

Pupillid land snails of eastern North America*

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Abstract: The Pupillidae form an important component of eastern North American land snail biodiversity, representing approx. 12% of the entire fauna, 25-75% of all species and individuals at regional scales, at least 30% of the species diversity, and 33% of individuals within any given site. In some regions pupillids represent 80-100% of total molluscan diversity within sites, notably in taiga, tundra, and the base-poor pine savannas and pocosins of the southeastern coastal plain. Adequate documentation of North American land snail biodiversity thus requires investigators to efficiently collect and accurately identify individuals of this group. This paper presents a set of annotated keys to the 65 species in this family known to occur in North America east of the Rocky Mountains. The distinguishing taxonomic features, updated county-scale range maps, and ecological conditions favored by each are presented in hopes of stimulating future research in this important group.

Key words: microsnail, biodiversity, ecology, biogeography, taxonomy

For the last dozen years, our interests in terrestrial gastropod biodiversity have lead us individually and collectively to observe molluscan communities over most of North America, ranging from central Quebec, Hudson's Bay and the north slope of Alaska to Florida, the Gulf Coast, desert southwest, and coastal California. In this time, we have recorded molluscs from over 1,700 stations and have become acutely aware of the importance of Pupillidae in North American land snail biodiversity. Here we consider this family in the expansive, historical sense as outlined by Pilsbry (1948) and Hubricht (1985), including the genera *Bothriopupa*, *Columella*, *Gastrocopta*, *Pupilla*, *Pupisoma*, *Pupoides*, *Sterkia*, and *Vertigo*. As thus defined, this family constitutes approx. 10% of the North American land snail fauna (Pilsbry 1948, Turgeon *et al.* 1998). Hubricht (1985) listed the Pupillidae as the third most diverse family east of the continental divide (12% of the total fauna), exceeded only by the Polygyridae (30%) and the former Zonitidae (22%). Because the North American Pupillidae do not demonstrate the high degree of local endemism of these other families, pupillid species tend to more fully saturate regional and site faunas. Our analyses indicate that pupillids generally constitute from 25 to 75% of all species and individuals at regional scales, and at least 30% of the species diversity and 33% of individuals within any given site. In some regions we have found that pupillids represent 80-100% of total molluscan diversity within sites, notably in taiga, tundra, and the base-poor pine savannas and pocosins of the southeastern coastal plain (Coles and Nekola 2007).

Adequate documentation of this diversity thus requires investigators to efficiently collect and accurately identify individuals from this family. Unfortunately, neither has been common. Two major reasons for this exist. First, none of the taxa exceeds 6 mm in maximum dimension. Consequently, accurate identification requires critical examination at 30-60× magnification and often cannot be accomplished in the field. Unfortunately, even museum holdings are suspect, with Hubricht (1985) lamenting about the high incidence of misidentification and mixed lots. Our observations validate this concern, with over 90% of the material in some collections having been misidentified. Second, most species are cryptic, being found primarily in decomposed leaf litter. As a consequence, they tend to be under-sampled by researchers who rely on locating individuals by eye or by use of traps. This has led to the lack of documentation not only of the normal range of morphological variation within and between populations and taxa but also of the true geographic and ecological ranges for most species. As a result, hasty (and in our view erroneous) conclusions concerning specific identity, biogeography, and ecology in this family have been commonplace in the published literature.

An overview of the current state-of-play of the taxonomy, biogeography, and ecology for this group across all of eastern North American would therefore be useful not only to malacologists, but also to conservation biologists and land managers. As both Burch (1962) and Hubricht (1985) provide information only for eastern U.S.A. taxa, we desired to expand our focus to also include eastern Canada. To assist identification, we have organized updated taxonomic, range

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map, and ecological information in the form of annotated species-level taxonomic keys for all pupillid taxa east of the Rocky Mountains. We have also provided figures which display representative shells of all valid taxa.

METHODOLOGY

Field and laboratory methods

We have endeavored to sample land snail faunas from all areas in North America east of the Rockies. However, there remain some regions for which we have not conducted fieldwork, including much of the central and northern Plains,

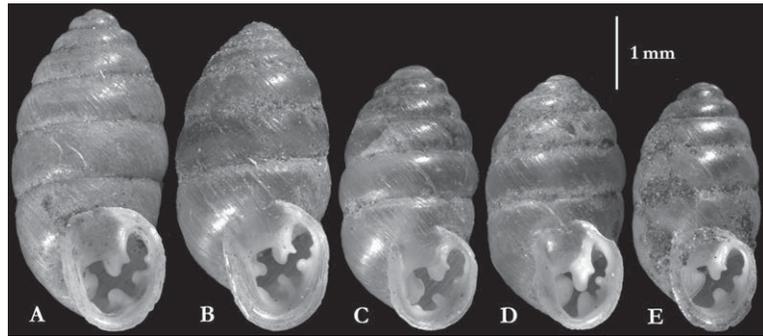


Figure 1. A, *Gastrocopta armifera*, Poultney River, Rutland Co., Vermont, 43°37'34"N, 73°21'16"W, JCN 10205; B, *Gastrocopta abbreviata*, Folsom, Union Co., New Mexico, 36°54'18"N, 103°46'59"W, JCN 16511; C, *Gastrocopta clappi*, Cedars of Lebanon State Park, Wilson Co., Tennessee, 36°20'40"N, 92°6'25"W, BFC 3032; D, *Gastrocopta ruidosensis*, Gallinas Canyon, San Miguel Co., New Mexico, 35°39'14"N, 105°19'22"W, JCN 12962; E, *Gastrocopta similis*, Beams Cabin, Jones Co., Iowa, 42°8'32"N, 91°20'44"W, JCN 11466.

