential species-level taxa. Additional sampling across northern Japan and boreal East Asia will also be required to assess the appropriate placement of the Japanese *V. lilljeborgi*, in particular whether these populations are disjunct from those in central Asia and Europe, and thus whether they deserve subspecies or species level recognition. Sampling from mainland China is required to assess the status of *V. teilhardi*.

Transcontinental biogeographic ranges again are conspicuous, being represented by individual species (*V. ovata*) and both species-groups. Particularly striking is the sister-status of geographically widely separated species, such as *V. antivertigo* and *V. oralis*, and *V. ventricosa* and ***V. kurilensis.***

SUBGENUS *STAURODON*

Analyses of the subgenus *Staurodon* was based on 70 individuals for CytB + 16S and 69 for ITS1 + ITS2. The CytB segment was 367 bases and the 16S segment 441–447 bases, with a total of 276 variable sites along the entire CytB + 16S construct. The analyzed ITS1 segment was 606–646 bases, the analyzed ITS2 segment was 672–736 bases, with a total of 99 variable sites along the entire ITS1 + ITS2 construct.

In combination with conchology and ecological preferences, fifteen species-level entities are suggested (Tables 11, 13, Figs. 18, 19): *V. bisulcata*, *V. calamitosa*, *V. californica*, *V. catalinaria*, *V. clementina*, *V. cupressicola*, *V. dalliana*, *V. diegoensis*, *V. farquhari*, *V. griqualandica*, *V. hemphilli*, *V. rowellii*, *V. saxicola* and *V. trinotata*, with ***V. pimuensis*** being described as a new species. We also recognize the subspecies *V. californica longa*.

Mean within-taxon variability in ITS1 + ITS2 ranged from none in *V. calamitosa*, *V. californica longa*, *V. cupressicola*, and *V. diegoensis* to 5.0 bases in *V. griqualandica.* In CytB + 16S, within-species variability ranged from none in *V. dalliana* and *V. saxicola* to 19.3 bases in *V. californica* and 32.0 in *V. griqualandica*. Mean pairwise variation between species in ITS1 + ITS2 ranged from less than 2 bases (*V. californica* vs. *V. catalinaria*; *V. californica* vs. *V. rowellii*; *V. calamitosa* vs. *V. clementina*) to 40.0 (*V. bisulcata* and *V. farquhari* vs. *V. diegoensis*, *V. trinotata*, *V. cupressicola*, and ***V. pimuensis***) and in CytB + 16S from 11.6 (*V. cupressicola* vs. *V. rowellii*) to 109.6 (*V. calamitosa* vs. *V. farquhari*) bases (Table 11).

Four main groups below the subgenus level are suggested with very high support (96–100) across both datasets and all reconstruction methods except for the NJ and ME trees of CytB + 16S (Fig. 18): (1) The *Staurodon* group: *V. saxicola*. (2) The *Nearctula* group: *V. californica*, *V. c. longa*, *V. catalinaria*, *V. cupressicola*, *V. diegoensis*, *V. rowellii* and *V. trinotata*; *V. dalliana* was shown as a separate branch from this group across all four methods in ITS1 + ITS2, however in CytB + 16S all four methods place it here. (3) The *Sterkia* group: *V. calamitosa*, *V. clementina*, *V. hemphilli* and ***V. pimuensis***. (4) The *Afripupa* group: *V. bisulcata*, *V. farquhari* and *V. griqualandica*. The *Nearctula* and *Sterkia* groups were shown to be members of the same highly supported (100) clade across all reconstruction methods in both datasets.

STAURODON GROUP

Vertigo (*Staurodon*) *saxicola*
(Lowe, 1852)
Fig. 19 (bottom row)

Pupa (*Staurodon*) *saxicola* Lowe, 1852: 278.

Type Locality: in Madera [sic].

Synonym: *Pupa* (*Staurodon*) *seminulum* Lowe, 1852: 278, type locality: “in Madera”.

Phylogenetics

This species existed across all reconstruction methods in both datasets as a highly supported (100) clade. NJ, ME, and ML reconstructions of the ITS1 + ITS2 data showed it as a non-coalescing long branch intermediately placed between the *Afripupa* and *Nearctula/Sterkia* groups, the Bayesian reconstruction associated it with high (100) support as a very long branch within *Afripupa*. In CytB + 16S, Bayesian, NJ and ME reconstructions all associated this species with high support (91–100) to the *Nearctula/Sterkia* groups. However, the ML reconstruction associated it with no support to

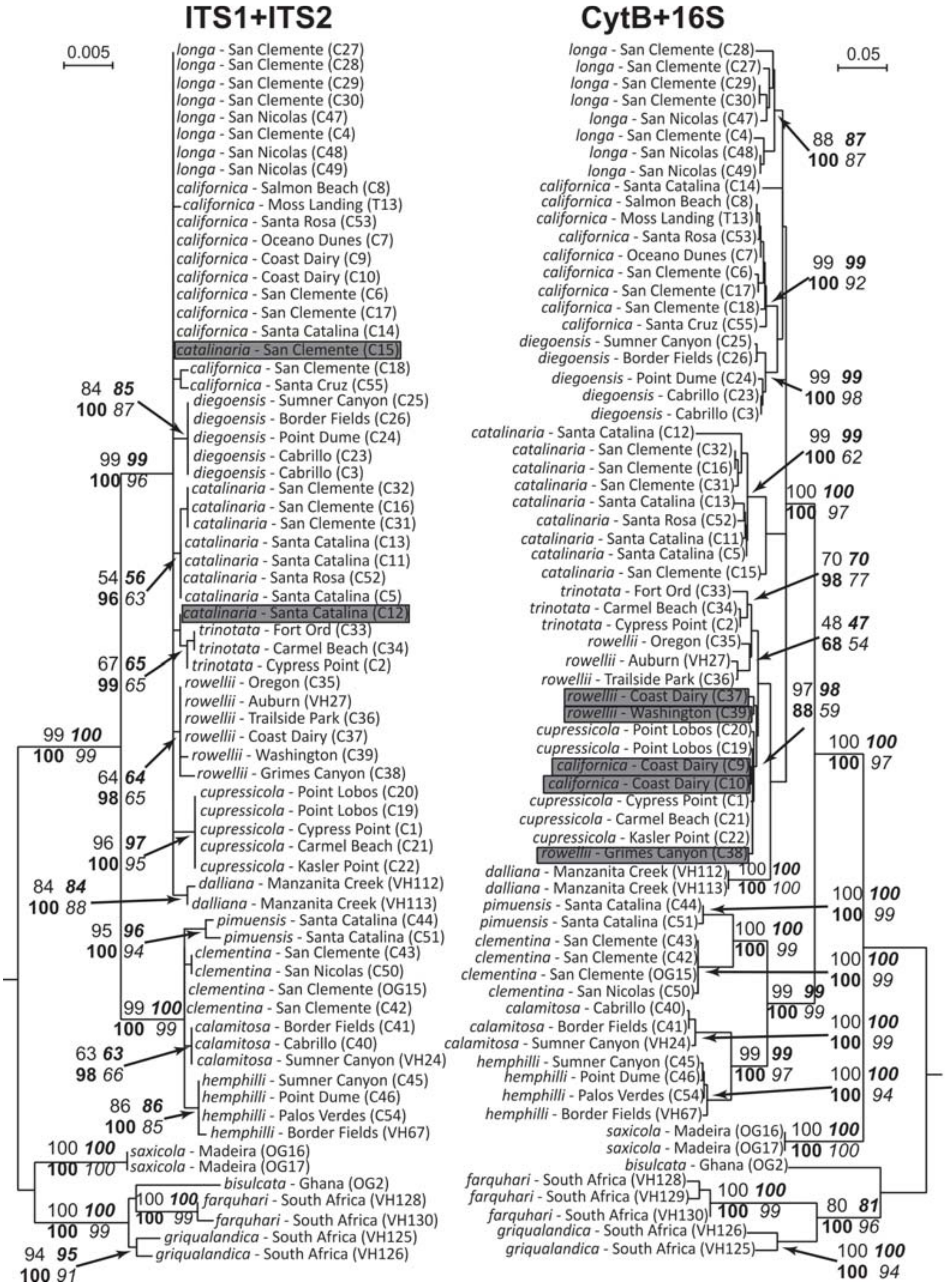


FIG. 18. Maximum-likelihood phylogenetic tree reconstructions in *Vertigo* (*Staurodon*) based on separate analysis of concatenated ITS1 + ITS2 and CytB + 16S data. Nodes with strong to moderate support have been labeled by four values: The upper left (normal font) is for Neighbor Joining. The upper right (***bold italic font***) is for Minimum Evolution. The lower left (**bold font**) is for Bayesian. The lower right (*italic font*) is for Maximum Likelihood. A grey box demarcates specimens which show incongruence in topologic location between the ITS1 + ITS2 and CytB + 16S trees, and likely represent examples of genetic introgression or incomplete sorting.

TABLE 11. Mean pairwise distances between *Vertigo* (*Staurodon*) species for the analyzed nDNA and mtDNA constructs, reported as nucleotide bases/construct. The lower half of the matrix represents distances in the ITS1 + ITS2 construct and the upper half (demarcated by *italic font*) represents distances in the CytB + 16S construct.

	californica	*c. longa*	*catalinaria*	*rowellii*	*diegoensis*	*dalliana*	*trinotata*	*cupressicola*	*clementina*	*calamitosa*	*hemphilli*	***pimuensis***	*saxicola*	*griqualandica*	*bisulcata*	*farquhari*
californica		*29.0*	*39.3*	*34.7*	*27.4*	*40.5*	*38.4*	*28.6*	*74.7*	*73.1*	*66.9*	*70.5*	*68.1*	*102.5*	*96.6*	*94.4*
c. longa	0.4		*40.5*	*39.5*	*28.1*	*46.6*	*42.9*	*33.6*	*77.8*	*80.8*	*72.1*	*73.1*	*71.9*	*104.8*	*96.4*	*95.7*
catalinaria	1.8	1.4		*44.6*	*39.4*	*51.7*	*45.5*	*39.6*	*76.4*	*74.2*	*65.8*	*73.4*	*73.8*	*108.3*	*94.4*	*96.4*
rowellii	1.9	1.5	2.9		*40.3*	*40.5*	*19.1*	*11.6*	*76.1*	*78.4*	*67.3*	*72.4*	*74.8*	*106.0*	*97.8*	*98.8*
diegoensis	2.4	2.0	3.4	3.5		*45.2*	*43.3*	*36.8*	*74.6*	*80.3*	*69.9*	*73.7*	*66.4*	*103.9*	*95.2*	*92.3*
dalliana	2.9	2.5	3.9	4.0	4.5		*42.3*	*38.2*	*80.3*	*81.7*	*73.0*	*80.5*	*80.0*	*106.5*	*103.0*	*108.0*
trinotata	3.1	2.7	3.8	4.2	4.7	5.2		*16.9*	*75.8*	*77.4*	*65.7*	*72.3*	*78.0*	*103.2*	*100.0*	*99.2*
cupressicola	3.4	3.0	4.4	4.5	5.0	5.5	5.7		*73.7*	*76.1*	*65.0*	*69.5*	*71.6*	*103.3*	*93.6*	*94.9*
clementina	16.9	16.5	17.5	18.0	18.5	18.0	19.2	19.5		*65.2*	*62.8*	*39.5*	*86.0*	*108.8*	*105.3*	*104.6*
calamitosa	17.4	17.0	18.0	18.5	19.0	18.5	19.7	20.0	1.5		*40.6*	*61.2*	*88.3*	*110.7*	*108.7*	*109.6*
hemphilli	18.3	18.3	19.3	19.8	20.3	19.8	20.9	21.3	2.8	3.3		*60.8*	*82.5*	*106.0*	*101.8*	*100.2*
pimuensis	20.9	20.5	21.5	21.9	22.5	22.0	23.2	23.5	5.0	5.5	6.8		*87.5*	*103.3*	*108.0*	*97.5*
saxicola	29.3	29.0	29.1	29.2	31.0	29.0	31.0	31.0	30.5	30.0	32.3	34.0		*96.0*	*90.0*	*103.7*
griqualandica	33.8	33.5	33.6	34.0	35.5	32.5	35.5	35.5	33.0	32.5	34.8	35.5	26.5		*83.5*	*75.5*
bisulcata	38.3	38.0	38.1	38.2	40.0	37.0	40.0	40.0	37.5	37.0	39.3	39.5	33.0	15.5		*90.0*
farquhari	38.3	38.0	38.1	38.5	40.0	37.0	40.0	40.0	37.5	37.0	39.3	40.0	32.0	13.5	19.5	

the *Afripupa* group. The consensus appears to be that *Staurodon* holds an intermediate position linking the *Nearctula* and *Sterkia* groups to the *Afripupa* group.

Conchology

Within *Staurodon*, *V. saxicola* is most similar to members of the *Sterkia* group, with which it shares a columnar shell < 1.8 mm tall. It differs from these by its sharply, regularly, and narrowly striate surface in conjunction with peg-shaped palatal lamellae and a forward-placed low, knob-like angular lamella. Outside of the subgenus, it is closest to some *Vertigo s. str.* such as *V. arthuri*, *V. hannai* and *V. inserta* that possess small, regularly striate shells with a prominent angular lamella. However *V. saxicola* differs from all these by lacking a crest, callus, and depression over the palatal lamella.

Ecology

Confined to shaded, low elevation rock outcrops and rock walls.

Biogeography

Macaronesia – Madeira, but present in Quaternary deposits on the neighboring island of Porto Santo.

NEARCTULA GROUP

Vertigo (*Staurodon*) *californica*
(Rowell, 1862)
Figs. 19 (top and second rows), 20A–G

Pupa californica Rowell, 1862: 287.

Type Locality: San Francisco, California, U.S.A.

Synonym: *Nearctula rowellii* (Newcomb, 1862) of Turgeon et al., 1998, and Roth & Sadeghian, 2003.

Phylogenetics

In ITS1 + ITS2 all but one individual shared identical sequence representing the base from which *V. catalinaria*, *V. cupressicola*, *V. diegoensis*, *V. rowellii* and *V. trinotata* have all diverged. In CytB + 16S *V. californica* existed as a highly supported (92–100) clade across all reconstruction methods. Although Santa Catalina and Santa Cruz Island specimens possessed divergent mtDNA sequence, they shared almost identical ITS1 + ITS2 sequence to the majority of *V. californica* specimens. Two individuals with typical shells from Coast Dairy Beach near Santa Cruz, California, were found to have CytB + 16S characteristic of *V. cupressicola.*

Conchology

On the mainland and Santa Rosa Island this species shell is characterized by its large size (often > 2.3 mm height), cylindrical to

FIG. 19. Shells of *Vertigo* (*Staurodon*). Bracketed DNA specimen codes precede each entry. Top row (left to right): *Vertigo californica*: [C7] Oceano Dunes, California, U.S.A. (35.1208°N, 120.6326°W); [C8] South Salmon Beach, California, U.S.A. (38.3492°N, 123.0659°W); [C10] Coast Dairy, California, U.S.A. (36.9893°N, 122.1672°W). *Vertigo californica longa*: [C4] Wilson Cove, San Clemente Island, California, U.S.A. (32.9953°N, 118.5516°W); [C48] Mineral Canyon, San Nicolas Island, California, U.S.A. (33.2537°N, 119.5032°W); [C47] Daytona Beach, San Nicolas Island, California, U.S.A. (33.2260°N, 119.4396°W). Second row (left to right): *Vertigo californica* (San Clemente form): [C6] Radar Station, San Clemente Island, California, U.S.A. (32.9745°N, 118.5317°W). *Vertigo californica* (Santa Catalina form): [C14] Cherry Canyon, Santa Catalina Island, California, U.S.A. (33.4505°N, 118.5138°W). *Vertigo catalinaria*: [C5] Bulrush Canyon, Santa Catalina Island, California, U.S.A. (33.3456°N, 118.4419°W); [C32] Thirst Peak, San Clemente Island, California, U.S.A. (32.8815°N, 118.4443°W); [C13] Two Harbors South, Santa Catalina Island, California, U.S.A. (33.4331°N, 118.5094°W). *Vertigo cupressicola*: [C1] Cypress Grove, Carmel, California, U.S.A. (36.5782°N, 121.9727°W); [C20] Point Lobos, California, U.S.A. (36.5215°N, 121.9519°W). Third row (left to right): *Vertigo diegoensis*: [C3] Point Loma, San Diego, California, U.S.A. (32.6720°N, 117.2449°W); [C24] Point Dume, Malibu, California, U.S.A. (34.0023°N, 118.8075°W); [C26] Border Field State Park, California, U.S.A. (32.5357°N, 117.1174°W). *Vertigo trinotata*: [C2] Cypress Grove, Carmel, California, U.S.A. (36.5782°N, 121.9727°W). *Vertigo dalliana*: [VH112] Manzanita Creek, California, U.S.A. (38.7396°N, 123.2446°W). *Vertigo rowellii*: [C36] Trailside Park, California, U.S.A. (38.7563°N, 122.6364°W). Bottom row (left to right): *Vertigo calamitosa*: [VH24] Sumner Canyon, La Jolla, California, U.S.A. (32.8734°N, 117.2483°W). *Vertigo hemphilli*: [VH67] Border Field State Park, California, U.S.A. (32.5428°N, 117.1061°W). *Vertigo clementina*: [OG15] Wilson Cove, San Clemente Island, California, U.S.A. (32.9953°N, 118.5516°W). ***Vertigo pimuensis***: [C44] USC Marine Lab, Santa Catalina Island, California, U.S.A. (33.4458°N, 118.4817°W). *Vertigo bisulcata*: [OG2] Fetish Grove, Ghana (5.3356°N, 0.0801°W). *Vertigo griqualandica*: [VH127] Biggarsberg, KwaZulu-Natal, South Africa (28.2000°S, 29.9170°E). *Vertigo farquhari*: [VH128] Burman Bush, KwaZulu-Natal, South Africa (29.8149°S, 31.0174°E). *Vertigo saxicola:* [OG16] Rua da Ribeira, Madeira (32.6928°N, 16.8044°W).

←

cylindrical-ovate shape, and presence of strong and irregular rib striae. It is most similar to *V. cupressicola* and some *V. diegoensis* which also commonly possess 3–4 apertural lamellae. It is readily distinguished from *V. cupressicola* by its larger size and denser and stronger rib striae. It can be most easily distinguished from *V. diegoensis* by its blade-shaped lamellae, less dense and blunter rib striae and larger size. On San Clemente, Santa Catalina, and Santa Cruz Islands a distinct shell form occurs which is smaller, and usually possesses a more domed apex and much weaker (to vestigal) rib striae as compared to *V. c. californica*, *V. c. longa* or *V. catalinaria*. However, these features are not completely reliable and DNA sequence may be required to confirm identification.

Ecology

Deep sandy soils where it occurs in cypress groves and/or open dune swales from Sonoma County south to Santa Rosa Island. It also has been observed in San Francisco on a shaded, seepy cliff. The small shell form on San Clemente, Santa Catalina and Santa Cruz Islands occurs in shaded upland habitats and avoids sandy substrates.

Biogeography

North America – Pacific coast from Bodega Bay in Sonoma County, California south to Oceano Dunes in San Luis Obispo County and Santa Rosa and Santa Cruz Islands off of Santa Barbara. On the mainland, it never occurs more than a kilometer from the marine shore. In upland sites on the Channel Islands it is present as the unique shell form described above.

Nomenclature

We retain *Vertigo californica* (Rowell, 1862) and *Vertigo rowellii* (Newcomb, 1862), as understood by all authors prior to Turgeon et al. (1998) and Roth & Saghedian (2003). The two species are unambiguously distinguished in their original descriptions, *rowellii* being “finely striated” and *californica* having “oblique rib-like striae”. The 10 shells in the *Pupa californica* paratype lot (ANSP 59392) match Rowell’s original description. In spite of this, Clarke (1960: 154, pl. 17, fig. 5, reproduced here as Fig. 20A) selected as the *Pupa rowellii* lectotype a shell from the putative type lot (CU29170) that conformed to the description of *Pupa californica*. For this reason, *californica* was regarded as a junior synonym of *rowellii* by Turgeon et al. (1998) and Roth & Sadeghian (2003). However, neither the shell currently identified as the *Vertigo rowellii* lectotype (CU29170A; Fig. 20B) nor the other paralectotypes in the lot (Fig. 20C–G) correspond to the illustrated Clarke (1960) lectotype, which appears to have been lost. To stabilize the nomenclature of these taxa we have selected a neotype from Newcomb’s paralectotypes that

FIG. 20. *Pupa rowellii* Newcomb, 1862 type lot (CU29170). A: Reproduction of the figure of the lectotype selected by Clarke (1960: pl. 17; fig. 5). Note that it does not agree with the *rowellii* description, and represents *V. californica*. This specimen is no longer extant; B: Shell currently labeled as the *rowellii* lectotype (CU29170A). Note that this shell appears intermediate between *rowellii* and *californica* and may represent a hybrid; C–G: Remaining paralectotypes, representing *V. californica*; H: The final remaining paralectotype, representing a shell in agreement with the *rowellii* description. This has been selected as the *rowellii* neotype (CU42441).

corresponds with the original description of *rowellii* (CU42441; Fig. 20H). This reinstates name usage according to their authors' original intent and subsequent use by Pilsbry (1919, 1948) and all other authors prior to 1998.

Vertigo (*Staurodon*) *californica longa*
Pilsbry, 1920: 377
Fig. 19 (top row)

Type Locality: San Clemente Island, California, U.S.A.

Synonyms: *Pupa californica* var. *elongata* Sterki, 1890: 8; *Vertigo californica elongata* Pilsbry, 1919: 142.

Phylogenetics

Although this subspecies shared identical ITS1 + ITS2 sequence with typical *V. californica*, it was found to differ in CytB + 16S on average by 29 bases. The subspecies formed a moderately to highly supported (87–100) clade divergent from the nominate subspecies across all reconstruction methods.