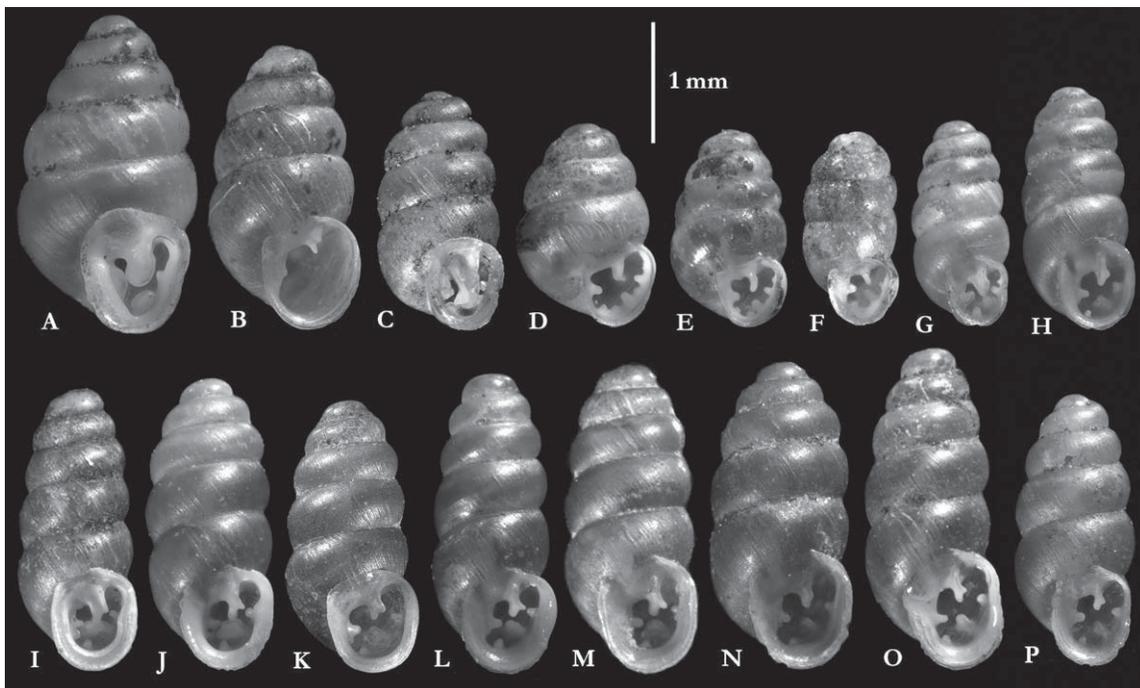


Figure 2. A, *Gastrocopta contracta*, Rowley Fen, Buchanan Co., Iowa, 42°22'26"N, 91°51'7"W, JCN 3762; B, *Gastrocopta corticaria*, Canton Glade, Jones Co., Iowa, 42°10'46"N, 90°59'52"W, JCN 3743; C, *Gastrocopta ashmuni*, Canyon del Agua, San Miguel Co., New Mexico, 35°29'45"N, 105°3'24"W, JCN 12791; D, *Gastrocopta tappaniana*, Faith Fen, Norman Co., Minnesota, 47°15'42"N, 96°5'11"W, JCN 6624; E, *Gastrocopta pentodon*, Lebanon State Forest, Burlington Co., New Jersey, 39°52'29"N, 74°30'58"W, JCN 12020; F, *Gastrocopta pilsbryana*, Devils Den Canyon, Eddy Co., New Mexico, 32°1'59"N, 104°48'17"W, JCN 14572; G, *Gastrocopta holzingeri*, Fults Prairie Nature Reserve, Monroe Co., Illinois, 38°9'19"N, 90°11'15"W, JCN 3913; H, *Gastrocopta pellucida*, Eden Chapel, Payne Co., Oklahoma, 36°0'52"N, 96°59'45"W, JCN 13315; I, *Gastrocopta rogersensis*, Beams Cabin, Jones Co., Iowa, 42°8'32"N, 91°20'44"W, JCN 11465; J, *Gastrocopta procera*, Fults Prairie Nature Reserve, Monroe Co., Illinois, 38°9'19"N, 90°11'15"W, JCN 3916; K, *Gastrocopta riparia*, Berkeley Co., South Carolina, 33°11'45"N, 79°58'22"W, JCN 10861; L, *Gastrocopta riograndensis*, Sacramento Canyon Falls, Otero Co., New Mexico, 32°42'51"N, 105°45'15"W, JCN 13192; M, *Gastrocopta sterkiana*, Tallgrass Prairie Preserve, Osage Co., Oklahoma, 36°48'22"N, 96°22'25"W, JCN 13282; N, *Gastrocopta cristata*, Ripley, Payne Co., Oklahoma, 35°59'10"N, 96°54'53"W, JCN 13348; O, *Gastrocopta rupicola*, Georgetown, Georgetown Co., South Carolina, 33°21'13"N, 79°17'33"W, JCN 10936; P, *Gastrocopta servilis*, Charlotte Harbor, Sarasota Co., Florida, BFC 3716.

taiga and tundra communities outside of central Manitoba and central Quebec, and the entirety of the Maritime Provinces of Canada. Documentation of pupillids was generally accomplished by litter collection, which provides the most complete faunal assessments (Oggier *et al.* 1998, Cameron and Pokryszko 2005). This procedure consists of throwing handfuls of litter onto a shallow sieve of 2-mm mesh nesting loosely inside a sieve of 0.6-mm mesh, accompanied by vigorous shaking, tapping, or other agitation (Kerney and Cameron 1979). Both coarse (>2 mm) and fine (0.6-2 mm) fractions are observed in the field (with magnification as necessary) to establish an estimate of species richness and abundance. With practice, this approach allows rapid and reliable field identification of preferred microhabitats. These appropriate microsites are then targeted for additional sampling, with approx. 50-500 ml of fine material (0.6-2.0 mm) being collected per site. Sievings are removed from the field, dried at room temperature, and then passed through a 0.6-mm sieve, with fractions being handpicked against a neutral background using low magnification as necessary. Through this process, typically 10^1 - 10^3 individuals per taxon were recovered per site, with 10^2 - 10^4 total individuals per taxon being observed across their entire ecological and geographic range. Over the last 15 years, we have collected >250,000 total pupillid individuals from the field, representing all but three valid eastern North American taxa. Material from the Coles collection is held at the National Museum of Wales (NMW) and the Florida Museum of Natural History (FM), while material from the Nekola collection is currently being maintained at the University of New Mexico.

Species concepts

Because pupillids demonstrate a high degree of aphallism and limited levels of anatomical variation (Pokryszko 1987), both species-level and supra-specific taxonomy has historically relied entirely upon conchological features. Some investigators have considered much of this variation to simply represent environmental plasticity, and have subsequently recommended the wholesale lumping of taxa (*e.g.*, Bequaert and Miller 1973, Metcalf and Smartt 1997). However, other investigators have advocated a much more liberal approach and have suggested that even the most subtle shell differences demarcate biologically distinct species (*e.g.*, Frest 1991). Throughout this work, we have chosen to let the observed variation in shell characters guide the determination of species level distinctions, rather than by blindly following either of these two camps. To do this we have used our extensive collections to define typical levels of variation for roughly 20 separate conchological features (Appendix 1) across all individuals in a given taxon both within and between populations across the entire known geographic and ecological range. We have then noted which features (if any) reliably

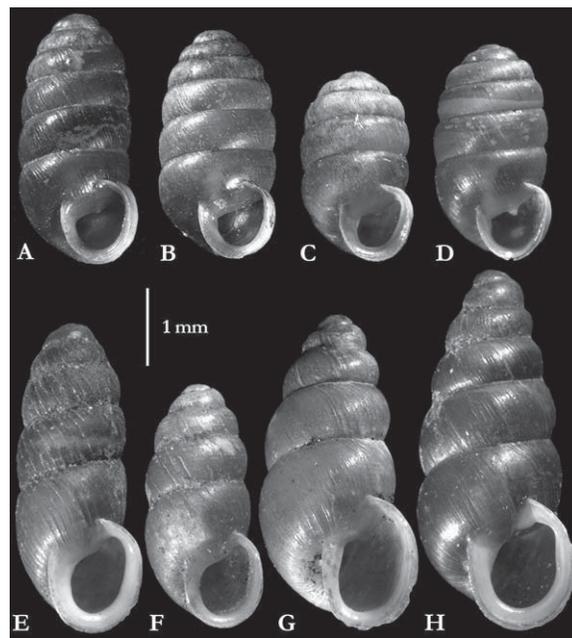


Figure 3. A, *Pupilla muscorum* (European exotic), Crawford Quarry, Linn Co., Iowa, 41°59'12"N, 91°44'24"W, JCN 14592; B, *Pupilla muscorum* (native), Lake Bemidji State Park, Beltrami Co., Minnesota, 47°31'58"N, 94°49'29"W, JCN 9054; C, *Pupilla muscorum xerobia*, Folsom, Union Co., New Mexico, 36°55'00"N, 103°46'48"W, JCN 16491; D, *Pupilla blandi*, Las Vegas, San Miguel Co., New Mexico, 35°35'35"N, 105°12'17"W, JCN 12788; E, *Pupoides hordaceus*, Duran, Torrance Co., New Mexico, 34°26'56"N, 105°25'6"W, JCN 14844; F, *Pupoides inornatus*, Folsom, Union Co., New Mexico, 36°54'18"N, 103°46'59"W, JCN 16521; G, *Pupoides modicus*, Cedar Key, Levy Co., Florida, CM 62.21320 (please note that shell has faded in long-term storage); H, *Pupoides albilabris*, Gettle Farm, Wright Co., Missouri, 37°10'57"N, 92°35'32"W, JCN 11938.

distinguish a given taxon, with a taxon being considered a distinct species when more variation in its key identifying features was noted between it and other taxa than was observed within that taxon. We have lumped taxa when we noted introgression between critical features either within a single population or between populations spread across either ecological or geographic space. Both morphometric (Nekola and Coles 2001, Pearce *et al.* 2007) and mtDNA sequence (Nekola *et al.* 2009) analyses have borne out this methodology, with the latter generally indicating at least 50 base-pair substitutions between concatenated CO1 and 16S mtDNA sequences of most recognized species (4.5% of all sequenced base pairs). These analyses have also demonstrated no more than 12 (and typically less than 5) base-pair differences exist between individuals within a given species at continental extents, even when they were sympatric at sub-meter scales with closely related species.

Nomenclature

Where possible, we have followed the nomenclature used by Hubricht (1985). However, the present account includes several taxa that have been elevated to species status since that time (e.g., Nekola 2001, Nekola and Coles 2001, Coles and Nekola 2007). In addition, while some pupillid “species” will probably prove to be species complexes, we are not yet in a position to provide definitive resolution regarding their taxonomy. We have provided our views, however, in the hope that other workers will be able to build on our observations. It should also be noted that we are in the process of revising the taxonomy of *Vertigo gouldii* group based on both conchological and DNA sequence data (Nekola *et al.* 2009). Although it is inappropriate to preempt these revisions, it should be noted that this work will ultimately change taxon rank in some cases. It will, however, otherwise not affect the following accounts.

Taxonomic keys

Using the suite of distinguishing conchological features detailed above, dichotomous taxonomic keys were written *de novo* to first assign a specimen to a given genus, followed by genus keys to allow assignment to a given species. An illustrated glossary for specialized pupillid conchological terms is presented (Appendix 1). The keys were written from a purely functional standpoint based solely on external shell features, and are thus artificial and should in no way be seen to construe any potential phylogenetic relationships. For accuracy and ease of use, occasionally a variable genus or species occurs multiple times in a given key. To aid use of the key, each couplet has been provided with a list of shell images which demonstrate the characters being defined. We have trialed these keys in a number of different public and academic

settings and have revised them accordingly with the hope that they will provide many types of users, ranging from amateur conchologists and high school students to academic biologists, with the means to accurately identify individuals to the species level. Annotated comments for each recognized species are alphabetically arranged within each genus. Favored habitats were determined by analysis of species abundance patterns across all principle habitat types in our North American data set. Favored microhabitats were determined from our field experience.