Conchology

Shells of *V. c. longa* and *V. californica* show a similar pattern of variation, but on average *longa* is slightly more cylindrical and possess coarser and less dense striae. It co-occurs on San Clemente Island with *V. catalinaria* and the local *V. c. californica* race, differing from both in its larger size, coarser rib striae and more cylindrical shell.

Ecology

Found across a wide range of xeric coastal scrub and woodland sites but appearing to avoid sandy substrates.

Biogeography

North America – Genetically confirmed populations are limited to San Clemente and San Nicolas in the California Channel Islands. It has also been reported from Santa Barbara Island.

Vertigo (*Staurodon*) *catalinaria*
(Sterki, 1890)
Fig. 19 (second row)

Pupa californica var. *catalinaria* Sterki, 1890: 9.

Type Locality: Santa Catalina Island, California, U.S.A.

Phylogenetics

In ITS1 + ITS2 the majority of specimens formed a poorly to highly supported (54–96) clade. However, two individuals from San Clemente and Santa Catalina Islands had divergent sequences being closest, respectively, to *V. californica* and *V. trinotata*. Both had shells closely resembling *V. catalinaria*. In CytB + 16S, the majority of specimens also formed a moderately to highly supported (62–100) clade. However, the two specimens discussed above again possessed divergent sequence only weakly associated with this clade.

Conchology

This species shares with *V. californica* and *V. c. longa* a rib-striate shell with four apertural lamellae. It differs from the southern Channel Island form of *V. c. californica* in its more tapered apex and denser and sharper rib striae. It differs from *V. c. longa* by a smaller, more conical shell with slightly denser and sharper striae. It may be differentiated from the race of *V. diegoensis* bearing palatal lamellae by having these be blade-shaped. These features are somewhat variable, however, and DNA sequence analysis may be required to confirm identification.

Ecology

Most often found in leaf litter in oak and cherry forest. On Santa Catalina, it also occurred in *Salvia-Artemisia* coastal scrub.

Biogeography

North America – Genetically confirmed populations are limited to San Clemente, Santa Catalina and Santa Rosa in the California Channel Islands. It has also been reported from Santa Barbara and Guadalupe Islands.

Vertigo (*Staurodon*) *cupressicola*
Sterki, in Pilsbry, 1919
Fig. 19 (second row)

Vertigo californica cupressicola Sterki, in Pilsbry, 1919: 143.

Type Locality: Cypress Point, Monterey, California, U.S.A.

Phylogenetics

This species existed as a highly supported (95–100) clade across all reconstruction methods in ITS1 + ITS2, and at lower support (59–98) in CytB + 16S across all four reconstruction methods. However, almost half of the mtDNA clade constituted *V. californica* or *V. rowellii* for which ITS1 + ITS2 sequence, shells, and ecological preferences were otherwise typical of those species. Thus, *V. cupressicola* appears to be a common mitochondrion donor to other *Nearctula* group members in the Monterey area, with these resultant populations having been widely dispersed. It is interesting to note that *V. cupressicola* mtDNA has not been found in *V. trinotata*, even though it is microsympatric at most *V. cupressicola* sites.

Conchology

This species closely resembles *V. catalinaria* and the Channel Islands form of *V. californica*. It differs from the former in its less dense rib-striae and less conical shell. It differs from the latter in its denser and more conspicuous rib-striae, deeper suture, and larger aperture relative to shell volume. On the central coast, it is sympatric with *V. californica*, *V. rowellii* and *V. trinotata*, from which it differs by its smaller shell and more remote striae. Intermediate individuals between these species have never been observed.

Ecology

Native Monterey cypress groves and fog belt chaparral within 1 km of the marine shore; it appears to avoid sandy substrates.

Biogeography

North America – Endemic to the Monterey, California, area where it ranges across only 16 km from Cypress Point in Carmel south to the

Rock Creek Bridge in the Big Sur. This species has the most limited range of any known mainland continental *Vertigo*.

Vertigo (*Staurodon*) *dalliana*
(Sterki, 1890)
Fig. 19 (third row)

Pupa dalliana Sterki, 1890: 19.

Type Locality: near Clear Lake, Lake County, California, U.S.A.

Phylogenetics

This species existed across all reconstruction methods in ITS1 + ITS2 and CytB + 16S as a moderately to highly supported (84–100) clade.

Conchology

Vertigo dalliana shells differ from all other *Staurodon* in their conic shape, weak striae and lack of apertural lamellae. Its shell shape and color are reminiscent of *V. meramecensis*, North America's only other obligately rupicolous *Vertigo*.

Ecology

Restricted to mossy limestone outcrops. It frequently covers its shell with dirt.

Biogeography

North America – Foothills of the central Sierra Nevada in Tuolumne County west to Lake County, California, and north into southern Oregon.

Vertigo (*Staurodon*) *diegoensis*
(Sterki, 1890)
Fig. 19 (third row)

Pupa californica var. *diegoensis* Sterki, 1890: 18.

Type Locality: False Bay near Asher Station, San Diego, California, U.S.A.

Phylogenetics

This species existed as a moderately to highly supported (84–100) clade in both datasets across all reconstruction methods. All specimens shared identical ITS1 + ITS2 sequence, but two highly supported (98–100) subclades were evident across all reconstruction methods in CytB + 16S; one represented by shells with 0–1 palatal lamellae, and the other by shells with 2 palatal lamellae.

Conchology

Populations of *V. diegoensis* possessing reduced to absent palatal lamellae are most similar to *V. trinotata* in their rib-striate shell and (when present) a peg-shaped palatal lamella. *Vertigo diegoensis* differs, however, in its somewhat smaller size, grey-brown color, and possession of a parietal lamella which points towards the upper palatal region. *Vertigo diegoensis* populations supporting two strong palatal lamellae appear closest to *V. californica* and *V. catalinaria*, but differ from both in the peg-like shape of those lamellae.

Ecology

Litter accumulations under dense scrub cover in fog-belt coastal scrub, usually not more than 1 km from the marine shore.

Biogeography

North America – Point Dume at Malibu, California, south through the Los Angeles Basin to San Diego and Baja California.

Vertigo (*Staurodon*) *rowellii*
(Newcomb, 1862)
Figs. 19 (third row), 20H

Pupa rowellii Newcomb, 1862: 146.

Type Locality: near Oakland, California, U.S.A.

Synonyms: *Nearctula* species of Turgeon et al., 1998 and Roth & Sadeghian, 2003; "Hoko *Vertigo*" of Burke (2013).

Phylogenetics

This species existed across all reconstruction methods as a moderately to highly supported (64–98) clade in ITS1 + ITS2, and as a poorly to moderately supported (47–68) clade in CytB + 16S. Although existing as an unresolved branch in ITS1 + ITS2, in CytB + 16S it was found to be a member of a moderately to highly supported (69–100) clade that included *V. trinotata*. One-half of the analyzed *V. rowellii* possessed typical ITS1 + ITS2, shells, and habitat preferences, but had CytB + 16S characteristic of *V. cupressicola*.

Conchology

This species differs from all others in the group by possessing a large tapered shell with irregular thread-like striae. We note that the putative, unnamed "Hoko *Vertigo*" of Burke (2013), and grey-literature citations therein, appears like *V. rowellii* with a somewhat more massive lower palatal lamella and additional vestigial lamellae between the lower and upper palatals. Given that this degree of palatal lamellae variation falls well within the range seen in other *Nearctula* group members – especially *V. californica* – and given that its conchology and habitat requirements are otherwise identical to *V. rowellii*, we strongly suspect that the "Hoko *Vertigo*" simply represents a shell form of *V. rowellii* with no taxonomic merit.

Ecology

Populations more than a few hundred meters from the marine shore are strictly arboreal on mossy deciduous tree trunks and branches. Immediately adjacent to the shore they may also live on small shrubs and in shaded leaf litter.

Biogeography

North America – British Columbia to the central California coast and inland to the foothills of the central Sierra Nevada Mountains. The record of this species from the San Bernardino Mountains (ANSP 46364) seems likely based on a labeling error, as its required habitat does not occur at the recorded station and we have been unable to find it there or other sites in the region.

Nomenclature

Selection by Clarke (1960) of a shell conforming to *Pupa californica* Rowell, 1862, to represent the *Pupa rowellii* Newcomb, 1862, lectotype (CU29170A; Fig. 20A) resulted in *rowellii* being applied to material that had previously been named *californica*, with material referable to the original description of *rowellii* lacking an available name. Because the Clarke lectotype has been lost (see above), we have chosen to stabilize the nomenclature by selecting a neotype from among Newcomb's paralectotypes that corresponds to the original description of *rowellii* (CU42441; Fig. 20H). This reinstates name usage according to the authors' original (and unambiguous) descriptions and subsequent use by Pilsbry (1919, 1948) and other authors prior to 1998.

Vertigo (*Staurodon*) *trinotata*
(Sterki, 1890)
Fig. 19 (third row)

Pupa californica var. *trinotata* Sterki, 1890: 18.

Type Locality: Monterey, California, U.S.A.

Phylogenetics

Across all reconstruction methods, this species existed as a moderately to highly supported (66–99) clade in ITS1 + ITS2 and CytB + 16S. Existing as an unresolved branch in ITS1 + ITS2, in CytB + 16S it was member of a moderately to highly supported (69–100) clade that included *V. rowellii*. One of the Santa Catalina Island *V. catalinaria* with a characteristic CytB + 16S sequence and shell of that species possessed aberrant ITS1 + ITS2 sequence similar to that of *V. trinotata*.

Conchology

This species shares with some *V. diegoensis* an aperture that has only one peg-shaped palatal lamella. It differs from that species in its slightly larger shell size, red-brown color, and possession of a parietal lamella which points towards the lower palatal lamella.

Ecology

Leaf litter accumulations under fog-belt scrub and cypress/oak forest. It often assumes higher densities around trunk bases. It may range inland a number of kilometers from the marine shore and can occur in deep sandy soils. It also colonizes litter accumulations under naturalized Hottentot Fig/Sea Fig (*Carpobrotus*) mats.

Biogeography

North America – Endemic to the Monterey, California, area where it ranges a little over 20 km from the former Fort Ord south to Garrapata State Park.

STERKIA GROUP

Even though not valid at the genus or subgenus level, *Sterkia* retains utility by categorizing this well-defined group within *Staurodon*. It is important to point out that we do not yet possess sequence data to evaluate whether Caribbean *Sterkia* (*Metasterkia*) of Pilsbry (1920) should be included here.

Vertigo (*Staurodon*) *calamitosa*
(Pilsbry, 1889)
Fig. 19 (bottom row), 21L

Pupa calamitosa Pilsbry, 1889: 61.

Type Locality: near the mouth of the San Tomas River, Baja California Norte, Mexico.

Phylogenetics

This species was defined across all reconstruction methods by a moderately to highly supported (63–98) clade in ITS1 + ITS2, and a highly supported clade (99–100) in CytB + 16S. Although existing as one of four unresolved branches in ITS1 + ITS2, in CytB + 16S *V. calamitosa* was a member of a highly supported (97–100) clade including *V. hemphilli*.

Conchology

This species is perhaps most similar to *V. hemphilli*, with which it shares a small, columnar shell with strong striae. However, it is easily distinguished by its somewhat smaller size, vertical crescent-shaped columellar lamella, very strong angular lamella, and shorter and less deeply inserted lower palatal lamella.

Ecology

Leaf litter accumulations in coastal fog-belt scrub within 200 meters of the marine shore.

Biogeography

North America – La Jolla on the north side of San Diego, California, U.S.A. south to central Baja California, Mexico; also found on San Martin Island just off the Baja California shore. It has yet to be observed more than 1 km from the marine shore.

Vertigo (*Staurodon*) *clementina*
(Sterki, 1890)
Figs. 19 (bottom row), 21I–K, O, Q

Pupa clementina Sterki, 1890: 44.

Type Locality: San Clemente Island, California, U.S.A.

Phylogenetics

Across all reconstruction methods in ITS1 + ITS2, this species appeared as the base from which the other three *Sterkia* species have diverged. In CytB + 16S, however, it was represented in all reconstruction methods by a highly supported (99–100) independent clade. These data also showed it to be a member of a highly supported (99–100) clade that includes ***V. pimuensis***.

Conchology

This species is closest to ***V. pimuensis***, sharing with it a small, columnar shell with reduced striation and simple apertural lamellae. It differs from that species by its shinier luster, more yellow-brown color, shallower suture, and blade-shaped angular lamella as seen in apertural view. Pilsbry (1948) placed this species in the section *Metasterkia* due to its reduced striae.

Ecology

This species is found across a wide range of habitats ranging from xeric fog-belt scrub to mesic canyon forest.

Biogeography

North America – Genetically confirmed populations are confined to San Clemente and San Nicolas in the California Channel Islands. All known Santa Catalina Island reports represent ***V. pimuensis***. While reported from Santa Barbara and Guadalupe Islands, we have yet to obtain specimens for genetic verification.

Vertigo (*Staurodon*) *hemphilli*
(Sterki, 1890)
Figs. 19 (bottom row), 21M

Pupa hemphilli Sterki, 1890: 27, pl. 1, fig. 6.

Type Locality: Bank of the San Tomas River, Baja California Norte, Mexico.

Phylogenetics

Across all reconstruction methods, this species existed as a moderately to highly

TABLE 12. Conchological traits for *Vertigo* (*Staurodon*) members.

Species	Height (mm)	Width (mm)	Shell Shape	Suture Depth	Striae	Luster	Color	Crest	Callus	Sinulus	Angular	Parietal	Columellar	Basal	Palatal	Palatal Depression	Other
bisulcata	1.7–1.9	0.9–1.0	Conical	Deep	Strong, sharp, regular	Dull	Yellow/red - brown	None	None to modest; at margin	Strong	Very strong	Long	Long, pointed downward	None	2	Groove over upper palatal	
calamitosa	1.4–1.9	0.7–0.9	Cylindrical	Moderate	Strong, sharp, regular	Dull	Yellow/red - brown	Weak to strong; deeply set	None to strong; at margin	Weak to modest	Very strong; long	Long, sinuous; infraparietal sometimes present	Long curved vertical plate	None	Lower peg; upper curved	Groove over upper palatal	Aperture margin strongly flared
californica	1.7–2.6	1.0–1.3	Cylindrical-ovate to cylindrical	Moderate	Very strong to weak; sharp to blunt; dense to remote	Dull	Dark brown-red	None	None	Weak	None to vestigal	Long	Peg	None	Lower strong to weak; Upper moderateto absent	None	
californica longa	2.1–2.7	1.0–1.3	Cylindrical to cylindrical-ovate	Moderate	Very strong, sharp, regular	Dull	Dark brown-red	None	None to weak	Weak	None to vestigal	Long	Peg	None	Lower strong; Upper moderateto absent	None	
catalinaria	1.6–2.1	1.0–1.2	Ovate-conical	Moderate	Strong, sharp, dense to remote	Dull	Dark brown-red	None	None	Weak to none	None	Long	Peg	None	2	None	
clementina	1.6–2.0	0.8–0.9	Cylindrical	Moderate to shallow	Weak, blunt, irregular	Silky - shiny	Yellow	None to modest; deeply set	None to modest; at margin	Weak to modest	Strong; blade	Long	Peg	None	2	Weak to modest groove over upper palatal	

(continues)

(continued)

Species	Height (mm)	Width (mm)	Shell Shape	Suture Depth	Striae	Luster	Color	Crest	Callus	Sinulus	Angular	Parietal	Columellar	Basal	Palatal	Palatal Depression	Other
cupressicola	1.6–2.2	1.0–1.1	Cylindrical-ovate	Moderate	Strong, blunt, remote	Silky-dull	Red-brown	None to very weak	None	None to weak	None	Long; sinuous	Peg	None	2	None	
dalliana	2.0–2.2	1.3–1.4	Conical	Deep	Weak to sharp, irregular	Silky-shiny	Red-brown	None	None to weak; at margin	None to weak	None	None	None	None	None	None	
diegoensis	1.7–2.2	1.0–1.2	Ovate-conical	Moderate	Strong, sharp, numerous	Dull	Brown	None to very weak	None	Weak	None	Long	Peg	None	None to 2 short	None	Parietal lamella points at upper palatal
farquhari	1.3–1.8	0.7–0.9	Conical	Moderate	Modest to strong, sharp, regular	Dull	Red-brown	None	None	Modest	Very strong; long	Very strong; long	Long	Peg to vestigal	Lower very long; Upper long	Weak groove over lower palatal	
griqualandica	1.3–1.5	0.7–0.9	Conical	Deep	Strong, sharp, regular	Dull	Yellow-brown	None	None to modest; at aperture margin	Modest to strong	Very strong; long	Very strong; long	Long	Blade parallel to aperture margin	Lower very deeply inserted; Upper very long, deeply inserted	Deep grooves over both	Aperture margin strongly flared
hemphilli	1.4–2.0	0.7–0.9	Cylindrical	Moderate	Strong, sharp, regular	Dull	Yellow-brown	None to weak	None to weak; at aperture margin	Modest to weak	Very strong; sinuous	Strong; sinuous	Narrow sinuous blade	None	Lower very deeply inserted; Upper very long, deeply inserted	Deep groove over upper palatal	Aperture margin strongly flared

(continues)

(continued)

Species	Height (mm)	Width (mm)	Shell Shape	Suture Depth	Striae	Luster	Color	Crest	Callus	Sinulus	Angular	Parietal	Columellar	Basal	Palatal	Palatal Depression	Other
pimuensis	1.5–2.0	0.8–0.9	Cylindrical	Shallow to moderate	Sharp threads; regular	Silky-dull	Red-yellow	Weak to modest; deeply set	None to modest; at aperture margin	Weak to modest	Strong; triangular	Long	Peg	None	2	Weak to modest	
rowellii	2.0–2.9	1.2–1.5	Narowly conic-ovate	Moderate	Numerous irregular threads; weak spiral lines	Dull-silky	Red to yellow-brown	None	None	Weak	None	Long; sinuous	Long	None	2	None	Aperture margin strongly flared
saxicola	1.3–1.5	0.7–0.8	Cylindrical	Moderate-deep	Numerous regular, sharp, threads; weak spiral lines	Dull	Brown	None	None	None	Weak to strong, blunt; at peristome margin	Moderate	Peg	None	Lower blade; Upper short	None	
trinotata	1.8–2.5	1.1–1.3	Ovate-conical	Moderate-deep	Strong, sharp, regular	Dull	Red-brown	None	None	Weak	None	Long	Peg	None	Lower peg; upper absent to weak	None	Parietal lamella points at lower palatal

supported (86–100) clade in ITS1 + ITS2 and CytB + 16S (94–100). In the latter it was also a member of a highly supported (97–100) clade including *V. calamitosa*.

Conchology

This species shares with *V. calamitosa* a small, columnar shell with strong striae. However, it is easily distinguished by its somewhat larger size, smaller horizontal crescent-shaped columellar lamella, lack of an angular lamella, and very long and deeply inserted lower palatal lamella.

Ecology

While often encountered in litter accumulations under xeric fog-belt scrub within 1 km of the marine coast, this species also occurs in inland oak/riparian forest. Pilsbry (1948) reported a station 90 km from the marine shore.

Biogeography

North America – Point Dume at Malibu, California, U.S.A. south along the coast into Baja California, Mexico, and inland to base of the San Bernardino Mountains.

Vertigo* (*Staurodon*) *pimuensis, n. sp.

Figs. 19 (bottom row), 21A–H, N, P, Table 12

GenBank Accessions: KY217264-5; KY216863-4; KY217661-2; KY216516-7.

Diagnosis

Shell small, cylindrical, similar to *V. clementina,* but differing in its stronger and more numerous striae, stronger microscopic pustulae covering the shell surface, duller luster, stronger suture, redder color, and possession of a strongly bowed angular lamella, causing the structure to appear broadly triangular in apertural view.

Description

Shell: 1.5–2.0 mm tall x 0.8–1.0 mm wide (Holotype 1.8 x 0.9 mm), translucent, pale yellow brown tending to reddish; approximately five whorls; narrowly cylindrical; normal suture and whorls for the *Sterkia* group (Fig. 21A–H); surface silky-dull from numerous fine striae and the presence of microscopic pustulae (Fig. 21P); aperture < $^1/_3$ of shell height, often somewhat taller than wide (Fig. 21A, E–H), in profile ascending onto body whorl (Fig. 21C); umbilicus closed by preceding whorls (Fig. 21B); peristome interrupted by body whorl, apertural lip distinctly flared (Fig. 21A–H); a weak to modest broad and deeply set crest sometimes present with weak to absent callus positioned at the apertural margin (Fig. 21C, E); five apertural lamellae, including a peg-shaped columellar, a long parietal, two blade-shaped palatals, and a strong sinuous angular (Fig. 21A, E–H); the proximal end of the angular lamella pointed towards the palatal wall (Fig. 21N) often obsolete midway so that the distal and proximal ends are separate; angular lamella also projected beyond the apertural margin (Fig. 21B, C), when observed in apertural view is broadly-triangular in shape (Fig. 21A, E–H); a very weakly to moderately developed depression on the palatal wall (Fig. 21D).

Holotype (Fig. 21A–D, P): ANSP 467373, Hillside lemonade berry scrub, USC Marine Laboratory, Santa Catalina Island, California, U.S.A.; 33°26'45"N, 118°28'54"W; October 2, 2013.

Paratypes: ANSP 467374, collected with holotype; 10 shells. SBMNH 141957; Under *Artemisia* & *Opuntia*, S-facing slope behind USC Marine Lab, Santa Catalina Island, California, U.S.A.; April 8, 1980; 56 shells. SBMNH 142040; Junk pile behind USC Marine Lab under logs, Fisherman’s Cove, Santa Catalina Island, California, U.S.A.; April 8, 1980; 35 shells. ANSP 467375, Coastal sagebrush scrub, Two Harbors South, Santa Catalina Island, California, U.S.A.; 33°25'59"N, 118°30'34"W; October 2, 2013; 5 shells. SBMNH 141956; leaf litter under *Lavateria* & *Opuntia*, Indian Rock, off Emerald Island Bay, Santa Catalina Island, California, U.S.A.; April 8, 1980; 13 shells. SBMNH 141958; In litter under *Opuntia*, to east above Salta Verde Point on flats just off road, Santa Catalina Island, California, U.S.A.; February 24, 1979; 6 shells. SBMNH 142010; Under *Opuntia* & *Salvia* $^2/_3$ way down slope, Silver Canyon, Santa Catalina Island, California, U.S.A.; April 23, 1991; 1 shell.