Range maps

County-scale ranges for each taxon recorded east of the Rockies were constructed based on our collections in conjunction with observed lots from the Field Museum of Natural History (FMNH), Carnegie Museum (CM), Academy of Natural Sciences, Philadelphia (ANSP), University of Michigan Museum of Zoology (UMMZ), Harvard Museum of Comparative Zoology (MCZ), Royal Ontario Museum (ROM), and the Canadian Museum of Nature (CMN). Additional occurrences were also mapped using references with known reliable pupillid identifications, in particular Hubricht (1985) but also Pilsbry (1948), Levi and Levi (1950; Wisconsin), Teskey (1954; northeastern Wisconsin), Dawley (1955; Minnesota), Frest (1981, 1982, 1987, 1990, 1991; northeastern Iowa), Frest and Dickson (1986; western Iowa), Theler (1997; western Wisconsin), and Ken Hotopp (pers. comm.; New York). As county-scale distributional data do not exist for Canada, range limits are indicated by plotting validated site occurrences in conjunction with locations provided in Brooks (1936), Brooks and Brooks (1940), Oughton (1948), and Pilsbry (1948).

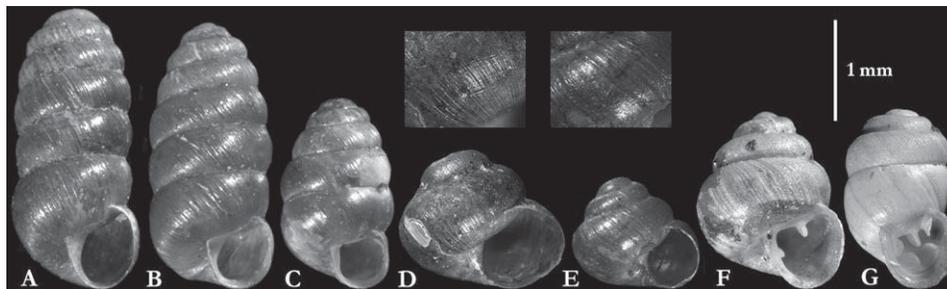


Figure 4. A, *Columella columella alticola*, Churchill, Manitoba, 58°45'6"N, 93°54'50"W, JCN 11321; B, *Columella simplex* (large morph), Rock Creek, Cedar Co., Iowa, 41°42'55"N, 91°9'31"W, JCN 11380; C, *Columella simplex* (normal morph), Haywood Landing, Jones Co., North Carolina, 34°49'10"N, 77°11'2"W, JCN 10716; D, *Pupisoma dioscoricola* (with high magnification inset of shell surface), Wadboo Creek, Berkeley Co., South Carolina, 33°11'50"N, 79°56'46"W, JCN 10903; E, *Pupisoma macneilli* (with high magnification inset of shell surface), Wadboo Creek, Berkeley Co., South Carolina, 33°11'50"N, 79°56'46"W, JCN 10904; F, *Bothriopupa variolosa*, Cuba, J. Bartlett, CM 62.21311 (please note that shell has faded in long-term storage); G, *Sterkia eyriesi rhoadsi*, Kyk-over-All, Kartabo, British Guiana, J. Bartlett, CM 62.19700 (please note that shell has faded in long-term storage).