Other, Non-Type Material Examined: Twenty-seven additional individuals in the Nekola collection from the USC Marine Laboratory and Two Harbors South sites.

Etymology

The specific epithet refers to Pimu, the name for Santa Catalina Island in the Tongva language of the original First Nations inhabitants of the southern California Channel Islands.

Phylogenetics

Across all reconstruction methods in both datasets this species existed as a highly supported (94–100) clade. In CytB + 16S across all reconstruction methods it was a member of the same highly supported (99–100) clade as *V. clementina*.

Comparisons with Other Species

Shells are similar to *V. clementina*, but differ in a duller shell luster due to the presence of stronger and more numerous striae and microscopic pustulae, a slightly more red-brown color, deeper suture, and most importantly a more strongly bowed angular lamella proximally

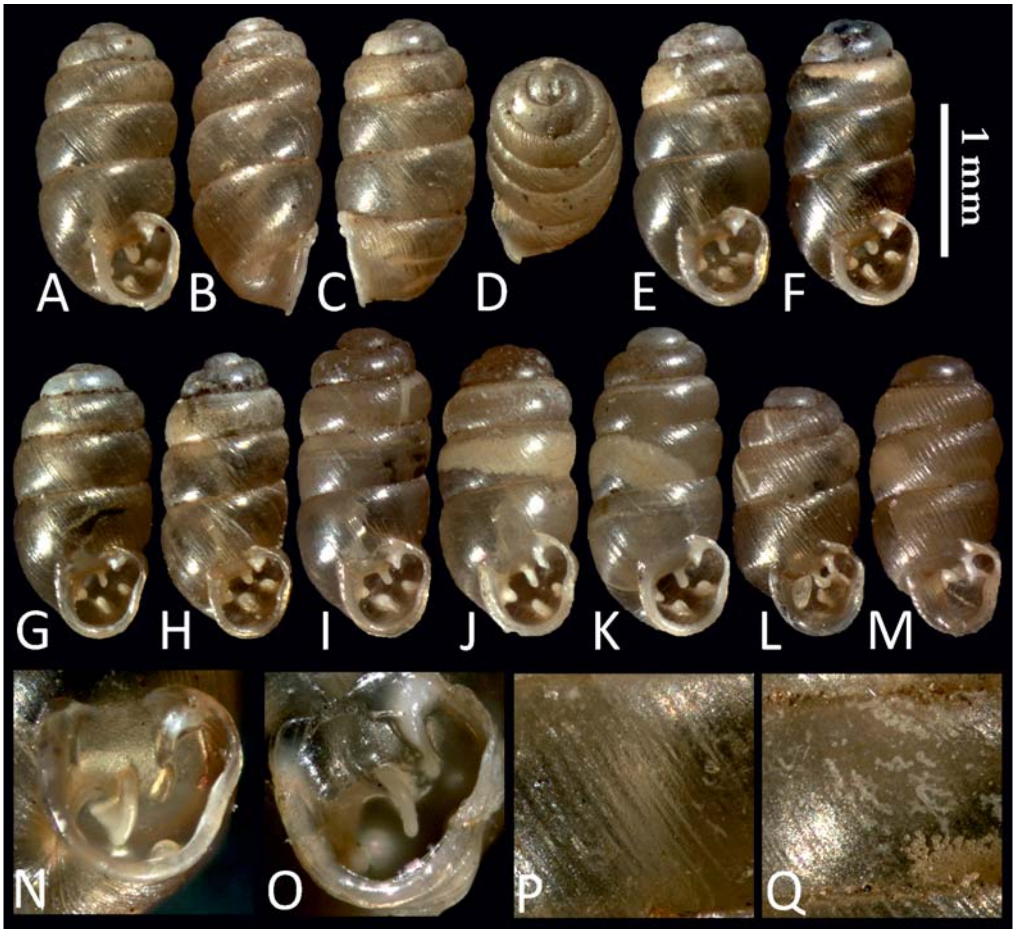


FIG. 21. ***Vertigo pimuensis*** n. sp. A–D, P: Holotype, ANSP 467373, Hillside lemonade berry scrub, USC Marine Laboratory, Santa Catalina Island, California, U.S.A. (33.4458°N, 118.4817°W); E, F: ANSP 467374 and [C44], Hillside lemonade berry scrub, USC Marine Laboratory, Santa Catalina Island, California, U.S.A. (33.4458°N, 118.4817°W); G, H, N: ANSP 467375 and [C51], Coastal sagebrush chaparral, Two Harbors South, Santa Catalina Island, California, U.S.A. (33.4331°N, 118.5094°W); *Vertigo clementina*. I: [C42] Island Cherry grove, Knob Canyon, San Clemente Island, California, U.S.A. (32.8384°N, 118.3751°W); J, O, Q: JCN 19109 and [OG15], Ice plant-sagebrush chaparral, Wilson Cove, San Clemente Island, California, U.S.A. (32.9953°N, 118.5516°W); K: [C50] *Coreopsis-Opuntia* chaparral, Desalinization Plant, San Nicolas Island, California, U.S.A. (33.2434°N, 119.4499°W); L: *Vertigo calamitosa* [C40] Coastal lemonade berry chaparral, Point Loma, San Diego County, California, U.S.A. (32.6730°N, 117.2449°W); M: *Vertigo hemphilli* [VH67] *Sambucus* grove on N-facing slope, Border Field State Park, San Diego County, California, U.S.A. (32.5428°N, 117.1061°W). When applicable, bracketed DNA specimen codes precede each entry.

pointed towards the palatal wall. As a result, the full face of the proximal end is visible in apertural view, causing the angular lamella to appear broadly triangular in apertural view. Additionally, the angular lamella is obsolete midway so that the distal and proximal ends are separate. In contrast, *V. clementina* possesses a shiny to silky shell surface from its much reduced striae and microscopic pustulae, is lighter yellow in color, has a shallower suture, and possesses a relatively straight, blade-shaped angular lamella with the proximal end being less strongly curved towards the parietal wall of the aperture, and which is not interrupted along its length. Both mainland species in the group (*V. calamitosa* and *V. hemphilli*) possess stronger striae and more complicated apertural lamellae architecture.

Geographic Distribution

North America – Santa Catalina Island from Silver Canyon in the southeast to Indian Rock in Emerald Bay off the northwest coast, for a range of 20.5 km. All known *Sterkia* group populations from Santa Catalina represent ***V. pimuensis***. ***Vertigo pimuensis*** does not occur on Santa Barbara, San Clemente, San Nicolas, Santa Cruz or Santa Rosa Islands. Surveys have yet to be made on Anacapa, Guadalupe and San Miguel Islands.

Ecology

Deep litter accumulations in xeric fog-belt coastal shrub and under Hottentot Fig/Sea Fig (*Carpobrotus*) mats.

AFRIPUPA GROUP

We find *Afripupa* to retain utility in categorizing this well-defined group in spite of the fact that the type species of *Afripupa* (*Pupa griqualandica* Melvill & Ponsonby, 1893) is shown by DNA sequence analysis to a member of *Vertigo* (*Staurodon*).

Vertigo (*Staurodon*) *bisulcata*
(Jickeli, 1872) Ethiopia
Fig. 19 (bottom row)

Pupa bisulcata Jickeli, 1872: 107.

Type Locality: Rora-Beir-Andu Plateau, Hamaszen Province and Keren Mts., Bogos, Ethiopia.

Phylogenetics

Because we have analyzed only a single specimen, no species level clade can be defined. However, this individual differed from the other two members of the group on average by 15.5–19.5 bases in ITS1 + ITS2, and 84.5–92.0 bases in CytB + 16S. Although the analyzed Ghanaian shell matches the description for *V. bisulcata*, because it was sourced so remotely from the type locality, analyses of Ethiopian material will be needed to ensure that a single species-level entity is present.

Conchology

This species shares with the other two group members a small conical shell with strong striae and dull luster. It differs in its lack of a basal lamella and shorter palatal blades.

Ecology

The analyzed specimen was collected in leaf litter of a remnant upland forest. The type material was collected under rotten leaves, wood, and stones.

Biogeography

Tropical Africa – Ethiopian highlands to Ghana and Victoria Falls.

Vertigo (*Staurodon*) *farquhari*
(Pilsbry, 1920)
Fig. 19 (bottom row)

Nesopupa farquhari Pilsbry, 1920: 50.

Type Locality: Grahamstown, South Africa.

Phylogenetics

This species existed across all reconstruction methods as a highly supported (99–100) clade in ITS1 + ITS2 and CytB + 16S. ML and Bayesian ITS1 + ITS2 reconstructions demonstrated it to be a member of the same poorly to moderately supported (50–66) clade as *V. bisulcata*; across all methods in CytB + 16S it was a member of the same moderately to highly supported (80–100) clade that included *V. griqualandica*.

Conchology

This species shares with the other two group members a small conical shell with strong striae and dull luster. It differs in its red-brown shell color and shallower suture. It also differs from *V. bisulcata* by the presence of a basal lamella and very long palatal blades. It differs from *V. griqualandica* by its less massive basal lamella, less deeply inserted lower palatal blade, less distinct palatal depression, and weaker flaring of the apertural margin.

Ecology

Leaf litter of upland afromontane forest.

Biogeography

Southern Africa – Eastern Cape and KwaZulu-Natal extending north into Mozambique. Restricted to areas within 400 km of the marine shore.

Vertigo (*Staurodon*) *griqualandica*
(Melvill & Ponsonby, 1893)
Fig. 19 (bottom row)

Pupa griqualandica Melvill & Ponsonby, 1893: 22.

Type Locality: Griqualand East, South Africa.

Phylogenetics

This species existed across all reconstruction methods as a highly supported (91–100) clade in ITS1 + ITS2 and CytB + 16S. In ITS1 + ITS2, NJ and ME reconstructions identified it as member of a poorly supported (53–54) clade containing *V. farquhari*. In CytB + 16S was a member of a moderately to highly supported (81–100) clade including *V. farquhari*.

Conchology

This species shares with the other two group members a small conical shell with strong striae and dull luster. It differs from *V. bisulcata* in its strong angular lamella and in having much longer palatal blades. It differs from *V. farquhari* in its yellow-brown shell, stronger basal lamellae, deeply inserted lower palatal lamella, and strongly flared apertural margin.

Ecology

Leaf litter of upland afromontane forest.

Biogeography

Southern Africa – Eastern Cape to KwaZulu-Natal, Gauteng and Limpopo. Largely an interior species.

STAURODON DISCUSSION

ITS1 + ITS2 sequence variation between *Nearctula* group species is modest compared to most other *Vertigo* (no more than 5.7 bases on average between taxa). Nevertheless, most were well-defined and possessed unique, diagnostic taxon-specific sequence. CytB + 16S sequence, conchology and/or ecological preferences also distinguish these taxa. For this reason, we are treating most as species-level entities. A similar pattern of limited – but diagnostic – ITS1 + ITS2 sequence variability in conjunction with well defined CytB + 16S, conchology, ecologic preferences, and biogeography has been noted in *Pupilla* (Nekola et al., 2015).

Some intriguing patterns were noted: for instance, why do $^1/_4$ of analyzed *V. catalinaria* specimens demonstrate divergent ITS1 + ITS2 sequence more closely related to mainland *V. californica* or *V. trinotata*? A hypothesis that could account for this is rare passive migration of these species to the Channel Islands, occasionally inserting mainland nDNA sequence into island *V. catalinaria* populations. Through random mutation and isolation, these sequences have ultimately diverged from their mainland counterparts. As shown by *V. californica longa*, given enough time such hybrid populations are capable of developing unique DNA and conchological attributes. A similar process is replicated in the *Sterkia* group, which possesses strongly defined island and mainland CytB + 16S clades.

A related issue is the converse: Why have *V. catalinaria*-specific sequences not been identified in mainland *Nearctula*? This is also possibly due to bird migration patterns, with resident island birds tending to be much more sedentary (Diamond & Jones 1980), thereby limiting potential movement of island *Vertigo* populations to the California mainland.

It is also notable that on San Clemente Island shells intermediate between the local *V. californica* race and *V. c. longa* have never been observed. Thus, even though their ITS1 + ITS2 sequences are identical, these two taxa must have begun the process of reproductive isolation as indicated by their divergent CytB

+ 16S. Paradoxically, intermediate shells exist between the local San Clemente race of *V. californica* and *V. catalinaria*, even though the genetics of these two races are more strongly differentiated.

As with the other subgenera, *Staurodon* exhibits a transcontinental range, extending from the North American Pacific Coast to the Macaronesian Islands of the eastern Atlantic and sub-Saharan Africa. *Vertigo saxicola*, which occurs at an intermediate geographical position between the *Nearctula / Sterkia* and *Afripupa* groups, also possesses intermediate DNA sequence. This suggests that the range of *Staurodon* may not actually be disjunct, with related species perhaps existing throughout tropical South America, Central America, and the Caribbean: for example, "*Sterkia*" *antillensis* Pilsbry, 1919, "*Sterkia*" *eyriesii* (Drouet, 1859) in *Sterkia (Metasterkia)* and some taxa currently assigned to *Nesopupa*.

SUBGENUS *ISTHMIA*

Analyses of the subgenus *Isthmia* represented 38 individuals for both CytB + 16S and ITS1 + ITS2. The CytB segment was 367 bases and the 16S segment 439–446 bases, with a total of 202 variable sites along the entire CytB + 16S construct. The analyzed ITS1 segment was 559–604 bases, the analyzed ITS2 segment was 596–656 bases, with a total of 111 variable sites along the entire ITS1 + ITS2 construct.

In combination with conchology and ecological preferences, these analyses suggested six species-level entities (Tables 13, 14, Figs. 22, 23): *V.* cf. *hirasei*, *V. kushiroensis*, *V. moulinsiana*, *V.* cf. *okinoerabuensis*, *V. pygmaea* and *V. tridentata.* We also recognize *V. botanicorum*, *V*. cf. *coreana* and *V. hachijoensis* as subspecies of *V. kushiroensis*.

Mean within-taxon variability ranged in ITS1 + ITS2 from 1.2 bases in *V. moulinsiana* to 7.8 in *V. k. botanicorum* and 8.0 in *V.* cf. *okinoerabuensis*. In CytB + 16S, within-taxon variability ranged from 0.8 in *V. moulinsiana* to 15.1 in *V. k. botanicorum* and 16.0 bases in *V.* cf. *hirasei*. Mean pairwise variation between taxa ranged in ITS1 + ITS2 from 5.3 (*V.* cf. *hirasei* vs. *V. kushiroensis*) to 50.6 (*V. moulinsiana* vs. *V. k. coreana* and *V. k. hachijoensis*) bases and in CytB + 16S from 17.0 (*V. k. coreana* vs. *V. k. hachijoensis*) to 93.8 bases (*V. moulinsiana* vs. *V.* cf. *okinoerabuensis*; Table 13).

Two groups below the subgenus level perhaps exist. One, identified across all reconstruction methods with high support (90–100) in ITS1 + ITS2 and in CytB + 16S with moderate to high support (62–99), consisted of the Central/East Asian and North American *V.* cf. *hirasei*, *V. kushiroensis*, *V.* cf. *okinoerabuensis* and *V. tridentata*. The other consisted of the European *V. moulinsiana* and *V. pygmaea*. However, this latter group was not identified across all reconstruction methods in ITS1 + ITS2 and not at all in CytB + 16S. As a result, it seems best to disregard these potential associations and, given the low number of taxa, ignore such divisions.

Vertigo (*Isthmia*) cf. *hirasei*
Pilsbry, 1901: 128
Figs. 5M, 23 (second row)

Type Locality: Yanagawa, Chikugo Province, Kiusiu [sic] Island, Japan.

Phylogenetics

This species existed across all reconstruction methods in ITS1 + ITS2 and CytB + 16S as a clade with moderate to high support (74–100). Shown in ITS1 + ITS2 to be a member of the highly supported (90–100) group including *V. kushiroensis, V.* cf. *okinoerabuensis* and *V. tridentata*, in CytB + 16S it was a member of a highly supported (91–100) clade including only *V*. cf. *okinoerabuensis*.

Conchology

This species shares with *V.* cf. *okinoerabuensis* a small straw-yellow shell almost lacking striae, a weak sinulus, and 3–4 apertural lamellae. It differs from that species in its more conic shell, with the body whorl making up more than $^1/_2$ of total shell height. It should be noted that shells from both analyzed populations agree with the characters for *V. h. glans*. We have not yet observed material referable to the nominate subspecies.

Ecology

Low herbaceous vegetation in riparian forest and the forested margins of rice paddies and wetlands.

Biogeography

East Asia – We found this species to be scattered within Tōhoku Region of Honshu. Pilsbry (1919) reported Hirase collections from Yanagawa in Kyushu and *V. h. glans* from Miyakejima in the Izu Archipelago.

Nomenclature

Because our sampled sites are so far removed from the type location for *V. hirasei* in Kyushu and *V. h. glans* on Miyakejima, we are uncomfortable definitively stating that the analyzed material is referable to either of these taxa. Verification of the correct name for the Tōhoku populations will require documentation and comparison of DNA sequence from the type locations of *V. hirasei* and *V. h. glans*.

Vertigo (Isthmia) kushiroensis
Pilsbry & Hirase, 1905
Figs. 5N, 23 (top row)

Vertigo hirasei kushiroensis Pilsbry & Hirase, 1905: 718.

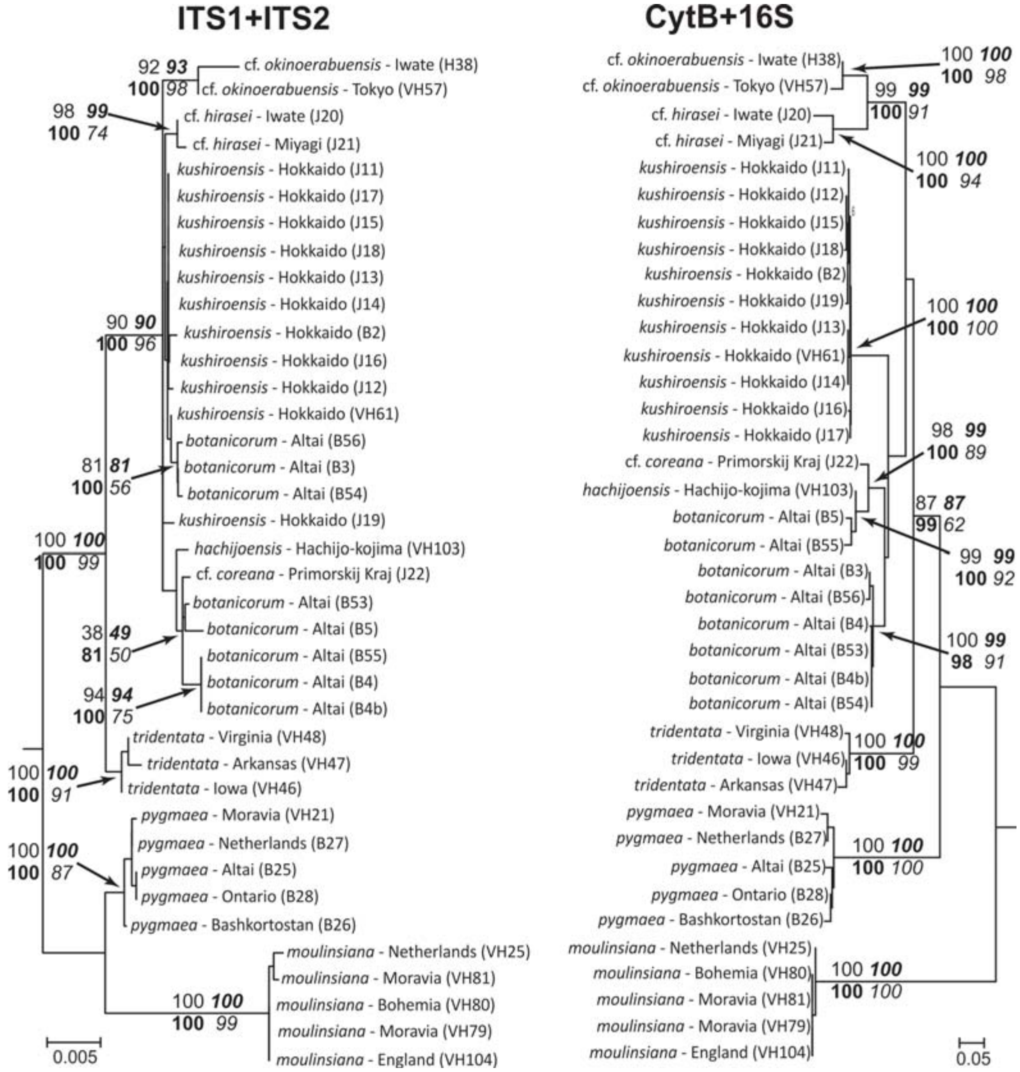


FIG. 22. Maximum-likelihood phylogenetic tree reconstructions in *Vertigo* (*Isthmia*) based on separate analysis of concatenated ITS1 + ITS2 and CytB + 16S data. Nodes with strong to moderate support have been labeled to the left of that node by four values: The upper left (normal font) is for Neighbor Joining. The upper right (***bold italic font***) is for Minimum Evolution. The lower left (**bold font**) is for Bayesian. The lower right (*italic font*) is for Maximum Likelihood.

TABLE 13. Mean pairwise distances between *Vertigo* (*Isthmia*) species for the analyzed nDNA and mtDNA constructs, reported as nucleotide base pairs/construct. The lower half of the matrix represents distances in the ITS1 + ITS2 construct and the upper half (demarcated by *italic font*) represents distances in the CytB + 16S construct.

	cf. *hirasei*	*kushiroensis*	*k. hachijoensis*	*k. botanicorum*	*k. coreana*	cf. *okinoerabuensis*	*tridentata*	*pygmaea*	*moulinsiana*
cf. *hirasei*		*60.5*	*65.5*	*59.0*	*62.0*	*42.5*	*69.0*	*89.3*	*91.8*
kushiroensis	5.3		*40.1*	*35.7*	*35.2*	*57.0*	*60.5*	*77.0*	*87.6*
k. hachijoensis	9.0	9.5		*22.5*	*17.0*	*59.5*	*59.7*	*67.8*	*86.8*
k. botanicorum	10.9	8.7	7.9		*24.5*	*55.0*	*55.3*	*67.4*	*87.6*
k. coreana	11.0	9.5	7.0	6.4		*58.0*	*57.7*	*68.0*	*86.8*
cf. *okinoerabuensis*	18.0	18.5	13.0	17.4	17.5		*64.7*	*82.0*	*93.8*
tridentata	23.7	23.1	22.0	23.6	21.3	26.0		*81.9*	*89.8*
pygmaea	40.4	39.0	34.8	36.4	35.8	36.9	37.0		*91.6*
moulinsiana	47.8	46.4	50.6	50.3	50.6	50.1	47.1	34.0	

Type Locality: Akkeshi, Kushiro, Hokkaidō, Japan.

Phylogenetics

Across all reconstruction methods in ITS1 + ITS2, this species was identified as a member of highly supported (90–100) clade from which other groups have diverged at lower levels of support. The taxon is more distinct in CytB + 16S, where it existed across all methods as a highly supported (100) clade. The complicating issue was the highly supported sister clades encompassing *V. k.* cf. *coreana*, *V. k. hachijoensis* and some *V. k. botanicorum* on one hand, and the remaining *V. k. botanicorum* on the other. As detailed below, the sorting of individuals between these groups was inconsistent between ITS1 + ITS2 and CytB + 16S. Because they do not appear to have yet achieved reproductive isolation, and given the large range of conchological variability in *V. kushiroensis* on Hokkaidō, it seems prudent at this time to regard *botanicorum*, *coreana* and *hachijoensis* as subspecies of *V. kushiroensis*.

Conchology

This species is closest to *V*. cf. *hirasei* and *V*. cf. *okinoerabuensis* from which it differs by its larger size, more ovate shape, and deeper suture. It encompasses a wide conchological range, varying by over 50% in size, possessing highly variable crest and callus development, with palatal lamellae varying from zero to two. This variability fully encompasses the three subspecies detailed below. The holotype (ANSP 90223) – which possesses a moderately strong callus – is atypical of the species even at its type locality.

Ecology

Almost exclusively above ground on low grass and sedge leaves in a wide variety of habitats, ranging from ocean shore dunes to old fields, roadsides, open riparian forest and wetland margins.

Biogeography

East Asia – As defined here, the nominate subspecies is limited to Hokkaidō, Japan, where we have documented populations throughout the southeastern third of the island.

Vertigo (*Isthmia*) *kushiroensis botanicorum*
Horsák & Pokryszko, 2010
Fig. 23 (top row)

Vertigo botanicorum Horsák & Pokryszko, 2010: 57.

Type Locality: 51°30'26.6''N, 85°35'48.6''E, Altai Mountains, Russia.

Phylogenetics

This taxon demonstrated polyphyly across both datasets and all reconstruction methods. In ITS1 + ITS2 some specimens existed within

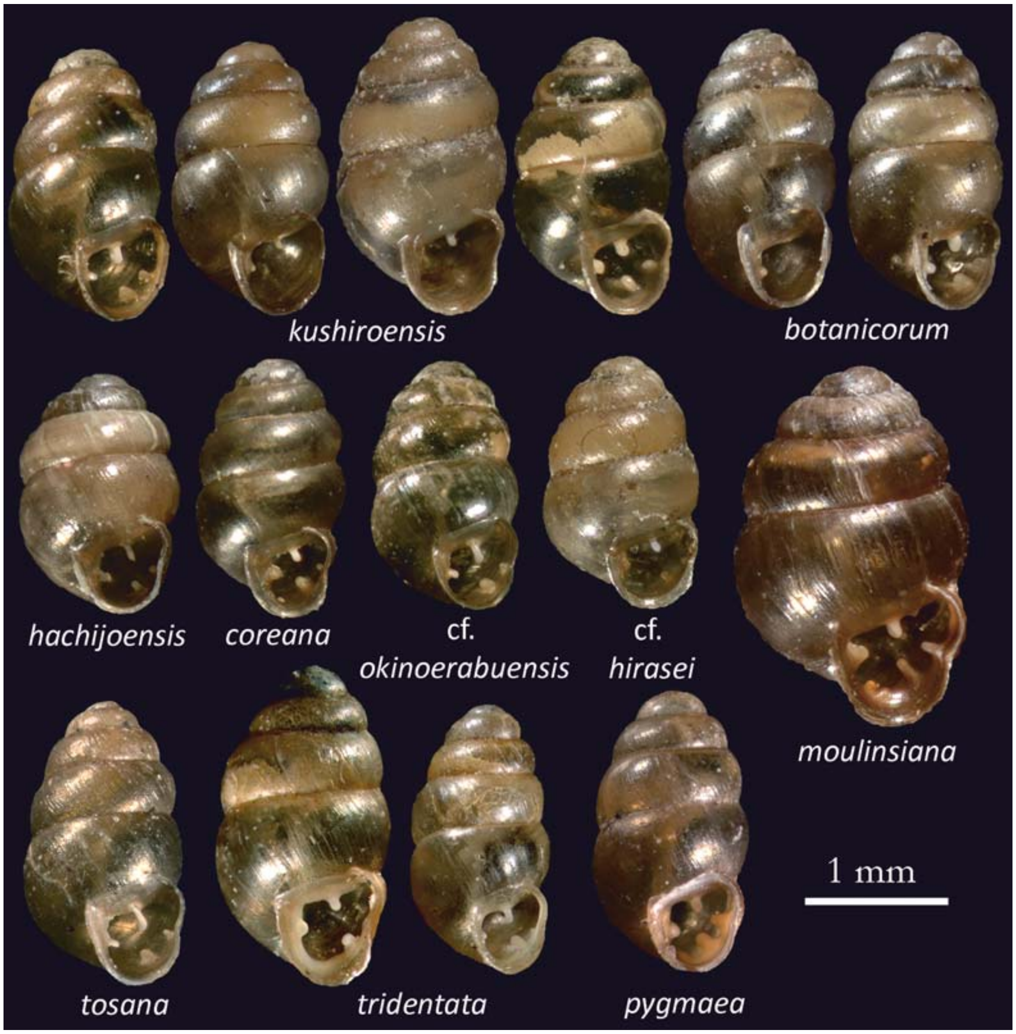


FIG. 23. Shells of *Vertigo* (*Isthmia*). Bracketed DNA specimen codes precede each entry. Top row (left to right): *Vertigo kushiroensis*: [VH61] Kushiro Marsh, Hokkaidō, Japan (43.0340°N, 144.3901°E); [B2] Lake Yudonuma, Hokkaidō, Japan (42.5877°N, 143.5358°E); [J12] Nishicha Bridge, Urakawa, Hokkaidō, Japan (42.1915°N, 142.8636°E); [J19] Hobetsu-fukuyama, Yufutsu, Hokkaidō, Japan (42.8860°N, 142.2500°E). *Vertigo kushiroensis botanicorum*: [B3] Aktel, Altai, Russia (51.5074°N, 85.5968°E); [B53] Ust-Muny West, Altai, Russia (51.7297°N, 85.7382°E). Second row (left to right): *Vertigo kushiroensis hachijoensis*: [VH103] Hachijo-kojima Island, Japan (33.1320°N, 139.6805°E). *Vertigo kushiroensis* cf. *coreana*: [J22] Gorno-Taezhnoye, Primorskij Kraj, Russia (43.6971°N, 132.1633°E). *Vertigo* cf. *okinoerabuensis*: [VH57] Renkoji Seep, Tama, Tōkyō, Japan (35.6325°N, 139.4677°E). *Vertigo* cf. *hirasei*: [J21] Minami-fukasawa, Tome, Miyagi, Japan (38.6740°N, 141.1103°E). *Vertigo moulinsiana*: [VH79] Žitková fen, Moravia, Czech Republic (48.9902°N, 17.9056°E). Bottom row (left to right): *Vertigo japonica tosana*: Nekola collection, Geibikei Gorge, Iwate, Japan (38.9873°N, 141.2557°E). *Vertigo tridentata*: [VH48] Falling Springs NE, Virginia, U.S.A. (37.8810°N, 79.9176°W); [VH46] Canton Glade, Iowa, U.S.A. (42.1795°N, 90.9979°W). *Vertigo pygmaea*: [VH21] Kotrle fen, Moravia, Czech Republic (49.3779°N, 18.0236°E).

a poorly to well supported (56–100) subclade most closely associated with *V. kushiroensis*, and the remainder within a poorly to moderately supported (38–81) subclade associated with *V. k.* cf. *coreana* and *V. k. hachijoensis*. In CytB + 16S this same topology was apparent with over 75% of individuals being members of a unique, highly supported (91–100) clade, and the remainder being associated at high support (89–100) with *V. k.* cf. *coreana* and *V. k. hachijoensis*. However, more than $^1/_3$ of individuals were assigned to different topological groups in ITS1 + ITS2 vs. CytB + 16S. Until the genetics of *V. kushiroensis* can be formalized across its entire range, the existence of the highly supported clade containing most *botanicorum* individuals suggests that it would be prudent to maintain this name at the subspecies level.

Conchology

The shells of *V. k. botanicorum* essentially fall within the range of variation seen on Hokkaidō within the nominate subspecies, although being slightly smaller on average and with a duller luster.

Ecology

In the Altai, this subspecies is characteristic of low to mid-elevation mesic steppe; it also occurs in adjacent hemiboreal and riparian forest.

Biogeography

Central Asia – North side of the Altai east to the Lake Baikal area (Richard Preece, *personal communication*), where it was previously reported as *Vertigo extima* (White et al., 2008).

Vertigo (*Isthmia*) *kushiroensis* cf. *coreana* Pilsbry, 1919

Fig. 23 (second row)

Vertigo japonica coreana Pilsbry, 1919: 156.

Type Locality: Island of Ko-je, South Korea.

Phylogenetics

As only a single far eastern Siberian specimen was analyzed, no characteristic clade could be identified. However, in ITS1 + ITS2 and CytB + 16S it was placed into the same poorly to highly supported (38–100) clade as *V. k. botanicorum* and *V. k. hachijoensis*. It differed from the other members of this clade by 4–8 bases in ITS1 + ITS2 and 17–19 bases in CytB + 16S.

Conchology

The shells of this subspecies are similar to *V. kushiroensis* and *V. k. botanicorum*, but differ in their slightly smaller size and stronger sinulus.

Ecology

The single analyzed shell was collected in an old-growth oak/maple forest.

Biogeography

East Asia – S-Primorskij Kraj in southeastern Siberia to Fusan and Geoje Island in South Korea.

Nomenclature

While the shell of the analyzed specimen is similar to the *Vertigo japonica coreana* holotype (ANSP 95772), because it was collected so far from the type location, we are not certain that our specimen actually represents this entity.

Vertigo (*Isthmia*) *kushiroensis hachijoensis* Pilsbry, 1919

Fig. 23 (second row)

Vertigo hachijoensis Pilsbry, 1919: 153.

Type Locality: Hachijojima, Izu, Japan.

Phylogenetics

As only a single specimen was analyzed, no characteristic clade could be identified. However, in both datasets it was placed into the same poorly to highly supported (38–100) clade as *V. k. botanicorum* and *V. k.* cf. *coreana*. It differed from the other members of this clade by 5–11 bases in ITS1 + ITS2 and 7–18 bases in CytB + 16S.

Conchology

This subspecies differs from others in the *V. kushiroensis* complex by possessing a more ovate and striate shell with a moderately strong crest and callus development. However, extreme *V. kushiroensis* individuals from Hokkaidō may exhibit these traits.

TABLE 14. Conchological traits for *Vertigo* (*Isthmia*) members.

Species	Height (mm)	Width (mm)	Shell Shape	Suture Depth	Striae	Luster	Color	Crest	Callus	Sinulus	Angular	Parietal	Columellar	Basal	Palatal	Palatal Depression	Other
cf. *hirasei*	1.5–1.9	1.0–1.1	Conic-ovate	Shallow	Very weak, blunt, irregular	Silky-shiny	Yellow	None	None	Weak	None	Long	Peg	None	2 short; upper weak to absent	None	Body whorl > $^{1}/_{2}$shell height
kushiroensis	1.7–2.2	0.8–1.2	Ovate-conic	Moderate	Weak, blunt, irregular	Silky	Dark yellow brown	None to modest	None to modest	Weak to modest	None	Long	Peg	None	2 to none	None to modest	Scaly surface
k. botanicorum	1.6–2.2	0.9–1.3	Ovate-conic	Moderate	Very weak, blunt irregular	Silky-dull	Dark yellow brown	None to modest	None	Weak to modest	None	Long	Peg	None	2 to none	None to modest	Very scaly surface
k. coreana	1.5–1.7	0.8–0.9	Ovate	Moderate	Weak, blunt, irregular	Silky	Yellow brown	Weak	None	Modest	None	Long	Peg	None	2	Weak	Scaly surface
k. hachijoensis	1.7–1.8	1.1–1.2	Ovate	Moderate	Fine, sharp	Silky-dull	Dark yellow brown	Modest	Weak to strong	Weak	None	Long	Peg	None	2	Weak	
moulinsiana	2.2–2.8	1.4–1.6	Broadly ovate	Shallow	Weak, irregular	Silky-shiny	Red brown	Modest	Strong to modest	Strong to modest	None to weak	Long	Peg	None or one	Lower short; Upper weak	Modest to weak	
cf. *okinoerabuensis*	1.6–1.9	0.9–1.1	Narrowly ovate to ovate	Shallow	Very weak, blunt, irregular	Silky	Yellow brown	None	None	Weak to modest	None	Long	Peg	None	Lower moderate Upper short	None	Body whorl < $^{1}/_{2}$ shell height
pygmaea	1.4–2.1	1.0–1.1	Narrowly ovate	Moderate	Sharp threads	Dull-silky	Red brown	Weak to strong	Absent to strong; white	Weak	None	Long	Peg; rarely bi-lobed	Strong	2; supra-palatal often present	Weak to modest	Scaly surface
tridentata	1.5–2.4	0.9–1.2	Broadly ovate	Moderate	Blunt, irregular	Silky-shiny	Honey yellow	Modest to strong	Weak to strong; yellow	Modest to strong	None	Long	Peg	None	2: Upper weak to absent	Weak to modest	

Ecology

Upland forest leaf litter.

Biogeography

East Asia – Only reported from Hachijimo in the Izo Archipelago.

Nomenclature

If additional analyses support the contention that this taxon, *V. k.* cf. *coreana* and some *V. k. botanicorum* represent a single distinct species-level entity, *V. hachijoensis* would have priority.

Vertigo (*Isthmia*) *moulinsiana*
(Dupuy, 1849)
Fig. 23 (second row)

Pupa moulinsiana Dupuy, 1849: 4.

Type Locality: Lyon, France.

Phylogenetics

Across all reconstruction methods in both datasets this species existed as a highly supported (99–100) clade.

Conchology

This species is unique in the subgenus by possessing red-brown shells > 2.2 mm tall and > 1.4 mm wide. It could perhaps be confused with some *Alaea*, in particular *V*. *teskeyae* and *V. ovata*, but it is even larger, has a more triangular apertural opening and reduced lamellae development.

Ecology

Low elevation calcareous wetlands. In the summer, it lives up to a meter above the ground surface on wide-leaved sedges and grasses; in the winter, it hibernates closer to the ground surface.

Biogeography

Europe and North Africa – Southern Sweden, Ireland and Morocco to the Caucasus. It perhaps penetrates into swamp forests of equatorial Africa (Ton de Winter, *personal communication*).

Nomenclature

Vertigo laevigata Gallenstein, 1848, may have priority. However, this name has rarely been used since 1900 and should be officially suppressed.

Vertigo (*Isthmia*) cf. *okinoerabuensis*
Pilsbry & Hirase, 1904
Fig. 23 (second row)

Vertigo hirasei okinoerabuensis Pilsbry & Hirase, 1904: 631.

Type Locality: Okinoerabushima, Ōsumi, Japan.

Phylogenetics

This species existed as a clade with high support (92–100) across all reconstruction methods in both datasets. While ITS1 + ITS2 analyses suggested it to be a member of the highly supported (90–100) group including *V. kushiroensis*, *V.* cf. *okinoerabuensis* and *V. tridentata*, in CytB + 16S it was shown to be a member of a highly supported (91–100) clade including *V*. cf. *hirasei*.

Conchology

This species shares with *V.* cf. *hirasei* a small yellow shell with almost absent striae, a weak sinulus, and 3–4 apertural lamellae. It differs from that species in its more ovate shape with the body whorl making up $^1/_2$ or less of total shell height.

Ecology

Occurs on low herbaceous vegetation in riparian forest and wetland margins.

Biogeography

East Asia – We found this species in scattered sites from Tōkyō to the Tōhoku Region of Honshu in Japan. Pilsbry (1919) reported it in the Satsunan Islands off the southern Kyushu coast.

Nomenclature

While shells of the analyzed individuals were closely similar to the *V. h. okinoerabuensis* holotype (ANSP 87690), our sampled populations were so far removed from the type location that assignment of our material to this taxon is provisional. Verification of the correct name for the Tōkyō and Tōhoku populations will require comparison with DNA sequence from the type location.

Vertigo (*Isthmia*) *pygmaea*
(Draparnaud, 1801)
Fig. 23 (bottom row)

Pupa pygmaea Draparnaud, 1801: 57.

Type Locality: France.

Phylogenetics

Across all reconstruction methods in both datasets, this species existed as a moderately to highly supported (87–100) clade. The North American specimen had identical ITS + ITS2 and only 8 base differences in CytB + 16S as compared to the Altai specimen. This is consistent with the conclusion that North American populations represent naturalized Eurasian material (Nekola & Coles, 2010).

Conchology

Within the subgenus, this species has a distinct shell, typically being dull red-brown with a narrowly ovate shape, a very strong crest, white callus and a strong basal lamella. However, populations possessing only a vestigal crest, callus, and basal lamella are known. It perhaps could be confused with some members of *Vertigo s. str.* but differs by possessing narrower thread-like striae.

Ecology

Generally a calcareous grassland species, ranging from upland pasture and steppe to roadsides, dunes and wetland margins. It is among the most anthropophilic of land snails, occurring throughout its range in abandoned limestone quarries, cement culverts (Hubricht, 1985), abandoned home foundations, suburban yards and compost piles. It also strays into native upland forest.

Biogeography

The native range extends from the European Atlantic coast north to southern Scandinavia and east to central Asia. Adventitious populations in North America range throughout the Great Lakes region south to Tennessee in the Appalachians and northeast to the Canadian Maritime Provinces. It also occurs in scattered sites throughout the intermountain West and Pacific Coast.

Vertigo (*Isthmia*) *tridentata*
Wolf, 1870: 198
Fig. 23 (bottom row)

Type Locality: Canton, Illinois, U.S.A.

Phylogenetics

Across all reconstruction methods in both datasets, this species existed as a highly supported (91–100) clade. It was part of the same moderately to highly supported (62–100) clade in ITS1 + ITS2 and CytB + 16S that includes *V*. cf. *hirasei*, *V. kushiroensis* and *V.* cf. *okinoerabuensis*.

Conchology

This species is unique in the subgenus for possessing a honey-yellow, broadly ovate shell with an apertural callus and 3–4 lamellae. Small individuals might be confused with *V. parvula* (in subgenus *Vertilla*) but differ in their more ovate shape, larger size, apertural callus and lighter yellow shell color.

Ecology

Characteristic of calcareous grassland habitats, it also occurs in upland forest and rock outcrops. In his species description, Wolf (1870) mentions that it was "abundant in shady copses on green weeds, climbing as high as three feet from the ground. I collected 12,000 from standing weeds and not one from the ground, although it was searched well to find them." A similar behavior has been seen in an Arkansas population.

Biogeography

North America – Southern Vermont and Ontario south down the Appalachians to Tennessee and west to southern Minnesota, eastern Kansas and eastern Texas.

ISTHMIA DISCUSSION

The status of taxonomic entities within *V. kushiroensis* is vexing, there being multiple well-supported subclades with inconsistent specimen placement between them in ITS1 + ITS2 vs. CytB + 16S. Combined with the large range of shell variability exhibited by *V. kushiroensis* on Hokkaidō and lack of sampling across much of mainland east Asia, it is difficult to know how many taxa are biologically supported and at what level. In this context, we have opted to recognize *botanicorum*, *coreana* and *hachijoensis* as subspecies of *V. kushiroensis*, mainly in deference to their current use. However, their true status must be further evaluated using empirical DNA sequence, conchological and ecological preference data from across their range. This will require sampling across eastern Siberia, northern China and Mongolia west to the Altai.

Determination of the status and correct nomenclature for central to northern Honshu populations of *V.* cf. *hirasei* and *V.* cf. *okinoerabuensis* requires analyses of populations from not only their respective type localities, but also intervening locations across southern Honshu, Kyushu and Shikoku. Additionally, it is essential that *V. japonica* and *V. j. tonsana* DNA sequence be analyzed to determine their correct taxonomic status and subgeneric assignment. It is remotely possible, for instance, that ***V. kodamai*** in *Vertigo s. str*. could represent a northern race of *V. japonica*.

Given how many members of this subgenus prefer to live off the ground on low-growing grasses, sedges, and herbs, we suspect that this behavior may represent an ancestral trait.

Isthmia again illustrates the transcontinental range of *Vertigo* subgenera, with members ranging from Europe and North Africa east across central Asia to East Asia and eastern North America. Given the large genetic distances seen between these species, it seems likely that the Holarctic range of the subgenus is related to fragmentation of once-continuous temperate/subtropical habitats during the late Tertiary.