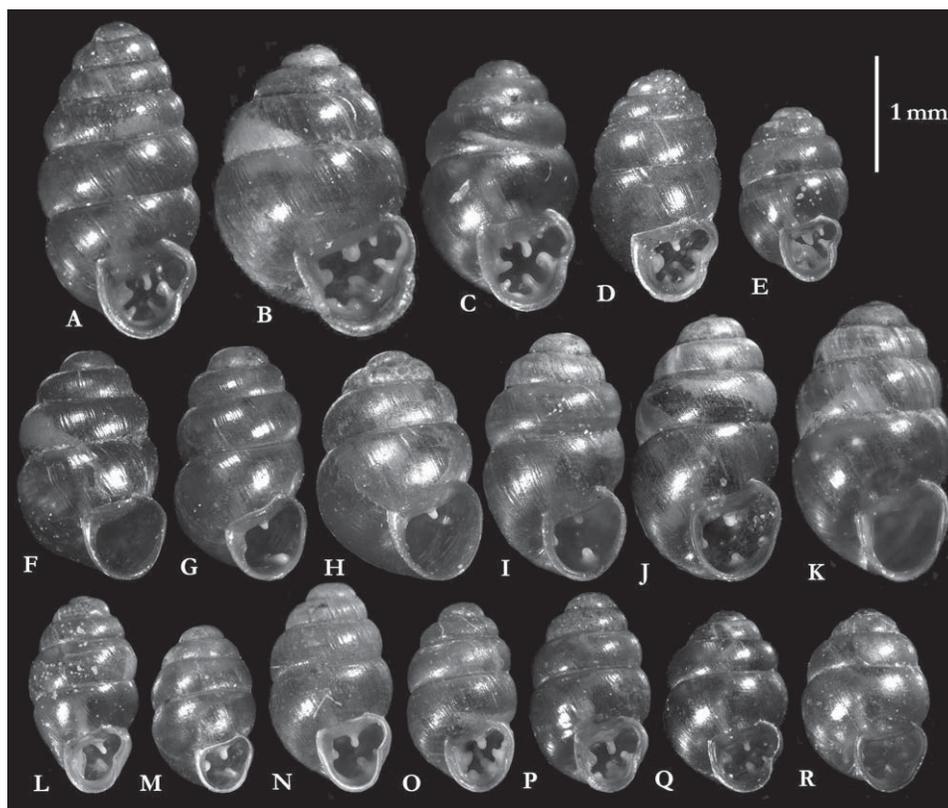


Figure 5. A, *Vertigo morsei*, Woodland Fen, Aroostook Co., Maine, 46°52'45"N, 68°8'21"W, JCN 10324; B, *Vertigo teskeyae*, Huffs Island Park, Lincoln Co., Arkansas, BFC 29; C, *Vertigo ovata*, Epworth Fen, Dubuque Co., Iowa, 42°25'24"N, 90°54'56"W, JCN 11506; D, *Vertigo binneyana*, LaSalle River, Winnipeg, Manitoba, 49°38'60"N, 97°24'17"W, JCN 10987; E, *Vertigo milium*, Berlin Fen, Green Lake Co., Wisconsin, 43°57'47"N, 88°45'20"W, JCN 6308; F, *Vertigo* aff. *genesi*, La Grande Pointe, Duplessis District, Quebec, 50°12'6"N, 63°24'5"W, JCN 13459; G, *Vertigo oughtoni*, West Twin Lake Fen, Churchill, Manitoba, 58°37'46"N, 93°50'35"W, JCN 11159; H, *Vertigo modesta hoppi*, Churchill Northern Studies Center, Manitoba, 58°43'60"N, 93°48'25"W, JCN 11319; I, *Vertigo modesta* form *arctica*, Churchill, Manitoba, 58°44'53"N, 93°51'13"W, JCN 11092; J, *Vertigo modesta*, South Fork Koyukuk River, Alaska, 67°1'11"N, 150°17'19"W, JCN 15241; K, *Vertigo modesta ultima*, Sunny Mountain, Nunavik District, Quebec, 55°3'53"N, 67°14'5"W, JCN 13781; L, *Vertigo oscariana*, Wadboo Creek, Berkeley Co., South Carolina, 33°11'50"N, 79°56'46"W, JCN 10908; M, *Vertigo parvula*, Buffalo Mountain, Washington Co., Tennessee, 36°13'38"N, 82°24'7"W, JCN 12474; N, *Vertigo tridentata*, Little Maquoketa River, Dubuque Co., Iowa, 42°28'17"N, 90°58'50"W, JCN 6375; O, *Vertigo pygmaea*, Kingfisher Farm, Manitowoc Co., Wisconsin, 43°57'50"N, 87°42'25"W, JCN 1770; P, *Vertigo elatior*, Karlstad South, Marshall Co., Minnesota, 48°32'14"N, 96°29'4"W, JCN 6909; Q, *Vertigo ventricosa*, Portage Lake, Aroostook Co., Maine, 46°47'6"N, 68°32'27"W, JCN 15915; R, *Vertigo perryi*, Clinton, Kennebec Co., Maine, 44°36'40"N, 69°26'35"W, JCN 15422.

Image figures

A representative, fresh shell of each eastern North American pupillid taxon was chosen from the authors' collections, except for *Bothriopupa variolosa*, *Pupoides modicus*, *Sterkia eyriesi*, and *Vertigo hebaridi*, which were obtained from CM collections. All specimens were imaged in apertural view at 15× (for *Pupilla*, *Pupoides*, and the *Gastrocopta armifera* group) or 30× magnification (all remaining taxa) using a digital camera attached to a stereomicroscope. Approximately 12 separate 1388 × 1040 pixel images were made of each specimen with the image focal lengths

positioned at 100 μm increments from the front to back of the shell. CombineZ5 freeware (<http://www.hadleyweb.pwp.blueyonder.co.uk/CZ5/combinez5.htm>) was used to assemble a final image from the focused parts of each separate image. This image was then imported into Adobe Photoshop, where brightness and contrast were optimized and the background made uniformly black. These images were then compiled into figures. Please note that because of their much older age, the four specimens imaged from the Carnegie collection have faded and do not represent the live shell color.