SUMMARY AND CONCLUDING REMARKS

Via consensus analyses of mtDNA, nDNA, conchology, biogeography and ecological preferences we have validated 88 *Vertigo* taxa: 80 species and 8 subspecies. Nine of these are new taxa and described herein: ***V. beringiana***, ***V. chiricahuensis***, ***V. chytryi***, ***V. genesioides***, ***V. kodamai***, ***V. kurilensis***, ***V. lilljeborgi vinlandica***, ***V. pimuensis*** and ***V. pisewensis***. Seven taxa (*V. berryi*, *V. kushiroensis botanicorum*, *V. kushiroensis* cf. *coreana*, *V. kushiroensis hachijoensis*, *V. occidentalis*, *V. perryi* and *V. ultimathule*) are only provisionally accepted due to indeterminate phylogenetics usually related to small sample size. Until incontrovertible empirical evidence exists to synonymize these, we maintain the *status quo*. Thirteen previously described taxa have been shown to be simple shell forms with no genetic basis for specific or subspecific status: *V. arthuri basidens*, *V. arthuri hubrichti*, *V. arthuri paradoxa* (= *V. arthuri*); *V. allyniana* (= *V. modesta castanea*); *V. andrusiana* (= *V. columbiana*); *V. alabamensis conecuhuensis* (= *V. alabamensis*); *V. dedecora tamagonari* (= *V. dedecora*); *V. elatior* (= *V. ventricosa*); *V. eogea* (= *V. ovata*); *V. idahoensis* (= *V. ventricosa*); *V. modesta insculpta* (= *V. modesta concinnula*); *V. modesta microphasma*, *V. modesta sculptilis* (= *V. modesta castanea*). Because some fraction of the 18 Holarctic taxa for which genetic material could not be obtained will undoubtedly be shown, following DNA sequence analysis, to represent valid specific or subspecific entities, and given that some number of supposed nesopupid genera (e.g., *Cylindrovertilla*, *Helenopupa,* and Neotropical and African *Nesopupa)* will also be shown to represent *Vertigo*, we conservatively estimate the global existence of at least 100 *Vertigo* taxa.

Across the six recognized subgenera, *Vertigo s. str.* is the most diverse, including 22 specific or subspecific taxa, followed by ***Boreovertigo*** (16), *Staurodon* (16), *Alaea* (15), *Vertilla* (10) and *Isthmia* (9). Across the entire genus, North America harbors by far the most taxa (58 or 2/3 of the total), followed by central/east Asia (22 or

TABLE 15. Total number of analyzed *Vertigo* taxa present within each subgenus within each biogeographic region.

Subgenus	North America	Europe	Central/East Asia	Africa/ Macaronesia	Caribbean
Vertigo	14	5	6		
Boreovertigo	12	5	6		
Vertilla	7	1	1		1
Alaea	12	2	3		2
Staurodon	12			4	
Isthmia	1	2	6	1?	
Total	58	15	22	4 (5?)	3

TABLE 16. Range type for analyzed *Vertigo* taxa within each subgenus. Transcontinental = distributed across more than one continent. Continental = distributed across extent of continental landmass. Sub-continental = distributed over $^1/_2$–$^1/_{10}$ of continental landmass. Regional = distributed over < $^1/_{10}$ of continental landmass. In this table, Europe and Asia are considered as single continent; North America and the Caribbean are considered separate.

Subgenus	Trans-continental	Continental	Subcontinental	Regional
Vertigo	3	2	11	6
Boreovertigo	4	2	8	2
Vertilla			4	6
Alaea	3	1	8	3
Staurodon			2	14
Isthmia			5	4
Total	10	5	38	35

25%), and Europe (15 or 17%; Table 15). This pattern generally holds as well at the subgenus level with all but *Isthmia* reaching maximum diversity within North America. North America is clearly the global biodiversity hotspot for *Vertigo* as it is for polygyrid land snails and unionid bivalves (Williams et al., 1993).

Ten species of *Vertigo* exhibit transcontinental and seven continental ranges (Table 16). Such widespread distribution is restricted to species within *Vertigo s. str.*, ***Boreovertigo*** and *Alaea,* and accounts for almost a third of the species of these subgenera. In contrast, no single species in *Isthmia*, *Staurodon* and *Vertilla* possess natural ranges of more than sub-continental extent. While a few of these are local endemics – notably *Staurodon* of the California coast (e.g., *V. cupressicola*, ***V. pimuensis***, and *V. trinotata*) – this appears to be an exception, with most species possessing distributions that extend at least 1,000 km. Evidently *Vertigo* species generally do not experience much dispersal limitation despite (or perhaps because of) their small size.

No single piece of research should ever be considered the final word on any given topic, and this contribution is no exception. There simply comes a time when data collection must cease and the results to date be presented. Much additional work awaits completion. We suggest the following as additional questions specifically relating to Holarctic *Vertigo* that should be addressed:

1. How many species-level entities should be recognized among the allies of ***V. chiricahuensis*** in the southwestern U.S.A. and northern Mexico?
2. Is *V. utahensis* the correct name for the documented Utah endemic?
3. Does the Yakutian form of ***V. genesioides*** warrant taxonomic designation?
4. Does the Minami-Iwo form of ***V. kodamai*** warrant taxonomic designation?
5. What are the correct taxonomic names for the entities here called *V. arctica, V. circumlabiata* & *V.* cf. *hoppi*?
6. How many biologically supported species exist within *V. coloradensis*? How distinct is it/are they from *V. cristata* and ***V. pisewensis***?
7. Does *V. ultimathule* warrant species, subspecies, or shell form status?
8. Does *Nesopupa maasseni* belong in *Vertigo* (*Vertilla*)?
9. Do East Asian populations of *V. lilljeborgi* warrant taxonomic designation?
10. How many biological species are present within the *V. milium* and *V. ovata* clades?
11. Does *V. perryi* warrant species, subspecies, or shell form status?
12. Should *V. kushiroensis* be considered a single variable species, two species (*V. hachijoensis, V. kushiroensis*), or four species (*V. botanicorum, V. coreana, V. hachijoensis, V. kushiroensis*)?
13. Are *V. hirasei* and *V. okinoerabuensis* the correct names for the two documented northern Honshu taxa?
14. Do any of the 18 unsampled Holarctic taxa represent valid specific or subspecific taxa and if so where do they fit into the global *Vertigo* tree?

This revision has been necessarily focused on Holarctic *Vertigo*, to which the genus has been historically restricted. It does not provide a complete global perspective because a number of genera presently regarded as nesopupids (e.g., *Cylindrovertilla*, *Helenopupa*, *Metasterkia* and some *Nesopupa*) likely also belong to *Vertigo*. We possess limited empirical data (and specimens) to document the diversity and phylogenetics of *Vertigo* in the Neotropics, Paleotropics, and southern temperate zones. A thorough phylogenetic survey of taxa from these areas is required to provide an accurate portrayal of global diversity patterns. Such research could significantly alter our current understanding of the biogeography, biodiversity, ecology and evolutionary history of the genus.

Lastly, the molecular phylogeny presented here is a consensus based on only two mitochondrial and two nuclear genes analyzed as two quasi-independent concatenated sets of sequence information. It is clear that some discrepancies exist between their results. Most appear to be due to mitochondrial or nuclear introgression, incomplete sorting and/or gene duplication. But are these explanations any more than a statement of the complexity of genetic exchange and evolutionary process? It has become clear from our preliminary efforts to identify additional nuclear genes suitable for phylogenetic analysis of pulmonate gastropods that regions from (presumed) different linkage groups can produce different sister-species relationships with high support (for a general discussion see Som, 2014), with the possibility existing that evolutionary history varies among linkage groups. For this reason phylogenetic analyses of genomic sequence in the absence of linkage information could be regarded as simplistic as it does not take into account the impact of non-independent sorting. However, rapid advances of genetic study, such as nextGen sequencing, in combination with breeding experiments to identify linkage groups, make understanding of this complex field a realistic prospect.

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APPENDIX. Collection and GenBank information for analyzed specimens. Because these represent the data used to inform analyses, except for new taxa, the following represent standard taxonomic convention prior to this study. The names recommended following DNA analyses are found in the body text.

Taxon/Location	Latitude/Longitude	Collection Date	Collection Acc. #	Specimen Acc. #	GenBank Acc. # CytB	16	ITS1	ITS2
Vertigo alabamensis Clapp, 1915								
North America								
U.S.A.								
Florida: Wolf Trap Bay	30.3680°N, 84.5700°W	4 May 2005	JCN12323	VH6	KF214516	KF214500	KF214491	KF214479
Georgia: Dickinson Memorial Forest	31.1698°N, 82.2243°W	3 May 2005	BC030039[1]	VH36	KY216922	KY216581	KY217330	KY216203
North Carolina: Johnson Mill Bay	34.7125°N, 78.5261°W	2 Jun 2003	JCN10612	VH5	KF214515	KF214501	KF214490	KF214478
Vertigo alabamensis form *conecuhensis* (Clapp, 1915)								
North America								
U.S.A.								
Alabama: Pond Creek	31.1036°N, 86.5343°W	5 May 2005	JCN12364	VH8	KF214517	KF214499	KF214492	KF214480
Georgia: Rayonier forest lands	31.3462°N, 81.8244°W	3 May 2005	BC030042[1]	VH38	KY216923	KY216582	KY217331	KY216204
North Carolina: Frying Pan Landing	35.8011°N, 76.1001°W	31 May 2003	BC024261[1]	VH37	KY216924	KY216583	KY217332	KY216205
Vertigo cf. *allyniana* Berry, 1919								
North America								
U.S.A.								
California: Little Pothole Lake	36.7693°N, 118.3518°W	1 Oct 2015		VH124	KY216925	KY216584	KY217333	KY216206
Vertigo alpestris Alder, 1838								
Europe								
Czech Republic								
Bohemia: Medvědičky Hill	50.5279°N, 13.9314°E	12 May 2010	JCN	T15	KY216926	JN941042	KY217334	KY216207
Norway								
Storfjord: Signaldalen	69.1911°N, 19.9873°E	16 Aug 2013	BC14511	B82	KY216927	KY216585	KY217335	KY216208
Sweden								
Lappland: Björkliden	68.3900°N, 18.6730°E	6 Jul 1990	BC	B35	KY216928	KY216586	KY217336	KY216209

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Taxon/Location	Latitude/Longitude	Collection Date	Collection Acc. #	Specimen Acc. #	GenBank Acc. #			
					CytB	16	ITS1	ITS2
United Kingdom								
England: Bowston, Cumbria	54.3619°N, 2.7733°W	27 Jun 2000	JCN	T16	KY216929	KY216587	KY217337	KY216210
				H37	KY216930	KY216588	KY217338	KY216211
Ukraine								
Crimea: Mramorne	44.7870°N, 34.2900°E	May 2011	Cameron	B36	KY216931	KY216589	KY217339	KY216212
Vertigo andrusiana Pilsbry, 1899								
North America								
U.S.A.								
Washington: Ocean Shores Rest Area	47.0167°N, 124.1656°W	30 May 2015	JCN20588	VH108	KY216932	KY216590	KY217340	KY216213
Centennial Trail	48.3065°N, 122.2131°W	28 May 2015	JCN20575	VH109	KY216933	KY216591	KY217341	KY216214
Vertigo angustior Jeffreys, 1830								
Europe								
Czech Republic								
Moravia: Pozděchov Fen	49.2339°N, 17.9864°E	17 Jul 2011	JCN	VH19	KY216934	KT008320	KY217342	KY216215
Netherlands								
Katwijk: Katwijk dunes	52.1826°N, 4.4008°E	22 Apr 2012	JCN	VH76	KY216935	KY216592	KY217343	KY216216
Sweden								
Skåne: Nymölla fen	56.0244°N, 14.4605°E	14 Aug 2006	MH	VH77	KY216936	KY216593	KY217344	KY216217
United Kingdom								
England: Gait Barrows, Lancashire	54.1901°N, 2.7977°W	28 Jun 2000	JCN	VH78	KY216937	KY216594	KY217345	KY216218
Vertigo antivertigo (Draparnaud, 1801)								
Europe								
Czech Republic								
Oravia: Pozděchov fen	49.2339°N, 17.9864°E	4 Apr 2011	MH	VH87	KY216938	KY216595	KY217346	KY216219
Netherlands								
Katwijk: Valkenburgse Meer	52.1590°N, 4.4331°E	22 Apr 2012	JCN	VH86	KY216939	KY216596	KY217347	KY216220

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Taxon/Location	Latitude/Longitude	Collection Date	Collection Acc. #	Specimen Acc. #	GenBank Acc. # CytB	16	ITS1	ITS2
Slovakia								
Sabinov: Bajerovce	49.2052°N, 20.7865°E	2 Jun 2005	MH	H28	KY216940	KY216597	KY217348	KY216221
United Kingdom								
Wales: Waun Eraud, Anglesey	53.3008°N, 4.2411°E	16 Jun 2000	JCN	T20	KY216941	KT008316	KY217349	KY216222
Vertigo arctica (Wallenberg, 1858)								
Europe								
Iceland								
Myvatn Lake	65.6289°N, 16.9928°W	7 Sep 2016	MH	B125	KY216942	KY216598	KY217350	KY216223
Norway								
Sør-Trøndelag: Kongsvall	62.3005°N, 9.6063°E	20 Aug 2006	MH	B71	KY216943	KY216599	KY217351	KY216224
Troms: Birtavarre	69.4947°N, 20.8247°E	15 Aug 2013	BC14507	B81	KY216944	KY216600	KY217352	KY216225
Slovakia								
Tatra National Park: Hlúpy Hill	49.2354°N, 20.2190°E	9 Jul 2011	MH	B70	KY216945	KY216601	KY217353	KY216226
Vertigo arizonensis (Pilsbry & Vanatta, 1900)								
North America								
U.S.A.								
Arizona: Nutrioso South	33.9039°N, 109.1619°W	26 Mar 2007	JCN14006	NS1	KY216946	GQ921524	KY217354	GQ921580
New Mexico: Emory Pass 2	32.9094°N, 107.7936°W	1 Apr 2007	JCN14217	NS2b	KY216947	GQ921525	KY217355	KY216227
Utah: Bullion Canyon 3	38.4171°N, 112.3126°W	7 Oct 2009	JCN17214	T4	KY216948	KY216602	KY217356	KY216228
Vertigo arthuri von Martens, 1884								
North America								
Canada								
Manitoba: Devils Lake Wayside	52.4035°N, 98.9119°W	17 Aug 2003	JCN11289	NS6	KY216949	GQ921487	KY217357	KY216229
U.S.A.								
Alaska: Chickaloon	61.7788°N, 148.4752°W	12 Aug 2007	JCN15401	NS4	KY216950	GQ921513	KY217358	GQ921562
Alaska: Falls Creek	60.9844°N, 149.5758°W	12 Aug 2007	JCN15354	NS5	KY216951	GQ921488	KY217359	KY216230

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Taxon/Location	Latitude/Longitude	Collection Date	Collection Acc. #	Specimen Acc. #	GenBank Acc. # CytB	16	ITS1	ITS2
Vertigo arthuri form *basidens* (Pilsbry & Vanatta, 1900)								
North America								
U.S.A.								
Colorado: Blanco River Campground	37.1452°N, 106.8857°W	26 Sep 2005	JCN13055	NS9	KY216952	GQ921490	KY217360	GQ921557
New Mexico: Tusas Ridge	36.6519°N, 106.0381°W	25 Sep 2005	JCN13016	NS8	KY216953	GQ921489	KY217361	GQ921566
Vertigo arthuri form *hubrichti* (Pilsbry, 1934)								
North America								
U.S.A.								
Wisconsin: Benderville Wayside	44.6132°N, 87.8420°W	16 Nov 2004	JCN645	NS28	KY216954	GQ921485	KY217362	GQ921571
Potawatomie State Park	44.8774°N, 87.4250°W	14 Aug 1996	JCN163	NS32	KY216955	GQ921501	KY217363	KY216231
Vertigo arthuri form *paradoxa* (Sterki, 1900)								
North America								
Canada								
Québec: La Grande Pointe	50.2017°N, 63.4013°W	2 Aug 2006	JCN13460	NS41	KY216957	GQ921484	KY217365	KY216233
U.S.A.								
Alaska: Nenana North, Alaska	64.6066°N, 149.0902°W	3 Aug 2007	JCN14949	NS42	KY216958	GQ921497	KY217366	GQ921569
Maine: Caribou	46.8590°N, 68.0119°W	23 Jul 2002	JCN9898	NS39	KY216959	GQ921494	KY217367	GQ921564
Russell Rock	46.3078°N, 67.8489°W	6 Sep 2007	JCN15567	T12	KY216960	KY216603	KY217368	KY216234
Vertigo beringiana n. sp.								
Asia								
Russia								
Altai: Aktash E2	50.3080°N, 87.6487°E	25 Jul 2011	JCN	B34	KY216961	KY216604	KY217369	KY216235
Camp Bolshoi Ilgumen	50.6411°N, 86.3512°E	5 Aug 2011	JCN	B33	KY216962	KY216605	KY217370	KY216236
Yakutia: Bestyakh SW	61.3624°N, 128.8433°E	10 Aug 2010	MH	T19	KY216963	KY216606	KY217371	KY216237
				H25	KY216964	KY216607	KY217372	KY216238

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Taxon/Location	Latitude/Longitude	Collection Date	Collection Acc. #	Specimen Acc. #	GenBank Acc. # CytB	16	ITS1	ITS2
North America								
U.S.A.								
Alaska: Berg 2	64.6066°N, 149.0902°W	3 Aug 2007	JCN14949	NS43	KY216965	GQ921515	KY217373	GQ921553
				T2	KY216966	KY216608	KY217374	KY216239
Ice Cut 1	69.0193°N, 148.8364°W	8 Aug 2007	JCN15118	B40	KY216967	KY216609	KY217375	KY216240
Clearwater Recreation Area	64.0530°N, 45.4332°W	11 Aug 2007	JCN15283	B41	KY216968	KY216610	KY217376	KY216241
Vertigo berryi Pilsbry, 1919								
North Ameica								
U.S.A.								
Utah: Mystic River seep	37.3743°N, 12.5945°W	6 Oct 2009	JCN17173	VH73	KY216970	KY216612	KY217378	KY216243
Vertigo binneyana Sterki, 1890								
North America								
Canada								
Saskatchewan: Ernfold East	50.4455°N, 06.8520°W	6 Sep 2012	BC14077	VH68	KY216971	KY216613	KY217379	KY216244
Manitoba: Sanford SE	49.6500°N, 97.4947°W	16 Aug 2003	BC02218[1]	VH69	KY216972	KY216614	KY217380	KY216245
Vertigo bisulcata (Jickeli, 1873)								
Africa								
Ghana								
Fetish Grove	5.3356°N, 0.0801°W	17 Mar 1995	dW 8846	OG2	KY216973	KT008314	KY217381	KY216246
Vertigo bollesiana (Morse, 1865)								
North America								
U.S.A.								
Maine: Mt. Carmel Wayside	47.3272°N, 68.1823°W	5 Sep 2007	JCN15493	NS10	KY216974	GQ921511	KY217382	KY216247
Russell Rock	46.3078°N, 67.8489°W	6 Sep 2007	JCN15564	NS11	KY216975	GQ921509	KY217383	GQ921574
Collins Siding	47.1113°N, 68.1316°W	13 Sep 2007	JCN16137	NS12	KY216976	GQ921510	KY217384	GQ921575

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		Collection	Collection	Specimen		GenBank Acc. #		
Taxon/Location	Latitude/Longitude	Date	Acc. #	Acc. #	CytB	16	ITS1	ITS2
Michigan: Maxton Plains Center	46.0789°N, 83.6569°W	17 Jun 1998	JCN2840	T5	KY216977	KY216615	KY217385	KY216248
Vertigo botanicorum Horsák & Pokryszko, 2010								
Asia								
<u>Russia</u>								
Altai: Aktel	51.5074°N, 85.5968°E	13 Aug 2005	MH	B3	KY216978	KY216616	KY217386	KY216249
Camp Cherga	51.6156°N, 85.5841°E	22 Jul 2011	JCN	B4	KY216979	KY216617	KY217387	KY216250
				B4b	KY216980	KY216618	KY217388	KY216251
4.5 km NE of Paspaul village	51.9679°N, 86.3997°E	26 Jul 2006	MH	B55	KY216981	KY216619	KY217389	KY216252
Ust-Muny W1	51.7346°N, 85.7318°E	23 Jul 2011	JCN	B5	KY216982	KY216620	KY217390	KY216253
Ust-Muny W3	51.7297°N, 85.7382°E	23 Jul 2011	JCN	B53	KY216983	KY216621	KY217391	KY216254
Ust Sema S	51.6134°N, 85.7926°E	23 Jul 2011	JCN	B54	KY216984	KY216622	KY217392	KY216255
Uzunkel Lake	50.4767°N, 87.6301°E	18 Jul 2006	MH	B56	KY216985	KY216623	KY217393	KY216256
Vertigo calamitosa (Pilsbry, 1889)								
North America								
<u>U.S.A.</u>								
California: Border Field State Park	32.5354°N, 117.1231°W	29 Sep 2013	JCN19190	C41	KY216986	KY216624	KY217394	KY216257
Point Loma	32.6730°N, 117.2449°W	21 Apr 2014	JCN19200	C40	KY216987	KY216625	KY217395	KY216258
Sumner Canyon	32.8734°N, 117.2483°W	2 Mar 2010	JCN18169	VH24	KY216988	KT008324	KY217396	KY216259
Vertigo californica (Rowell, 1862)								
North America								
<u>U.S.A.</u>								
California: Coast Dairy	36.9893°N, 122.1672°W	6 Oct 2013	JCN19288	C9	KY216989	KY216626	KY217397	KY216260
				C10	KY216990	KY216627	KY217398	KY216261
Moss Landing Beach	36.8095°N, 121.7884°W	25 Nov 2006	JCN13934	T13	KY216991	KT008315	KY217399	KY216262
Oceano Dunes	35.1208°N, 120.6326°W	4 Oct 2013	JCN19216	C7	KY216992	KY216628	KY217400	KY216263

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Taxon/Location	Latitude/Longitude	Collection Date	Collection Acc. #	Specimen Acc. #	GenBank Acc. # CytB	16	ITS1	ITS2
South Salmon Creek Beach	38.3492°N, 123.0659°W	12 Sep 2013	JCN19187	C8	KY216993	KY216629	KY217401	KY216264
San Clemente Island								
Knob Canyon	32.8384°N, 118.3751°W	19 Apr 2014	JCN19755	C17	KY216994	KY216630	KY217402	KY216265
				C18	KY216995	KY216631	KY217403	KY216266
Radar Station	32.9745°N, 118.5317°W	14 Jul 2013	JCN19155	C6	KY216996	KY216632	KY217404	KY216267
Santa Catalina Island								
Cherry Canyon	33.4505°N, 118.5138°W	2 Oct 2013	JCN19234	C14	KY216997	KY216633	KY217405	KY216268
Santa Rosa Island								
Carrington Point	34.0220°N, 120.0706°W	16 Jun 2016	JCN	C53	KY216998	KY216634	KY217406	KY216269
Vertigo californica longa Pilsbry, 1920								
North America								
U.S.A.								
California: San Clemente Island								
Wilson Cove S1	32.9953°N, 118.5516°W	12 Jul 2013	JCN19111	C4	KY216999	KY216635	KY217407	KY216270
Old Airport East	32.9526°N, 118.5163°W	18 Apr 2014	JCN19750	C27	KY217000	KY216636	KY217408	KY216271
Middle Ranch Canyon	32.8767°N, 118.4909°W	14 Jul 2013	JCN19164	C28	KY217001	KY216637	KY217409	KY216272
China Point	32.8042°N, 118.4271°W	13 Jul 2013	JCN19124	C29	KY217002	KY216638	KY217410	KY216273
				C30	KY217003	KY216639	KY217411	KY216274
San Nicolas Island								
Daytona Beach	33.2260°N, 119.4396°W	4 Oct 2015	JCN20697	C47	KY217004	KY216640	KY217412	KY216275
Mineral Canyon 2	33.2537°N, 119.5032°W	3 Oct 2015	JCN20659	C48	KY217005	KY216641	KY217413	KY216276
Corral Harbor E	33.2749°N, 119.5124°W	3 Oct 2015	JCN20674	C49	KY217006	KY216642	KY217414	KY216277
Vertigo catalinaria (Sterki, 1890)								
North America								
U.S.A.								
California: San Clemente Island								
Grove Canyon	32.8772°N, 118.4348°W	6 Sep 2014	JCN20152	C31	KY217007	KY216643	KY217415	KY216278

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Taxon/Location	Latitude/Longitude	Collection Date	Collection Acc. #	Specimen Acc. #	GenBank Acc. #			
					CytB	16	ITS1	ITS2
Old Airport East	32.9526°N, 118.5163°W	18 Apr 2014	JCN19749	C15	KY217008	KY216644	KY217416	KY216279
Thirst Peak	32.8815°N, 118.4443°W	14 Jul 2013	JCN19160	C32	KY217009	KY216645	KY217417	KY216280
Upper China Canyon	32.8340°N, 118.4233°W	13 Jul 2013	JCN19129	C16	KY217010	KY216646	KY217418	KY216281
Santa Catalina Island								
Bulrush Canyon 2	33.3456°N, 118.4419°W	1 Oct 2013	JCN19213	C5	KY217011	KY216647	KY217419	KY216282
Two Harbors South	33.4331°N, 118.5094°W	2 Oct 2013	JCN19227	C12	KY217012	KY216648	KY217420	KY216283
Santa Catalina Island								
Upper Coffee Pot	33.3360°N, 118.3864°W	1 Oct 2013	JCN19214	C11	KY217014	KY216650	KY217422	KY216285
Santa Cruz Island								
Navy Road	34.0034°N, 119.6477°W	19 Sep 2016	JCN	C55	KY217015	KY216651	KY217423	KY216286
Santa Rosa Island								
Cherry Canyon	33.9864°N, 120.0730°W	16 Jun 2016	JCN	C52	KY217016	KY216652	KY217424	KY216287
Vertigo chiricahuensis n. sp.								
North America								
U.S.A.								
Arizona: Buena Vista Peak	31.9176°N, 109.2722°W	20 Mar 2005	JCN12560	NS15	KY217017	GQ921526	KY217425	KY216288
Vertigo cf. *chiricahuensis*								
Central America								
Mexico								
Sonora: Sierra el Tigre	30.6003°N, 109.2199°W	13 Aug 2015	Van Devender	VH115	KY217018	KY216653	KY217426	KY216289
				VH121	KY217019	KY216654	KY217427	KY216290
North America								
U.S.A.								
Texas: Davis Mountains	30.6386°N, 104.1616°W	8 Nov 2015	JCN20728	VH122	KY217020	KY216655	KY217428	KY216291
	30.6371°N, 104.1781°W	8 Nov 2015	JCN20780	VH123	KY217021	KY216656	KY217429	KY216292
Vertigo chytryi n. sp.								
Asia								

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Taxon/Location	Latitude/Longitude	Collection Date	Collection Acc. #	Specimen Acc. #	GenBank Acc. # CytB	16	ITS1	ITS2
Russia								
Altai: Zalesovo, Peshcherka	54.1335°N, 84.7584°E	10 Jul 2012	MH	B52	KY217022	KY216657	KY217430	KY216293
Tyumenskaya: Nizhnie Aremzyany	58.5269°N, 68.6815°E	10 Aug 2013	MH	B75	KY217023	KY216658	KY217431	KY216294
Vertigo circumlabiata Schileyko, 1984								
Asia								
Japan								
Hokkaidō: Tsukiji, Urakawa,	42.1717°N, 142.7649°E	23 Jul 2012	JCN	B72	KY217024	KY216659	KY217432	KY216295
Kotanuka, Shibetsu Pass	43.7527°N, 144.8426°E	25 Jul 2012	JCN	B73	KY217025	KY216660	KY217433	KY216296
North America								
U.S.A.								
Alaska: Earthquake Park, Anchorage	61.1990°N, 149.9889°W	12 Aug 2007	JCN15313	B103	KY217026	KY216661	KY217434	KY216297
	61.1990°N, 149.9795°W	19 Aug 2007	BC12469	B116	KY217027	KY216662	KY217435	KY216298
Vertigo clappi Brooks & Hunt, 1936								
North America								
U.S.A.								
Tennessee: Blue Hole, Rock Island SP	35.8111°N, 85.6370°W	8 Jul 2001	BC00544[1]	VH43	KY217028	KY216663	KY217436	KY216299
Lynn Mountain	36.3545°N, 82.1535°W	10 Sep 2002	UF299578	VH20	KY217029	KT008321	KY217437	KY216300
				VH20b	KY217030	KY216664		KY216301
Tellico Gorge	35.3294°N, 84.1833°W	5 Jul 2001	BC00510[1]	VH42	KY217031	KY216665		KY216302
Virginia: Back Creek Trail 1	38.0631°N, 79.8885°W	26 Oct 2012	JCN19500	VH55	KY217032	KY216666	KY217438	KY216303
Vertigo clementina (Sterki, 1890)								
North America								
U.S.A.								
California: San Clemente Island								
Wilson Cove S1	32.9953°N, 118.5516°W	12 Jul 2013	JCN19109	OG15	KY217033	KT008325	KY217439	KY216304
Knob Canyon	32.8384°N, 118.3751°W	19 Apr 2014	JCN19753	C42	KY217034	KY216667	KY217440	KY216305

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		Collection	Collection	Specimen		GenBank Acc. #		
Taxon/Location	Latitude/Longitude	Date	Acc. #	Acc. #	CytB	16	ITS1	ITS2
Middle Ranch Canyon	32.8769°N, 118.4909°W	14 Jul 2013	JCN19163	C43	KY217035	KY216668	KY217441	KY216306
San Nicolas Island								
Desalinization Plant W	33.2434°N, 119.4499°W	4 Oct 2015	JCN20692	C50	KY217036	KY216669	KY217442	KY216307
Vertigo coloradensis (Cockerell, 1891)								
North America								
<u>Canada</u>								
British Columbia: Duncan Lake 2	50.6280°N, 117.0356°W	2 Sep 2011	JCN18652	B39	KY217037	KY216670	KY217443	KY216308
<u>U.S.A.</u>								
Alaska: Clearwater State Rec.Area	64.0530°N, 145.4332°W	11 Aug 2007	JCN15286	B38	KY217038	KY216671	KY217444	KY216309
Earthquake Park 1	61.1990°N, 149.9889°W	12 Aug 2007	JCN15312	NS46	KY217039	GQ921538	KY217445	KY216310
Toolik Field Station 2	68.6243°N, 149.5931 W	9 Aug 2007	JCN15211	B37	KY217040	KY216672	KY217446	KY216311
Arizona: Mt. Lemmon	32.4413°N, 110.7848°W	27 Mar 2007	JCN14044	NS14	KY217041	GQ921540	KY217447	GQ921587
Vertigo columbiana Sterki, 1892								
North America								
<u>Canada</u>								
British Columbia: Slocan River	49.7544°N, 117.4767 W	28 Aug 2011	JCN18459	VH93	KY217042	KY216673	KY217448	KY216312
<u>U.S.A.</u>								
Alaska: Old Crow Mine Rd	60.9752°N, 149.1211°W	13 Aug 2007	JCN15363	VH94	KY217043	KY216674	KY217449	KY216313
				VH95	KY217044	KY216675	KY217450	KY216314
Oregon: Manhattan Beach	45.6413°N, 123.9410°W	2 Aug 2012	JCN18739	VH92	KY217045	KY216676	KY217451	KY216315
Washington: Centennial Trail	48.3065°N, 122.2131°W	28 May 2015	JCN20576	VH110	KY217046	KY216677	KY217452	KY216316
Vertigo concinnula Cockerell, 1897								
North America								
<u>U.S.A.</u>								
Arizona: Nutrioso South	33.9039°N, 109.1619°W	26 Mar 2007	JCN14007	NS54	KY217047	GQ921535	KY217453	GQ921586
Colorado: Ptarmigan Trailhead	38.8029°N, 106.3744°W	14 Aug 2005	JCN12914	B108	KY217048	KY216678	KY217454	KY216317
Tincup	38.7171°N, 106.4987°W	14 Aug 2005	JCN12921	VH96	KY217049	KY216679	KY217455	KY216318

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		Collection	Collection	Specimen	GenBank Acc. #			
Taxon/Location	Latitude/Longitude	Date	Acc. #	Acc. #	CytB	16	ITS1	ITS2
New Mexico: Nogal Canyon	33.4980°N, 105.7611°W	30 Sep 2005	JCN13086	VH88	KY217050	KY216680	KY217456	KY216319
Utah: Bullion Canyon 3	38.4171°N, 112.3126°W	7 Oct 2009	JCN17215	T1	KY217051	KY216681	KY217457	KY216320
Cobblerest seep	40.5948°N, 110.9905°W	21 Sep 2010	BC13184	VH107	KY217052	KY216682	KY217458	KY216321
Vertigo cristata (Sterki, 1919)								
North America								
Canada								
Québec: Sunny Mountain	55.0647°N, 67.2348°W	12 Aug 2006	JCN13786	NS44	KY217053	GQ921544	KY217459	GQ921584
U.S.A.								
Maine: Blind Brook	46.5788°N, 68.9291°W	7 Sep 2007	JCN15736	NS19	KY217054	GQ921542		GQ921589
Roque Bluffs Road	44.6363°N, 67.4961°W	2 Oct 2004	BC02647[1]	NS16	KY217055	GQ921541		KY216322
Vertigo cupressicola Sterki, 1919								
North America								
U.S.A.								
California: Carmel Beach	36.5232°N, 121.9300°W	26 Nov 2006	JCN13940	C21	KY217056	KY216683	KY217460	KY216323
Crocker Grove, Carmel	36.5782°N, 121.9727°W	5 Oct 2013	JCN19266	C1	KY217057	KY216684	KY217461	KY216324
Kasler Point N	36.4230°N, 121.9135°W	5 Oct 2013	JCN19285	C22	KY217058	KY216685	KY217462	KY216325
Point Lobos	36.5215°N, 121.9519°W	5 Oct 2013	JCN19274	C19	KY217059	KY216686	KY217463	KY216326
				C20	KY217060	KY216687	KY217464	KY216327
Vertigo dalliana (Sterki, 1890)								
North America								
U.S.A.								
California: Manzanita Creek	38.7396°N, 123.2446°W	4 Jan 1981	Roth1233	VH112	KY217061	KY216688	KY217465	KY216328
				VH113	KY217062	KY216689	KY217466	KY216329
Vertigo dedecora (Pilsbry, 1902)								
Asia								

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Taxon/Location	Latitude/Longitude	Collection Date	Collection Acc. #	Specimen Acc. #	CytB	GenBank Acc. # 16	ITS1	ITS2
Japan								
Tōkyō: Chichijima Island	27.0948°N, 142.2166°E	2012	Chiba	VH23	KY217063	KT008323	KY217467	KY216330
Toriyama, Chichijima Island	27.0550°N, 142.2338°E	Oct 2015	Chiba	VH133	KY217064	KY216690	KY217468	KY216331
Vertigo dedecora tamagonari Pilsbry & Hirase, 1904								
Asia								
Japan								
Okinawa: Minami-daitoujima	25.8191°N, 131.2465°E	9 Jun 1995	ANSP421190	VH134	KY217065			
Tōkyō: Hahajima Island	26.6537°N, 142.1536°E	2012	Chiba	VH28	KY217066	KY216691	KY217469	KY216332
Higashiyama, Hahajima Island	26.7005°N, 142.1503°E	7 Nov 2013	Chiba	VH135	KY217067		KY217470	KY216333
Vertigo diegoensis (Sterki, 1890)								
North America								
U.S.A.								
California: Border Field State Park 2	32.5357°N, 117.1174°W	22 Apr 2014	JCN19777	C26	KY217068	KY216692	KY217471	KY216334
Point Dume	34.0023°N, 118.8075°W	4 Oct 2013	JCN19257	C24	KY217069	KY216693	KY217472	KY216335
Point Loma	32.6720°N, 117.2449°W	30 Sep 2013	JCN19202	C3	KY217070	KY216694	KY217473	KY216336
		21 Apr 2014	JCN19202	C23	KY217071	KY216695	KY217474	KY216337
Sumner Canyon	32.8734°N, 117.2483°W	2 Mar 2010	JCN18171	C25	KY217072	KY216696	KY217475	KY216338
Vertigo elatior Sterki, 1894								
North America								
Canada								
Alberta: Ghost Hills	51.3435°N, 114.9680°W	31 Aug 2012	BC13941	B87	KY217073	KY216697	KY217476	KY216339
Québec: La Grande Pointe	50.2017°N, 63.4013°W	2 Aug 2006	JCN13456	B89	KY217074	KY216698	KY217477	KY216340
U.S.A.								
Arizona: Blind Canyon 1	31.3823°N, 110.3187°W	23 Mar 2016	JCN21192	VH132	KY217075	KY216699	KY217478	KY216341
Iowa: Rowley North fen	42.3764°N, 91.8507°W	21 Sep 2012	JCN5746	B88	KY217076	KY216700	KY217479	KY216342
New Mexico: Sacramento Canyon	32.7148°N, 105.7557°W	1 Oct 2005	JCN13169	B118	KY217077	KY216701	KY217480	KY216343

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Taxon/Location	Latitude/Longitude	Collection Date	Collection Acc. #	Specimen Acc. #	GenBank Acc. # CytB	16	ITS1	ITS2
Vertigo eogea Pilsbry, 1919								
Asia								
Japan								
Iwate: Kashiwagidaira, Tono	39.3083°N, 141.7146°E	29 Jul 2012	JCN	J7	KY217078	KY216702	KY217481	KY216344
Hokkaidō: Hamataura	42.5898°N, 141.2602°E	22 Jul 2012	JCN	VH58	KY217079	KY216703	KY217482	KY216345
Kushiro Marsh	43.0340°N, 144.3901°E	23 Jul 2012	JCN	J1	KY217080	KY216704	KY217483	KY216346
Lake Abashiri	43.9200°N, 144.1586°E	25 Jul 2012	JCN	J3	KY217081	KY216705	KY217484	KY216347
Lake Utonai, Tomakomai	42.7056°N, 141.7146°E	26 Jul 2012	JCN	J5	KY217082	KY216706	KY217485	KY216348
				J6	KY217083	KY216707	KY217486	KY216349
Yanbetsu, Shari District	43.9154°N, 144.5379°E	25 Jul 2012	JCN	J2	KY217084	KY216708	KY217487	KY216350
Tōkyō: Renkoji seep, Tama	35.6325°N, 139.4677°E	31 Jul 2012	JCN	VH56	KY217085	KY216709	KY217488	KY216351
Vertigo extima (Westerlund, 1876)								
Asia								
Russia								
Yamalo-Nenets: Tazovskii	67.1815°N, 78.8589°E	22 Aug 2013	MH	B77	KY217086	KY216710	KY217489	KY216352
Europe								
Norway								
Finnmark: Basecakka	69.6612°N, 25.8886°E	30 Jul 1991	TvP	B111		KY216711		
		16 Jul 2014	TvP	B114	KY217087	KY216712	KY217490	KY216353
Sweden								
Lappland: Kiruna	67.8626°N, 20.2579°E	4 Jul 1990	BC	B69	KY217088	KY216713		KY216354
Sarek National Park	67.2833°N, 17.7000°E	5 Aug 1996	TvP	B83	KY217089	KY216714	KY217491	KY216355
Vertigo farquhari (Pilsbry, 1920)								
Africa								
South Africa								
KwaZulu-Natal: Burman Bush	29.8149°S, 31.0174°E	29 Mar 2011	NMSA.W7887	VH128	KY217090	KY216715	KY217492	KY216356
Pietermaritzburg	29.5033°S, 30.5037°E	19 Dec 2001	NMSA.V9872	VH129	KY217091	KY216716	KY217493	
Thukela River	29.2270°S, 31.5980°E	9 Apr 1999	NMSA.V7096	VH130	KY217092	KY216717	KY217494	KY216357

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Taxon/Location	Latitude/Longitude	Collection Date	Collection Acc. #	Specimen Acc. #	GenBank Acc. # CytB	16	ITS1	ITS2
Vertigo genesii (Gredler, 1856)								
Europe								
Italy								
Belluno: Pocol	46.5207°N, 12.0985°E	9 Jul 2013	MH	B99	KY217093	KY216718	KY217495	KY216358
Norway								
Sør-Trøndelag: Kongsvoll	62.2672°N, 9.5855°E	20 Aug 2006	MH	H31	KY217094	JN941043	KY217496	KY216359
Sweden								
Jämtland: Hammerdal	63.5802°N, 15.2311°E	15 Aug 2006	MH	B8	KY217095	KY216719	KY217497	KY216360
Lappland: Abisko Tourist Station	68.3426°N, 18.8353°E	5 Aug 2013	TvP	B101	KY217096	KY216720	KY217498	KY216361
Switzerland								
Alp Astras: Tamangur Valle	46.6741°N, 10.3522°E	10 Aug 2012	MH	B9	KY217097	KY216721	KY217499	KY216362
Vertigo genesioides n. sp.								
Asia								
Japan								
Hokkaidō: Hamanaka	43.1108°N, 145.1068°E	24 Jul 2012	JCN	B15	KY217098	KY216722	KY217500	KY216363
Russia								
Altai: Camp Belshoi Ilgumen	50.6389°N, 86.3484°E	5 Aug 2011	MH	AP24	KY217099	KY216723	KY217501	KY216364
Mukhor-Tarkhata E	49.9929°N, 88.5496°E	3 Aug 2011	JCN	B6	KY217100	KY216724	KY217502	KY216365
Kemerovo: Leninsk-Kuznetskii	54.3446°N, 85.2223°E	8 Jul 2012	MH	B7	KY217101	KY216725	KY217503	KY216366
Yakutia: Kangalassy SW	62.3292°N, 129.9282°E	4 Aug 2010	MH	H24	KY217102	KY216726	KY217504	KY216367
Kil'demsty Village	62.2822°N, 129.7570°E	3 Aug 2010	MH	B17	KY217103	KY216727	KY217505	KY216368
North America								
Canada								
Manitoba: Twin Lakes Road, Churchill	58.6464°N, 93.8245°W	23 Aug 2003	JCN11342	H33	KY217104	KY216728	KY217506	KY216369
Québec: La Grande Pointe	50.2017°N, 63.4014°W	2 Aug 2006	JCN13459	B14	KY217105	KY216729	KY217507	KY216370
U.S.A.								
Alaska: Milepost 346, Dalton Hwy	69.3100°N, 148.7300°W	9 Aug 2007	JCN15192	H35	KY217106	KY216730	KY217508	KY216371
Yukon Crossing, Dalton Hwy	65.8787°N, 149.7151°W	6 Aug 2007	JCN15027	B13	KY217107	KY216731	KY217509	KY216372

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Taxon/Location	Latitude/Longitude	Collection Date	Collection Acc. #	Specimen Acc. #	GenBank Acc. # CytB	16	ITS1	ITS2
Vertigo geyeri Lindholm, 1925								
Europe								
Poland								
Chełmski: Brzeźno	51.1568°N, 23.6000°E	11 Jul 2010	MH	H30	KY217108	KY216732	KY217510	KY216373
Slovakia								
Kežmarok: Výborná	49.2144°N, 20.3903°E	29 May 2003	MH	H29	KY217109	KY216733	KY217511	KY216374
Sweden								
Skåne: Sjöbo, Röddinge	55.5883°N, 13.7850°E	13 Aug 2006	MH	H23	KY217110	KY216734	KY217512	KY216375
Switzerland								
Scuol: Lac Noir	46.7772°N, 10.2681°E	8 Aug 2012	MH	B16	KY217111	KY216735	KY217513	KY216376
United Kingdom								
England: Tarn Moor, Kirkby Stephen	54.4596°N, 2.5082°W	4 Nov 2002	Colville	H32	KY217112	KY216736	KY217514	KY216377
Vertigo gouldii (A. Binney, 1843)								
North America								
U.S.A.								
Arkansas: Panther Creek	36.0858°N, 92.5649°W	3 Apr 2007	JCN14342	NS22	KF214509	GQ921507	KF214485	KF214473
Iowa: Brush Creek Canyon	42.7796°N, 91.6890°W	20 Jul 2007	JCN1554	NS21	KF214508	GQ921506	KF214484	KF214472
Maine: Russell Rock	46.3078°N, 67.8489°W	6 Sep 2007	JCN15566	NS20	KY217113	GQ921505	KY217515	KY216378
Missouri: 11-Point River Bridge	36.7931°N, 91.3334°W	1 May 2010	JCN18206	T6	KF214510	KF214506	KF214486	KF214474
Tennessee: Beauty Spot Gap Road	36.1277°N, 82.3086°W	5 Apr 2005	JCN12451	VH65	KY217114	KY216737	KY217516	KY216379
Virginia: Falling Spring NE	37.8810°N, 79.9176°W	25 May 2013	JCN18911	VH49	KY217115	KY216738	KY217517	KY216380
West Virginia: Big Ugly WMA	38.0859°N, 82.0009°W	20 Nov 2013	Dourson	VH66	KY217116	KT008330	KY217518	KY216381
Vertigo griqualandica (Melvill & Ponsonby, 1893)								
Africa								