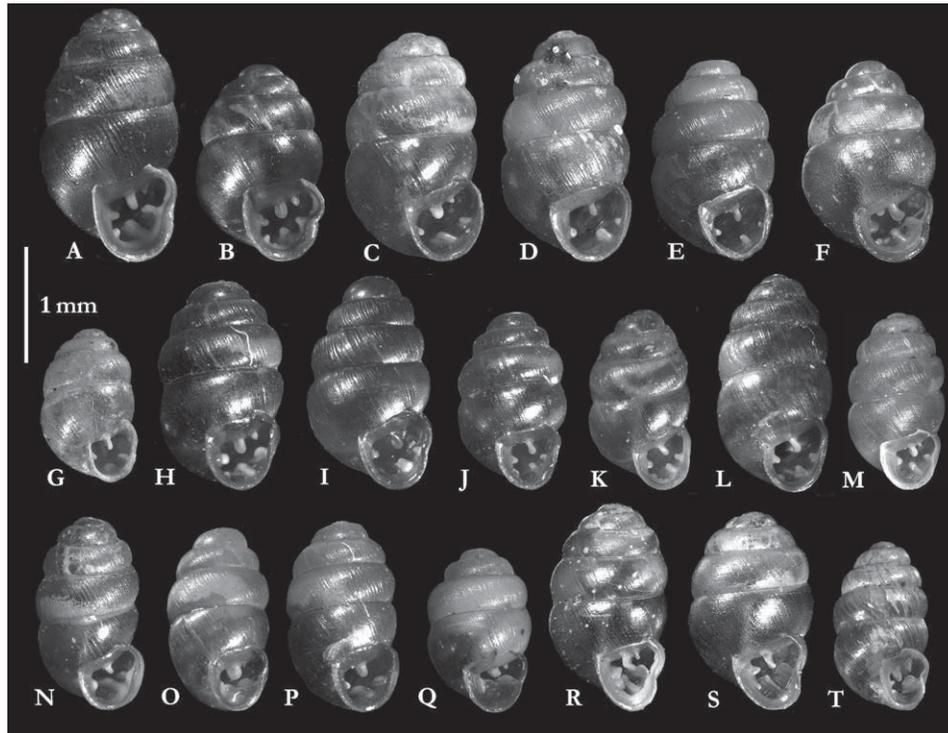


Figure 6. A, *Vertigo rugulosa*, Lock and Dam #5 Park, Jefferson Co., Arkansas, BFC 1297; B, *Vertigo oralis*, Rayonier Wildlife Management Area, Brantley Co., Georgia, 31°20'36"N, 81°49'34"W, JCN 12313; C, *Vertigo concinnula*, Neutrioso South, Apache Co., Arizona, 33°54'14"N, 109°9'43"W, JCN 14007; D, *Vertigo cristata* (large morph), Sunny Mountain, Nunavik District, Quebec, 55°3'51"N, 67°14'2"W, JCN 13686; E, *Vertigo cristata* (small morph), Sugar Camp Bog, Oneida Co., Wisconsin, 45°50'60"N, 89°17'45"W, BFC 11635; F, *Vertigo malleata*, Holly Shelter Game Lands, Pender Co., North Carolina, 34°31'57"N, 77°44'41"W, BFC NMW.Z.2005.011.03831 (paratype); G, *Vertigo hebardi*, Porgy Key, Dade Co., Florida, CM 73090 (please note that color has faded in long-term storage); H, *Vertigo hannai*, Happy Valley, Alaska, 69°20'8"N, 148°43'49"W, JCN 15144; I, *Vertigo meramecensis*, North Bear Creek, Winneshiek Co., Iowa, 43°26'52"N, 91°37'19"W, JCN 5192; J, *Vertigo bollesiana*, Collins Siding, Aroostook Co., Maine, 47°6'41"N, 68°7'54"W, JCN 16137; K, *Vertigo gouldii* (small southern form), Tellico Gorge, Monroe Co., Tennessee, 35°19'49"N, 84°10'59"W, BFC 1332; L, *Vertigo gouldii* (normal form), Deer Creek, Fillmore Co., Minnesota, 43°43'56"N, 92°20'39"W, JCN 14646; M, *Vertigo arizonensis*, Devils Den Canyon, Eddy Co., New Mexico, 32°1'59"N, 104°48'17"W, JCN 14582; N, *Vertigo arthuri*, Devils Lake Wayside, Manitoba, 52°24'13"N, 98°54'43"W, JCN 11289; O, *Vertigo hubrichti*, Blue Springs East, Winneshiek Co., Iowa, 43°24'35"N, 91°56'29"W, JCN 8883; P, *Vertigo paradoxa*, Caribou, Aroostook Co., Maine, 46°51'32"N, 68°0'43"W, JCN 9898; Q, *Vertigo nylanderi*, Sturgeon Gill Road, Manitoba, 53°28'23"N, 99°9'55"W, BFC 10708/504s; R, *Vertigo alabamensis*, Lanier Quarry, Pender Co., North Carolina, 34°37'49"N, 77°40'27"W, JCN 10781; S, *Vertigo alabamensis* ('conecuhensis' morph), Pond Creek seep, Covington Co., Alabama, 31°6'12"N, 86°32'3"W, JCN 12364; T, *Vertigo clappi*, Tellico Gorge, Monroe Co., Tennessee, 35°19'49"N, 84°10'59"W, BFC 110.

ANNOTATED KEYS TO EASTERN NORTH AMERICAN PUPILLIDS

Generic key

- 1. At least one lamella in the aperture (Figs. 1, 2, 6) 2
 - No apertural lamellae (Figs. 3A-C, 3E-H, 4A-E, 5F, 5K) 7
- 2. Parietal lamella fused with angular forming a complex bilobed structure (Figs. 1, 2C, 2G-P) *Gastrocopta*
 - Parietal lamella a simple peg or plate (occasionally absent); angular lamellae (if present) not fused with the parietal (Figs. 2A, 2D-F, 5A-E, 5G-J, 5L-R, 6) 3
- 3. Fresh shells waxy white to clear (Fig. 2A, 2D-F) *Gastrocopta*
 - Fresh shells pale to deep reddish brown (Figs. 3D, 4F-G, 5A-E, 5G-J, 5L-R) 4
- 4. Shell >3 mm tall (Fig. 3D) *Pupilla*
 - Shell <3 mm tall (Figs. 4F-G, 5, 6) 5
- 5. Entire shell surface pitted; shell almost as tall as wide; three lamellae in aperture (Fig. 4F) *Bothriopupa*
 - Shell lacking pits; shell taller than wide or if as tall as wide, then no apertural lamellae (Figs. 4G, 5A-E, 5G-J, 5L-R, 6) 6

- 6. Shell apex strongly domed; body whorl $\frac{2}{3}$ shell height (Fig. 4G) *Sterkia*
- Shell apex tapered; body whorl $\sim\frac{1}{2}$ shell height or less (Figs. 5, 6) *Vertigo*
- 7. Shell >3 mm tall (Figs. 3A-C, 3E-H) 8
- Shell <3 mm tall (Figs. 4A-E, 5F, 5K) 9
- 8. Shell ovoid or conical with tapered apex (Figs. 3E-H) *Pupoides*
- Shell cylindrical with domed apex (Figs. 3A-C) *Pupilla*
- 9. Adult shell height and width approximately equal; note that many immature pupillids will also key here (Figs. 4D-E) *Pupisoma*
- Adult shell distinctly taller than wide (Figs. 4A-C, 5F, 5K) 10
- 10. Shell ovoid or cylindrical; shell surface smooth (Figs. 5F, 5K) *Vertigo*
- Shell cylindrical or slightly conical; shell surface striate (Figs. 4A-C) *Columella*

Annotated species keys

Bothriopupa Pilsbry, 1898:

Bothriopupa variolosa (Gould, 1848); Figs. 4F, 7A

Pilsbry (1948) reported this species from Little Marco Island, Key Marco, and Big Pine Key off the extreme southern Florida coast, and speculated that it might favor mossy rocks or trees. It has apparently not been seen alive in our region in over 75 years (Hubricht 1985).