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Taxon/Location	Latitude/Longitude	Collection Date	Collection Acc. #	Specimen Acc. #	GenBank Acc. # CytB	16	ITS1	ITS2
South Africa								
KwaZulu-Natal: Paulpietersburg	27.5274°S, 20.7276°E	13 Jul 2012	NMSA.W9293	VH125	KY217117	KY216739	KY217519	KY216382
Biggarsberg	28.2000°S, 29.9170°E	7 Jan 1997	NMSA.V4934	VH127	KY217118			
Limpopo: Forest Glens	23.9712°S, 29.9185°E	17 Jun 2006	NMSA.W7776	VH126	KY217119	KY216740	KY217520	KY216383
Vertigo hachijoensis Pilsbry, 1919								
Asia								
Japan								
Tōkyō: Hachijo-kojima Island	33.1320°N, 139.6805°E	2013	Chiba	VH103	KY217120	KY216741	KY217521	KY216384
Vertigo hannai Pilsbry, 1919								
North America								
Canada								
Alberta: Waiparous River bridge	51.3681°N, 114.9905°W	31 Aug 2012	BC13888	B115	KY217121	KY216742	KY217522	KY216385
Manitoba: Launch Road, Churchill	58.7447°N, 93.8716°W	22 Aug 2003	BC02294[1]	NS23	KY217122	GQ921520	KY217523	GQ921573
U.S.A.								
Alaska: Coldfoot North	67.3512°N, 150.1359°W	6 Aug 2007	JCN15040	NS26	KY217123	GQ921519	KY217524	GQ921565
Happy Valley	69.3355°N, 148.7302°W	8 Aug 2007	JCN15144	NS24	KY217124	GQ921518	KY217525	GQ921556
Last Tree South, Dalton Hwy	67.9406°N, 149.7970°W	7 Aug 2007	JCN15072	NS25	KY217125	GQ921517	KY217526	GQ921560
Nenana North	64.6066°N, 149.0902°W	3 Aug 2007	JCN14953	NS27	KY217126	GQ921516	KY217527	KY216386
South Fork Koyukuk	67.0197°N, 150.2886°W	10 Aug 2007	JCN15240	T7	KY217127	KY216743	KY217528	KY216387
Vertigo hebardi Vanatta, 1912								
North America								
U.S.A.								
Florida: Elliott Key	25.4553°N, 80.1925°W	30 Apr 2010	UF437837	VH2	KF214512	KF214504	KF214511	KF214476
Long Key	24.8146°N, 80.8211°W	2 May 2010	UF437841	VH1	KF214511	KF214505	KF214487	KF214475
Plantation Key	24.9845°N, 80.5450°W	12 Apr 2016	JCN	VH137	KY217128	KY216744	KY217529	KY216388

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		Collection	Collection	Specimen		GenBank Acc. #		
Taxon/Location	Latitude/Longitude	Date	Acc. #	Acc. #	CytB	16	ITS1	ITS2
Vertigo hemphilli (Sterki, 1890)								
North America								
U.S.A.								
California: Border Field 3	32.5428°N, 117.1061°W	22 Apr 2014	JCN19780	VH67	KY217129	KT008331	KY217530	KY216389
Palos Verdes Hills	33.7480°N, 118.3952°W	18 Jun 2016	JCN	C54	KY217130	KY216745	KY217531	KY216390
Point Dume	34.0023°N, 118.8075°W	4 Oct 2013	JCN19256	C46	KY217131	KY216746	KY217532	KY216391
Sumner Canyon	32.8734°N, 117.2483°W	2 Mar 2010	JCN18170	C45	KY217132	KY216747	KY217533	KY216392
Vertigo hinkleyi Pilsbry, 1920								
North America								
U.S.A.								
Arizona: Cave Creek Canyon 2	31.8670°N, 109.1889°W	31 Mar 2007	JCN14187	VH54	KY217133	KY216748	KY217534	KY216393
Miller Canyon	31.4105°N, 110.2824°W	28 Mar 2007	JCN14091	NS53	KY217134	GQ921545	KY217535	GQ921592
Vertigo cf. *hirasei* Pilsbry, 1901								
Asia								
Japan								
Iwate: Takameda, Nagayama, Shizukishi	39.6942°N, 140.9562°E	28 Jul 2012	JCN	J20	KY217135	KY216749	KY217536	KY216394
Miyagi: Minami-fukasawa, Tome	38.6740°N, 141.1103°E	30 Jul 2012	JCN	J21	KY217136	KY216750	KY217537	KY216395
Vertigo cf. *hoppii* (Möller, 1842)								
Asia								
Russia								
Khanty-Mansi: Salym	59.9880°N, 71.2883°E	12 Aug 2013	MH	B79	KY217137	KY216751	KY217538	KY216396
Yamalo-Nenets: Tazovskii	67.2726°N, 78.8365°E	21 Aug 2013	MH	B78	KY217138	KY216752	KY217539	KY216397
North America								
Canada								
Manitoba: Acid palsa, Churchill	58.7333°N, 93.8069°W	21 Aug 2003	BC02336[1]	B58	KY217139	KY216753	KY217540	KY216398

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Taxon/Location	Latitude/Longitude	Collection Date	Collection Acc. #	Specimen Acc. #	GenBank Acc. # CytB	16	ITS1	ITS2
Vertigo idahoensis Pilsbry, 1934								
North America								
<u>Canada</u>								
British Columbia: Incomappleux 1	50.9227°N, 117.5787°W	29 Aug 2011	JCN18516	B94	KY217140	KY216754	KY217541	KY216399
<u>U.S.A.</u>								
Colorado: Trujillo Meadows	37.0539°N, 106.4626°W	25 Sep 2005	JCN13035	B95	KY217141	KY216755	KY217542	KY216400
Utah: Mystic River seep	37.3743°N, 112.5945°W	6 Oct 2009	JCN17175	VH72		KY216756	KY217543	KY216401
Vertigo inserta Pilsbry, 1919								
North America								
<u>U.S.A.</u>								
Arizona: Bear Wallow 2	32.4211°N, 110.7302°W	27 Mar 2007	JCN14062	NS30	KY217142	GQ921527	KY217544	KY216402
				T9	KY217143	KY216757	KY217545	KY216403
Bigelow Campground	32.4154°N, 110.7282°W	27 Mar 2007	JCN14072	NS31	KY217144	GQ921528	KY217546	GQ921579
Nutrioso South	33.9039°N, 109.1619°W	26 Mar 2007	JCN14008	NS29	KY217145	GQ921529	KY217547	GQ921578
Blind Canyon 1	31.3823°N, 110.3187°W	23 Mar 2016	JCN21191	VH136	KY217146	KY216758	KY217548	KY216404
Vertigo japonica cf. *coreana* Pilsbry, 1919								
Asia								
<u>Russia</u>								
Primorskij Kraj: Gorno-Taezhnoye	43.6971°N, 132.1633°E	19 Jul 2012	Meng	J22	KY217147	KY216759	KY217549	KY216405
Vertigo kodamai n. sp.								
Asia								
<u>Japan</u>								
Hokkaidō: Cape Shirepa, Kushiro	42.9517°N, 144.7370°E	24 Jul 2012	JCN	VH100	KY217148	KY216760	KY217550	KY216406
			JCN	VH101	KY217149	KY216761	KY217551	KY216407
Hobetsu-fukuyama, Yufutsu	42.8869°N, 142.2500°E	26 Jul 2012	JCN	VH102	KY217150	KY216762	KY217552	KY216408

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Taxon/Location	Latitude/Longitude	Collection Date	Collection Acc. #	Specimen Acc. #	GenBank Acc. # CytB	16	ITS1	ITS2
Kamikineusu, Urakawa	42.2201°N, 142.9594°E	22 Jul 2012	JCN	VH59	KY217151	KY216763	KY217553	KY216409
Samani	42.1815°N, 143.0003°E	22 Jul 2012	JCN	VH98	KY217152	KY216764	KY217554	KY216410
Tsubetsu, Abashiri	43.5104°N, 143.9862°E	25 Jul 2012	JCN	VH60	KY217153	KY216765	KY217555	KY216411
Tōkyō: Minami Iwo	24.2385°N, 141.4695°E	2012	Chiba	VH22	KY217154	KY216766	KY217556	KY216412
				VH22b			KY217557	KY216413
Vertigo kurilensis n. sp.								
Asia								
Japan								
Hokkaidō: Akkeshi North	43.0817°N, 144.8442°E	24 Jul 2012	JCN	J10	KY217155	KY216767	KY217558	KY216414
Hamanaka	43.1108°N, 145.1068°E	24 Jul 2012	JCN	B97	KY217156	KY216768	KY217559	KY216415
Tokotan	43.4352°N, 145.2616°E	24 Jul 2012	JCN	B98	KY217157	KY216769	KY217560	KY216416
Vertigo kushiroensis (Pilsbry & Hirase, 1905)								
Asia								
Japan								
Hokkaidō: Chisata Pass, Saru	42.9750°N, 142.7481°E	26 Jul 2012	BC13832	J18	KY217158	KY216770	KY217561	KY216417
Hamanaka, Akkeshi	43.1108°N, 145.1068°E	24 Jul 2012	JCN	J14	KY217159	KY216771	KY217562	KY216418
			JCN	J15	KY217160	KY216772	KY217563	KY216419
Hobetsu-fukuyama, Yufutsu	42.8860°N, 142.2500°E	26 Jul 2012	JCN	J19	KY217161	KY216773	KY217564	KY216420
Kushiro Marsh	43.0340°N, 144.3901°E	23 Jul 2012	JCN	VH61	KY217162	KY216774	KY217565	KY216421
				J13	KY217163	KY216775	KY217566	KY216422
Nakashibetsu, Nemura	43.5511°N, 144.9697°E	25 Jul 2012	BC13761	J16	KY217164	KY216776	KY217567	KY216423
			BC13762	J17	KY217165	KY216777	KY217568	KY216424
Nishicha Bridge, Urakawa	42.1915°N, 142.8636°E	23 Jul 2012	JCN	J12	KY217166	KY216778	KY217569	KY216425
Samani	42.1815°N, 143.0003°E	22 Jul 2012	JCN	J11	KY217167	KY216779	KY217570	KY216426
Lake Yudonuma	42.5877°N, 143.5358°E	23 Jul 2012	JCN	B2	KY217168	KY216780	KY217571	KY216427

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Taxon/Location	Latitude/Longitude	Collection Date	Collection Acc. #	Specimen Acc. #	GenBank Acc. # CytB	16	ITS1	ITS2
Vertigo lilljeborgi (Westerlund, 1871)								
Asia								
Japan								
Hokkaidō: Lake Abashiri	43.9200°N, 144.1586°E	25 Jul 2012	JCN	J4	KY217169	KY216781	KY217572	KY216428
Russia								
Khanty-Mansi: Urengoi	59.9880°N, 71.2883°E	19 Aug 2013	MH	B76	KY217170	KY216782	KY217573	KY216429
Europe								
Czech Republic								
Moravia: Louky u Černého lesa Reserve	49.5855°N, 15.9423°E	4 Aug 2012	MH	B60	KY217171	KY216783	KY217574	KY216430
Norway								
Sør-Trøndelag: Kongsvoll	62.3558°N, 9.6832°E	21 Aug 2006	MH	B61	KY217172	KY216784	KY217575	KY216431
United Kingdom								
England: Little Langdale Tarn, Cumbria	54.4210°N, 3.0672°W	28 Jun 2000	JCN	B62	KY217173	KY216785	KY217576	KY216432
Vertigo lilljeborgi vinlandica n. subsp.								
North America								
Canada								
Québec: Schefferville Airport	54.8071°N, 66.8036°W	8 Aug 2006	JCN13681	B93	KY217174	KY216786	KY217577	KY216433
Lac John	54.8138°N, 66.7920°W	10 Aug 2006	JCN13746	B119	KY217175	KY216787	KY217578	KY216434
U.S.A.								
Maine: Portage Lake	46.7850°N, 68.5408°W	9 Sep 2007	JCN15914	VH51	KY217176	KY216788	KY217579	KY216435
Vertigo malleata Coles & Nekola, 2007								
North America								
U.S.A.								
Alabama: Pond Creek	31.1036°N, 86.5343°W	5 May 2005	JCN12365	VH10	KY217177	KY216789	KY217580	KY216436
North Carolina: Holly Shelter	34.5492°N, 77.7817°W	1 Apr 2003	UF449308	VH9	KY217178	KT008318	KY217581	KY216437
Maine: Saco Heath 3	43.5477°N, 70.4586°W	8 Aug 2004	JCN12099	VH11	KY217179	KY216790	KY217582	KY216438
				VH11b	KY217180	KY216791	KY217583	KY216439

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		Collection	Collection	Specimen		GenBank Acc. #		
Taxon/Location	Latitude/Longitude	Date	Acc. #	Acc. #	CytB	16	ITS1	ITS2
Vertigo marciae Nekola & Rosenberg, 2013								
Caribbean								
Jamaica								
John Crow Peak	18.1132°N, 76.6685°W	22 May 1999	ANSP402244	VH3b	KY217181	KY216792		
				VH4	KF214514	KF214502	KF214489	KF214477
Vertigo meramecensis Van Devender, 1979								
North America								
U.S.A.								
Iowa: Brush Creek Canyon	42.7796°N, 91.6890°W	20 Jul 2007	JCN1555	NS34	KY217182	GQ921532	KY217584	GQ921552
				NS35	KY217183	GQ921533	KY217585	KY216440
Clark Cabin	43.4458°N, 91.5724°W	8 May 1999	JCN5340	NS33	KY217184	GQ921531	KY217586	KY216441
Kentucky: Cave Hollow	37.9379°N, 85.6334°W	8 Feb 2013	Schroeder	VH75	KY217185	KT008329	KY217587	KY216442
Missouri: 11-Point River Bridge	36.7931°N, 91.3334°W	1 May 2010	JCN18207	T10	KY217186	KY216793	KY217588	KY216443
Virginia: Maury Neck 1	37.8199°N, 79.4251°W	24 Oct 2013	JCN19448	VH62	KY217187	KY216794	KY217589	KY216444
Vertigo microsphaera Schileyko, 1984								
Asia								
Japan								
Hokkaidō: Akkeshi North	43.0817°N, 144.8442°E	24 Jul 2012	JCN	J9	KY217188	KY216795	KY217590	KY216445
Kami-ashoro Motomachi	43.3551°N, 143.7880°E	25 Jul 2012	JCN	B74	KY217189	KY216796	KY217591	KY216446
Kushiro Marsh	43.0340°N, 144.3901°E	23 Jul 2012	JCN	J8	KY217190	KY216797	KY217592	KY216447
Tsukiji, Urakawa	42.1717°N, 142.7649°E	23 Jul 2012	JCN	B12	KY217191	KY216798	KY217593	KY216448
				B12b	KY217192	KY216799	KY217594	KY216449
				B12c	KY217193	KY216800	KY217595	KY216450
Russia								
Altai: Camp Cherga 2	51.6186°N, 85.5771°E	24 Jul 2011	JCN	B10	KY217194	KY216801	KY217596	KY216451
Seminski Pass S	50.9855°N, 85.6817°E	5 Aug 2011	JCN	B11	KY217195	KY216802	KY217597	KY216452

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Taxon/Location	Latitude/Longitude	Collection Date	Collection Acc. #	Specimen Acc. #	GenBank Acc. # CytB	16	ITS1	ITS2
North America								
U.S.A.								
Alaska: Eagle River Nature Center	61.2298°N, 149.2692°W	13 Aug 2007	JCN15382	B1	KY217196	KY216803	KY217598	KY216453
Vertigo milium (Gould, 1840)								
North America								
U.S.A.								
Arizona: Blind Canyon	31.3823°N, 110.3187°W	23 Mar 2016	JCN21192	VH131	KY217197	KY216804	KY217599	KY216454
Arkansas: Blanchard Springs 2	35.9582°N, 92.1778°W	6 Apr 2007	JCN14544	VH53	KY217198	KY216805	KY217600	KY216455
Florida: Lake Annie	27.2108°N, 81.3490°W	31 Dec 2009	JCN17909	VH18	KY217199	KY216806	KY217601	KY216456
Iowa: Rowley North fen	42.3764°N, 91.8507°W	21 Sep 2012	JCN5747	VH30	KY217200	KT008328	KY217602	KY216457
Michigan: Tiplady fen	42.4307°N, 83.9793°W	11 Oct 2008	JCN16546	VH143		KY216807		KY216458
North Carolina: Sheep Ridge pocosin	34.9355°N, 77.0707°W	24 Feb 2003	BC02133[1]	VH140	KY217201	KY216808		KY216459
Texas: McKinney Falls park	30.1874°N, 97.7179°W	9 Feb 2016	JCN20828	VH142	KY217202	KY216809	KY217603	KY216460
Vermont: Benson Road bluff	43.7674°N, 72.9812°W	28 Jul 2002	BC01399[1]	VH141	KY217203	KY216810		KY216461
Vertigo modesta (Say, 1824)								
North America								
Canada								
British Columbia: New Denver East	49.9966°N, 117.3455°W	31 Aug 2011	JCN18588	VH97	KY217204	KY216811	KY217604	KY216462
Alberta: McAbee Creek	50.6440°N, 114.4860°W	10 Sep 2012	BC14174	B120	KY217205	KY216812	KY217605	KY216463
				B121	KY217206	KY216813	KY217606	KY216464
				B122	KY217207	KY216814	KY217607	KY216465
				B123	KY217208	KY216815	KY217608	KY216466
Labrador: Elizabeth Lake Road	54.7478°N, 66.8436°W	8 Aug 2006	BC12365	B57	KY217209	KY216816	KY217609	KY216467
Manitoba: Goose Creek Road	58.7086°N, 94.1230°W	20 Aug 2003	JCN11103	B65	KY217210		KY217610	KY216468
Québec: La Grande Pointe	50.2017°N, 63.4013°W	2 Aug 2006	JCN13457	B64	KY217211	KY216817	KY217611	KY216469

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Taxon/Location	Latitude/Longitude	Collection Date	Collection Acc. #	Specimen Acc. #	GenBank Acc. # CytB	16	ITS1	ITS2
<u>U.S.A.</u>								
Alaska: South Fork Koyukuk River	67.0197°N, 150.2886°W	10 Aug 2007	JCN15241	B66	KY217212	KY216818	KY217612	KY216470
Old Crow Mine Road	60.9752°N, 149.1211°W	13 Aug 2007	JCN15366	B102	KY217213	KY216819	KY217613	KY216471
Vertigo modesta castanea Pilsbry & Vanatta, 1900								
North America								
<u>U.S.A.</u>								
California: Luther Pass Road	38.7900°N, 120.0093°W	9 Oct 2009	JCN17249	B104	KY217214	KY216820	KY217614	KY216472
Vertigo modesta insculpta Pilsbry, 1919								
North America								
<u>U.S.A.</u>								
Arizona: Mt. Lemmon	32.4413°N, 110.7848°W	27 Mar 2007	JCN14046	B105	KY217215	KY216821	KY217615	KY216473
Vertigo modesta microphasma Berry, 1919								
North America								
<u>U.S.A.</u>								
California: Osita Camp E	34.2240°N, 116.9251°W	3 Oct 2013	JCN19252	B106	KY217216	KY216822	KY217616	KY216474
Vertigo modesta sculptilis Pilsbry, 1934								
North America								
<u>Canada</u>								
British Columbia: Healy Creek 1	50.6368°N, 117.1918°W	30 Aug 2011	JCN18538	B109	KY217217	KY216823	KY217617	KY216475
<u>U.S.A.</u>								
Nevada: Bear Creek summit	41.7903°N, 115.4575°W	19 Sep 2010	JCN18302	B107	KY217218	KY216824	KY217618	KY216476
Vertigo morsei Sterki, 1894								
North America								
<u>Canada</u>								
Manitoba: North Twin Creek fen	52.8694°N, 99.0454°W	25 Aug 2003	BC02233[1]	VH91	KY217219	KY216825	KY217619	KY216477