Columella Westerlund, 1878 (Figs. 4A-C):

- Shell cylindrical; apex domed; adult shell with 6-7 whorls, >2½ mm tall (Fig. 4A) *C. columella alticola*
- Shell tapered; apex conical; adult shell with 5½-6½ whorls, ≤2½ mm tall (Figs. 4B-C) *C. simplex*

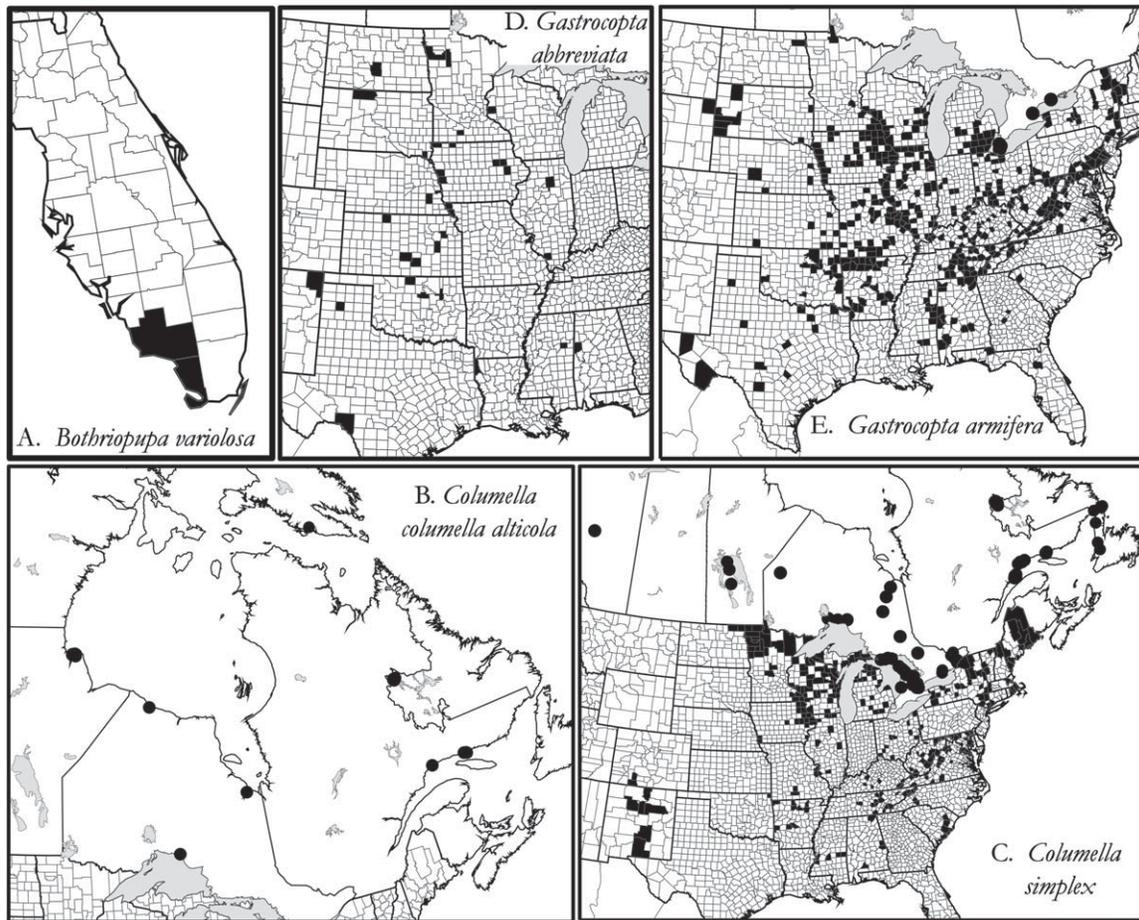


Figure 7. Range maps for *Bothriopupa variolosa*, *Columella columella alticola*, *Columella simplex*, *Gastrocopta abbreviata*, and *Gastrocopta armifera*.

Columella columella alticola (Ingersoll, 1875); Figs. 4A, 7B

Individuals prefer willow and dwarf birch litter accumulations in taiga shrub carr communities and a wide variety of tundra habitats. At the southern edge of its range, it is restricted to seeps and coastal turf.

Columella simplex (Gould, 1841); Figs. 4B-C, 7C

This species, as currently defined, is found across a wide range of forested and open habitats, ranging from subtropical to taiga, xeric to wet, and acidic to calcareous. In the north, it is commonly found climbing on ferns and other herbaceous vegetation up to a meter above the ground.

In such situations leaf litter sieving underestimates population size. In the south, however, it most commonly appears in leaf litter accumulations. *Columella* “*simplex*” encompasses such a large variation of shell sizes, shapes, and shell surface sculptures that Pilsbry (1948), Oughton (1948), and Hubricht (1985) all suggest this name likely refers to a problematic species complex. Our own observations confirm this view, but we have not yet resolved the problem. Large forms in this complex have been commonly confused with *Columella columella* in the southwestern U.S.A. (Bequaert and Miller 1973, Metcalf and Smartt 1997).

Gastrocopta Wollaston, 1878 (Figs. 1-2):