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Taxon/Location	Latitude/Longitude	Collection Date	Collection Acc. #	Specimen Acc. #	GenBank Acc. # CytB	16	ITS1	ITS2
U.S.A.								
Maine: Woodland fen	46.8795°N, 68.1391°W	11 Oct 2002	BC01563[1]	VH90	KY217220	KY216826	KY217620	KY216478
Michigan: Maxton Plains	46.0754°N, 83.6684°W	29 Sep 2009	JCN17095	ET6	KY217221	KY216827	KY217621	KY216479
Vertigo moulinsiana (Dupuy, 1849)								
Europe								
Czech Republic								
Bohemia: Ráj, Kokořínsko	50.4573°N, 14.5891°E	9 Aug 1998	MH	VH80	KY217222	KY216828	KY217622	KY216480
Moravia: Břežany pond	48.8738°N, 16.3309°E	9 Apr 2011	MH	VH81	KY217223	KY216829	KY217623	KY216481
Žitková fen	48.9902°N, 17.9056°E	17 Jul 2011	JCN	VH79	KY217224	KY216830	KY217624	KY216482
Netherlands								
Woubrugge: Widje Aa	52.1710°N, 4.6119°E	27 Apr 2012	JCN	VH25	KY217225	KT008326	KY217625	KY216483
United Kingdom								
England: Chingford Pond, Petworth	50.9473°N, 0.6163°W	12 Dec 2014	Willing	VH104	KY217226	KY216831	KY217626	KY216484
Vertigo nitidula (Mousson, 1876)								
Asia								
Georgia								
Kakheti: Lagodekhi NE	41.4578°N, 46.3105°E	Sep 2015	Mumladze	VH117	KY217227	KY216832	KY217627	KY216485
				VH118	KY217228			
Imereti: Sairme N	41.9274°N, 42.7498°E	Jun 2013	Mumladze	VH119	KY217229	KY216833	KY217628	KY216486
Samtskhe-Javakheti: Borjomi Nat. Park	41.8540°N, 43.2392°E	Aug 2011	Mumladze	VH120	KY217230	KY216834	KY217629	KY216487
Vertigo nylanderi Sterki, 1909								
North America								
Canada								
Manitoba: Sturgeon Gill Road	53.4731°N, 99.1653°W	25 Aug 2003	JCN11204	NS37	KY217231	GQ921493	KY217630	GQ921577
Ontario: Wolford Bog	44.9230°N, 75.7738°W	18 Oct 2008	JCN16661	T11	KY217232	KY216835	KY217631	KY216488
U.S.A.								
Maine: McConnell Brook	46.6120°N, 68.5953°W	7 Sep 2007	JCN15709	NS36	KY217233	GQ921483	KY217632	GQ921576

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Taxon/Location	Latitude/Longitude	Collection Date	Collection Acc. #	Specimen Acc. #	GenBank Acc. # CytB	16	ITS1	ITS2
Wisconsin: Blueberry Marsh	44.5323°N, 87.8924°W	16 Nov 2004	JCN12266	NS38	KY217234	GQ921491	KY217633	GQ921554
Vertigo occidentalis Sterki, 1907								
North America								
U.S.A.								
California: Yellow Post fen	34.2230°N, 116.9410°W	28 Sep 2013	JCN19196	B96	KY217235	KY216836	KY217634	KY216489
Vertigo cf. *okinoerabuensis* (Pilsbry & Hirase, 1904)								
Asia								
Japan								
Iwate: Sarusawa, Ichinoseki	38.9869°N, 141.2550°E		Chiba	H38	KY217236	JN941044	KY217635	KY216490
Tōkyō: Renkoji Seep, Tama	35.6325°N, 139.4677°E	31 Jul 2012	JCN	VH57	KY217237	KY216837	KY217636	KY216491
Vertigo oralis (Sterki, 1898)								
North America								
U.S.A.								
Arkansas: Bayou Meto WMA	34.2765°N, 91.6491°W	Mar 2004	UF449316	VH15	KY217238	KY216838	KY217637	KY216492
Florida: Highlands Hammock State Park	27.4726°N, 81.5550°W	2 Jan 2010	JCN17958	VH14	KY217239	KY216839	KY217638	KY216493
Georgia: Rayonier forest lands	31.3462°N, 81.8244°W	3 May 2005	BC030431[1]	VH40	KY217240	KY216840	KY217639	KY216494
South Carolina: Lewis Ocean Bay	33.7890°N, 78.8503°W	2 Jun 2003	BC022021[1]	VH41	KY217241	KY216841	KY217640	KY216495
Vertigo oscariana (Sterki, 1890)								
North America								
U.S.A.								
Alabama: Chewacla State Park	32.5481°N, 85.4855°W	16 Feb 2002	BC01474[1]	VH39	KY217242	KY216842	KY217641	KY216496
Arkansas: Blanchard Springs 2	35.9582°N, 92.1778°W	6 Apr 2007	JCN14545	VH12	KF214518	KF214498	KF214493	KF214481
South Carolina: Wadboo Creek	33.1971°N, 79.9461°W	23 Feb 2003	JCN10908	VH13	KF214519	KF214497	KF214494	KF214482
Vertigo oughtoni (Pilsbry, 1948)								
North America								

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Taxon/Location	Latitude/Longitude	Collection Date	Collection Acc. #	Specimen Acc. #	GenBank Acc. # CytB	16	ITS1	ITS2
<u>Canada</u>								
Manitoba: Goose Creek Road, Churchill	58.7264°N, 94.1171°W	20 Aug 2003	JCN11117	H34	KY217243	KY216843	KY217642	KY216497
<u>U.S.A.</u>								
Alaska: Mile 341, Dalton Hwy.	69.2408°N, 148.7763°W	9 Aug 2007	JCN15186	B18	KY217244	KY216844	KY217643	KY216498
Sukakpak Mountain	67.5988°N, 149.7846°W	7 Aug 2007	JCN15107	T14	KY217245	KY216845	KY217644	KY216499
Vertigo ovata Say, 1822								
North America								
<u>U.S.A.</u>								
Iowa: Boar Power fen	42.2815°N, 91.8323°W	23 Sep 2012	JCN18785	VH31	KY217246	KY216846	KY217645	KY216500
Maine: Orient	45.8362°N, 67.8482°W	16 Sep 2007	JCN16298	VH111	KY217247	KY216847	KY217646	KY216501
Massachusetts: Tispaquin Street 1	41.9010°N, 70.8521°W	12 Aug 2004	JCN12156	B117	KY217248	KY216848	KY217647	KY216502
Nevada: Lamoille fen	40.7813°N, 115.4126°W	18 Sep 2010	JCN18276	VH139	KY216969	KY216611	KY217377	KY216242
New Mexico: Santo Domingo fen	35.5356°N, 106.3519°W	28 Sep 2010	JCN18422	VH74	KY217249	JN941045		
New York: Swan Lake bog	40.8946°N, 72.7945°W	6 Aug 2004	JCN12061	VH63	KY217250	KY216849	KY217648	KY216503
North Carolina: Sheep Ridge	34.9345°N, 77.0100°W	24 Feb 2003	JCN10972	VH32	KY217251	KY216850	KY217649	KY216504
Tennessee: Lady Finger Bluff trail	35.6904°N, 88.0207°W	2 Jul 2000	BC00625[1]	VH33	KY217252	KY216851	KY217650	KY216505
Texas: Powderhorn Ranch	28.4551°N, 96.5082°W	12 Feb 2016	JCN21084	VH138	KY217253	KY216852	KY217651	KY216506
Vertigo parcedentata (Braun, 1847)								
Asia								
<u>Russia</u>								
Altai: Camp Kuyuktanar	50.1510°N, 88.3031°E	3 Aug 2011	JCN	B20	KY217254	KY216853	KY217652	KY216507
Camp Zhuma-ly 2	49.5211°N, 88.0164°E	28 Jul 2011	JCN	B19	KY217255	KY216854	KY217653	KY216508
Uzunkel Lake	50.4767°N, 87.6301°E	18 Jul 2006	MH	B21	KY217256	KY216855	KY217654	KY216509
Europe								
<u>Norway</u>								
Sør-Trøndelag: Dovrefjäll	62.2672°N, 9.5855°E	8 Aug 1988	TvP	B86	KY217257	KY216856	KY217655	KY216510

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Taxon/Location	Latitude/Longitude	Collection Date	Collection Acc. #	Specimen Acc. #	GenBank Acc. #			
					CytB	16	ITS1	ITS2
Vertigo parvula Sterki, 1890								
North America								
U.S.A.								
Tennessee: Davis Springs	36.1553°N, 82.3089°W	31 May 2001	BC00490[1]	VH44	KY217258	KY216857		
Straight Creek, Buffalo Mt.	36.2272°N, 82.4020°W	5 Apr 2005	JCN12474	VH50	KY217259	KY216858	KY217656	KY216511
Virginia: Fortney Branch 2	37.9272°N, 79.9861°W	27 May 2013	JCN19001	VH45	KY217260	KY216859	KY217657	KY216512
Vertigo perryi Sterki, 1905								
North America								
U.S.A.								
Maine: Clinton SE	44.6112°N, 69.4430°W	4 Sep 2007	JCN15422	B63	KY217261	KY216860	KY217658	KY216513
Massachusetts: Tispaquin Street	41.9010°N, 70.8521°W	12 Aug 2004	JCN12157	VH89	KY217262	KY216861	KY217659	KY216514
Wisconsin: Sugar Camp bog	45.8498°N, 89.2952°W	12 Nov 2004	BC02781[1]	B92	KY217263	KY216862	KY217660	KY216515
Vertigo pimuensis n. sp.								
North America								
U.S.A.								
California: Santa Catalina Island								
USC Marine Lab	33.4458°N, 118.4817°W	2 Oct 2013	JCN19222	C44	KY217264	KY216863	KY217661	KY216516
Two Harbors South	33.4331°N, 118.5094°W	2 Oct 2013	JCN19226	C51	KY217265	KY216864	KY217662	KY216517
Vertigo pisewensis n. sp.								
North America								
Canada								
Alberta: Big Horn	51.2642°N, 114.7326°W	25 Aug 2011	BC00020[2]	B48	KY217266	KY216865	KY217663	KY216518
Manitoba: Pisew Falls	55.1982°N, 98.3918°W	17 Aug 2003	BC02264[1]	B47	KY217267	KY216866	KY217664	KY216519
U.S.A.								
Alaska: Clearwater Recreation Area	64.0530°N, 145.4332°W	11 Aug 2007	JCN15285	B46	KY217268	KY216867	KY217665	KY216520
Coldfoot	67.6461°N, 150.1688°W	7 Aug 2007	JCN15093	B45	KY217269	KY216868	KY217666	KY216521

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Taxon/Location	Latitude/Longitude	Collection Date	Collection Acc. #	Specimen Acc. #	GenBank Acc. # CytB	16	ITS1	ITS2
Vertigo pseudosubstriata Ložek, 1954								
Asia								
Russia								
Altai: Lesosek	49.6416°N, 87.7629°E	27 Jul 2011	JCN	B22	KY217270	KY216869	KY217667	KY216522
Seminski Pass S	50.9855°N, 85.6817°E	5 Aug 2011	JCN	B23	KY217271	KT008317	KY217668	KY216523
Uzunkel Lake	50.4767°N, 87.6301°E	18 Jul 2006	MH	B24	KY217272	KY216870	KY217669	KY216524
Vertigo pusilla O. F. Müller, 1774								
Asia								
Russia								
Tyumenskaya: Nizhniye Aremzyany	58.5256°N, 68.6791°E	8 Aug 2013	MH	VH84	KY217273	KY216871	KY217670	KY216525
Europe								
Czech Republic								
Moravia: Podyjí National Park	48.8586°N, 15.8960°E	Aug 2011	MH	mtG-V	KF214520	KF214496	KY217671	KF214483
Netherlands								
Katwijk: Katwijk dunes	52.1826°N, 4.4008°E	22 Apr 2012	JCN	VH82	KY217274	KY216872	KY217672	KY216526
Norway								
Troms: Signaldalen	69.1911°N, 19.9873°E	16 Aug 2013	BC14510	VH85	KY217275	KY216873	KY217673	KY216527
United Kingdom								
England: Bowston Stone Wall, Cumbria	54.3619°N, 2.7733°W	27 Jun 2000	JCN	VH83	KY217276	KY216874	KY217674	KY216528
Vertigo pygmaea (Draparnaud, 1801)								
Asia								
Russia								
Altai: Seminski Pass S	50.9855°N, 85.6817°E	5 Aug 2011	JCN	B25	KY217277	KY216875	KY217675	KY216529
Bashkortostan: Novoaleksandrovka	52.0894°N, 57.3226°E	19 Jul 2007	MH	B26	KY217278	KY216876	KY217676	KY216530
Europe								
Czech Republic								
Moravia: Kotrle fen	49.3779°N, 18.0236°E	17 Jul 2011	JCN	VH21	KY217279	KT008322	KY217677	KY216531

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		Collection Date	Collection Acc. #	Specimen Acc. #	GenBank Acc. #			
Taxon/Location	Latitude/Longitude				CytB	16	ITS1	ITS2
Netherlands								
Katwijk: Valkenburgse Meer	52.1590°N, 4.4331°E	22 Apr 2012	JCN	B27	KY217280	KY216877	KY217678	KY216532
North America								
Canada								
Ontario: Burnt Lands Alvar 1	45.2548°N, 76.1514°W	19 Oct 2008	JCN16704	B28	KY217281	KY216878	KY217679	KY216533
Vertigo ronnebyensis (Westerlund, 1871)								
Asia								
Russia								
Altai: Camp Ilbegem 2	49.6281°N, 87.6574°E	2 Aug 2011	JCN	B29	KY217282	KY216879	KY217680	KY216534
Yakutia: Kysyl-Syr E	62.5671°N, 130.5288°E	5 Aug 2010	MH	H27	KY217283	KY216880		KY216535
Europe								
Norway								
Troms: Signaldalen	69.1911°N, 19.9873°E	16 Aug 2013	BC14512	B80	KY217285	KY216882	KY217682	KY216537
Sweden								
Jämtland: Hammerdal W	63.5802°N, 15.2311°E	15 Aug 2006	MH	H22	KY217286		KY217683	KY216538
Lappmark: Kiruna	67.8660°N, 20.2478°E	2 Jul 1990	BC14512	B30	KY217287	KY216883		KY216539
Blekinge: Ronneby, Persborg	56.1976°N, 15.2624°E	18 May 2003	TvP	B84	KY217288	KY216884		KY216540
North America								
Canada								
Manitoba: Churchill	58.7709°N, 94.1640°W	22 Aug 2003	BC10555	B44	KY217289	KY216885	KY217684	KY216541
U.S.A.								
Alaska: Atigun Valley	68.3156°N, 149.3531°W	10 Aug 2007	JCN15222	B42	KY217290	KY216886		KY216542
Berg 2	64.6066°N, 149.0902°W	3 Aug 2007	JCN14950	NS47	KY217291	GQ921536	KY217685	KY216543
Circle Hot Springs	65.4874°N, 144.6501°W	5 Aug 2007	JCN15012	B51	KY217292	KY216887	KY217686	KY216544
Clearwater Recreation Area	64.0530°N, 145.4332°W	11 Aug 2007	JCN15284	B43	KY217293	KY216888	KY217687	KY216545
Ice Cut 1	69.0193°N, 148.8364°W	8 Aug 2007	JCN15120	B49	KY217294	KY216889	KY217688	KY216546
Milepost 188, Dalton Hwy.	67.4313°N, 150.0734°W	10 Aug 2007	JCN15230	B50	KY217295	KY216890		KY216547

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Taxon/Location	Latitude/Longitude	Collection Date	Collection Acc. #	Specimen Acc. #	GenBank Acc. # CytB	 16	 ITS1	 ITS2
Vertigo rowellii (Newcomb, 1862)								
North America								
<u>U.S.A.</u>								
California: Auburn	38.9072°N, 121.0516°W	9 Oct 2009	JCN17232	VH27b	KY217296	KT008327	KY217689	KY216548
Coast Dairy	36.9893°N, 122.1672°W	6 Oct 2013	JCN19289	C37	KY217297	KY216891	KY217690	KY216549
Grimes Canyon	36.2081°N, 121.7347°W	5 Oct 2013	JCN19281	C38	KY217298	KY216892	KY217691	KY216550
Trailside Park	38.7563°N, 122.6364°W	11 Sep 2013	JCN19174	C36	KY217299	KY216893	KY217692	KY216551
Oregon: Manhattan Beach	45.6413°N, 123.9410°W	2 Aug 2012	JCN18740	C35	KY217300	KY216894	KY217693	KY216552
Washington: Cougar Mountain Park	47.5113°N, 122.0891°W	28 May 2015	JCN20554	C39	KY217301	KY216895	KY217694	KY216553
Vertigo rugosula Sterki, 1890								
North America								
<u>U.S.A.</u>								
Arkansas: 0.5 miles S L&D #5	34.4040°N, 92.1020°W	11 Nov 2002	UF409059	VH16	KY217302	KT008319	KY217695	KY216554
Huff's Island Park	34.1575°N, 91.6807°W	27 Apr 2003	UF409294	VH17	KY217303	KY216896	KY217696	KY216555
Vertigo saxicola (Lowe, 1852)								
Macaronesia								
<u>Madeira</u>								
Santa Cruz: Rua da Ribeira 1	32.6928°N, 16.8044°W	7 Jul 2016	MH	OG16	KY217304	KY216897	KY217697	KY216556
Rua da Ribeira 2	32.6928°N, 16.8044°W	7 Jul 2016	MH	OG17	KY217305	KY216898	KY217698	KY216557
Vertigo substriata (Jeffreys, 1833)								
Asia								
<u>Russia</u>								
Altai: Seminski Pass S	50.9855°N, 85.6817°E	5 Aug 2011	JCN	B31	KY217306	KY216899	KY217699	KY216558
Bashkortostan: Yuldybaevo Village	52.5909°N, 56.9400°E	13 Jul 2007	MH	B32	KY217307	KY216900		KY216559
Europe								
<u>Netherlands</u>								
Driehuis: Zuid-Kennemerland	52.4413°N, 4.6267°E	23 Apr 2012	JCN	VH26	KY217308	KY216901	KY217700	KY216560

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Taxon/Location	Latitude/Longitude	Collection Date	Collection Acc. #	Specimen Acc. #	CytB	GenBank Acc. # 16	ITS1	ITS2
Slovakia								
Poprad: Liptovská Teplička	48.9632°N, 20.1044°E	29 May 2010	MH	T17	KY217309	JN941046	KY217701	KY216561
United Kingdom								
Wales: Waun Eraud, Anglesey	53.3008°N, 4.2411°W	16 Jun 2000	JCN	T18	KY217310	KY216902	KY217702	KY216562
Vertigo teskeyae Hubricht, 1961								
North America								
U.S.A.								
Arkansas: Huffs Island Park	34.1575°N, 91.6807°W	29 Jun 1997	BC00012[1]	VH52	KY217311	KY216903		
Florida: Cow Creek	29.7951°N, 82.7659°W	9 Apr 2011	Slapcinsky	VH35	KY217312	KY216904	KY217703	KY216563
Tennessee: Lady Finger Bluff trail	35.6904°N, 88.0207°W	2 Jul 2000	BC00626[1]	VH34	KY217313	KY216905	KY217704	KY216564
Vertigo tridentata Wolf, 1870								
North America								
U.S.A.								
Arkansas: Norfolk	36.2025°N, 92.2906°W	2 Jun 1996	BC00066[1]	VH47	KY217314	KY216906	KY217705	KY216565
Iowa: Canton glade	42.1795°N, 90.9979°W	23 Sep 1999	BC00069[1]	VH46	KY217315	KY216907	KY217706	KY216566
Virginia: Falling Spring NE	37.8810°N, 79.9176°W	25 May 2013	JCN18913	VH48	KY217316	KY216908	KY217707	KY216567
Vertigo trinotata (Sterki, 1890)								
North America								
U.S.A.								
California: Carmel Beach	36.5232°N, 121.9300°W	26 Nov 2006	JCN13941	C34	KY217317	KY216909	KY217708	KY216568
Crocker Grove	36.5782°N, 121.9727°W	5 Oct 2013	JCN19268	C2	KY217318	KY216910	KY217709	KY216569
Fort Ord	36.6561°N, 121.7540°W	13 May 2006	JCN13404	C33	KY217319	KY216911	KY217710	KY216570
Vertigo ultima (Pilsbry, 1919)								
North America								
U.S.A.								
Alaska: Earthquake Park 3	61.1997°N, 149.9667°W	12 Aug 2007	JCN15325	B68	KY217320	KY216912	KY217711	KY216571

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Taxon/Location	Latitude/Longitude	Collection Date	Collection Acc. #	Specimen Acc. #	GenBank Acc. # CytB	 16	 ITS1	 ITS2
Fox Spring, Fairbanks	64.9645°N, 147.6259°W	2 Aug 2007	JCN14903	B110	KY217321	KY216913	KY217712	KY216572
Happy Valley 2	69.3366°N, 148.7314°W	8 Aug 2007	JCN15151	B67	KY217322	KY216914	KY217713	KY216573
Vertigo ultimathule Proschwitz, 2007								
Europe								
Norway								
Finnmark: Basecakka	69.6612°N, 25.8886°E	30 Jul 1991	TvP	B85	KY217323	KY216915		KY216574
		16 Jul 2014	TvP	B112	KY217324	KY216916	KY217714	KY216575
North America								
U.S.A.								
Alaska: Oil Spill Hill, Dalton Hwy.	68.9428°N, 148.8689°W	9 Aug 2007	JCN15171	B59	KY217325	KY216917	KY217715	KY216576
Vertigo cf. *utahensis* (Sterki, 1900)								
North America								
U.S.A.								
Utah: Bullion Canyon 3	38.4171°N, 112.3126°W	7 Oct 2009	BC13081	VH106	KY217326	KY216918	KY217716	KY216577
Cobblerest West	40.5948°N, 110.9905°W	21 Sep 2010	JCN18350	VH71	KY217327	KY216919	KY217717	KY216578
Vertigo ventricosa (Morse, 1865)								
North America								
Canada								
Labrador: Leo fen	54.6727°N, 66.6075°W	11 Aug 2006	JCN13755	B90	KY217328	KY216920	KY217718	KY216579
U.S.A.								
Maine: Salmon Brook Lake	46.9004°N, 68.2466°W	8 Sep 2007	JCN1519	B119991	KY2129	KY2121	KY2119	KY2180

Notes: Collectors/collections – ANSP = Academy of Natural Sciences Philadelphia, BC = Brian Coles, dW = Ton de Winter, JCN = Jeffrey C. Nekola, MH = Michal Horsák, NMSA = National Museum of South Africa, TvP = Ted von Proschwitz, UF = University of Florida Museum of Natural History; for others see Acknowledgements. For BC collections – [1, 2] indicate accession numbers of the National Museum of Wales these are preceded by NMW.Z.2005.011. and NMW.Z.2015.009., respectively, otherwise lot numbers refer to BC collections not yet donated to the Museum.