1. Shell $3\frac{1}{4}$ mm tall; ovoid-conical; color white to brown (Fig. 2) 2
Shell >math>3\frac{1}{4}</math> mm tall, cylindrical or barrel-shaped; translucent white when fresh (Fig. 1; subgenus *Albinula*) 5
2. Angulo-parietal lamella a simple peg-like tooth (Figs. 2D-F, 2N) 9
Angulo-parietal lamellae not peg-shaped (Figs. 2A-C, 2G-M, 2O-P) 3
3. Angulo-parietal lamella a single large, folded sheet (Figs. 2A) *G. contracta*
Angular and parietal lobes of angulo-parietal lamellae distinct (Figs. 2C, 2G-M, 2O-P) 4
4. Fresh shells whitish to pale horn yellow (Figs. 2C, 2G-H, 2O-P) 12
Fresh shells yellow-brown to brown-red (Figs. 2I-M) 17
5. Columellar lamella triangular or round in cross section (Figs. 1A-B) 6
Columellar lamella a more or less vertical, flat plate (Figs. 1C-E) 7
6. Columellar lamella with both forward and basally pointing components, appearing more or less pyramidal in apertural view;
shell usually >4 mm tall (Fig. 1A) *G. armifera*
Columellar lamella lacking a basal lobe, making the entire structure appear as a downward-pointing peg in apertural view;
shell <4 mm tall (Fig. 1B) *G. abbreviata*
7. Columellar lamella a simple plate, with lower end slightly more deeply inserted into aperture; lower palatal lamella taller than wide,
inserted at same depth into the aperture as the upper palatal lamella (Fig. 1C) *G. clappi*
Columellar lamella creased in the middle, more deeply inserted at the top; lower palatal lamella as wide or wider than tall,
inserted more deeply into aperture than upper palatal (Figs. 1D-E) 8
8. Lamellae massive, filling over $\frac{3}{4}$ of the aperture, lower end of the parietal lamellae overlapping the upper end of the lower palatal;
shell with domed apex (Fig. 1D) *G. ruidosensis*
Lamellae less massive, filling less than $\frac{3}{4}$ of the aperture, lower end of the parietal lamellae at most approaching the upper end of the lower palatal;
shell with tapered apex (Fig. 1E) *G. similis*
9. Fresh shells brown-red (Fig. 2N) *G. cristata*
Fresh shells white-transparent (Figs. 2D-F) 10
10. Shell approximately cylindrical (Fig. 2F) *G. pilsbryana*
Shell ovoid-conical (Figs. 2D-E) 11
11. Shell narrowly conical, with height more than $1\frac{1}{2}$ times width; lower palatal lamella deeply entering aperture (Fig. 2E) *G. pentodon*
Shell broadly conical, with height less than $1\frac{1}{2}$ times width; lower palatal lamella not deeply entering aperture (Fig. 2D) *G. tappaniana*
12. Lobes of angulo-parietal lamella distinct, more or less parallel (Figs. 2B-C, 2G) 13
Angulo-parietal lobes intersecting, in form of a curved X-like structure (Figs. 2H, 2O-P) 15
13. Basal and palatal lamellae absent; shell >2.4 mm tall (Fig. 2B) *G. corticaria*
Basal and palatal lamellae present; shell <2.4 mm tall (Figs. 2C, 2G) 14
14. Angulo-parietal lamella massive, almost filling aperture; height >math>1\frac{3}{4}</math> mm (Fig. 2C) *G. ashmuni*
Angulo-parietal lamella filling only $\frac{1}{4}$ of aperture; height $1\frac{3}{4}$ mm (Fig. 2G) *G. holzingeri*
15. Shell approximately cylindrical, with bottom three whorls of similar diameter (Fig. 2H) *G. pellucida*
Shell narrowly conical, with each whorl of increasing diameter (Figs. 2O-P) 16
16. Aperture margin with thickened callus (Fig. 2O) *G. rupicola*
Aperture margin unthickened (Fig. 2P) *G. servilis*
17. Alive or recently dead clean shells deep tan to brown, opaque (Figs. 2I-N) 18
Alive or recently dead clean shells horn-yellow to light yellow-brown, translucent (Figs. 2H, 2O-P) 24
18. Angular lobe of angulo-parietal lamella reduced to a small protuberance (Fig. 2N) *G. cristata*
Angulo-parietal lamella distinctly bi-lobed (Figs. 2I-M, 2O-P) 19
19. Angulo-parietal lobes parallel throughout (Fig. 2I) *G. rogersensis*
Angulo-parietal lobes intersecting, in form of a curved X-like structure (Figs. 2J-M) 20
20. Lower palatal lamella parallel to and inserted at roughly the same depth into aperture as upper palatal lamella (Figs. 2K-L) 21
Lower palatal lamella angled away from upper palatal lamella, and inserted more deeply into shell (Figs. 2J, 2M) 22
21. Shell strongly tapered, with body whorl wider than the penultimate; callus plate of variable thickness on aperture margin in front of
palatal lamellae (Fig. 2L) *G. riograndensis*
Shell columnar to ovate, with body and penultimate whorls of approximately same width; aperture margin unthickened (Fig. 2K) *G. riparia*

22. Shell tapered, with body whorl wider than the penultimate (Fig. 2L) *G. riograndensis*
 Shell columnar to ovate, with body and penultimate whorls of approximately the same width (Figs. 2H, 2J, 2M, 2O-P) 23
23. Angular lobe flaring upwards, triangular in shape, distinct from and crossing over the parietal lobe; lower palatal lamella inserted moderately deep, lying at a 45° angle to aperture axis; shell height usually >2.4 mm; thick callus plate present on aperture margin (Fig. 2M) *G. sterki*
 Angular lobe linear and fused to the middle of the parietal lobe; lower palatal lamella inserted deeply, lying parallel to aperture; shell height usually <2.4 mm; no callus (Fig. 2J) *G. procera*
24. Shell more or less cylindrical, with bottom three whorls of similar diameter (Fig. 2H) *G. pellucida*
 Shell narrowly conical, with each whorl of increasing diameter (Figs. 2O-P) 25
25. Aperture margin with thickened callus (Fig. 2O) *G. rupicola*
 Aperture margin unthickened (Fig. 2P) *G. servilis*

Gastrocopta abbreviata (Sterki, 1909); Figs. 1B, 7D

This is the characteristic member of the subgenus *Albinula* in the central and western plains, where it is found under stones, within loess bank fissures, and in thin litter accumulations in riparian forests and grasslands. Towards the east it becomes largely limited to xeric habitats associated with bedrock outcrops or sand deposits. Our observations support Hubricht (1972) who noted that even though it frequently co-occurs with *Gastrocopta armifera* and *Gastrocopta similis*, intermediate individuals never occur.

Gastrocopta armifera (Say, 1821); Figs. 1A, 7E

This species is found in leaf litter accumulations on bedrock glades, rich rocky woodlands, and floodplain forests. As noted by Hubricht (1985), mapped reports of this species west from the eastern Plains and northwest of southern Minnesota are questionable. All material from these locations should be re-examined to determine if they represent *Gastrocopta abbreviata* or *Gastrocopta similis*, respectively.

Gastrocopta ashmuni (Sterki, 1898); Figs. 2C, 8A

East of the Rockies, populations are limited to leaf accumulations in somewhat mesic juniper, piñon pine, and oak forest on bedrock outcrops.

Gastrocopta clappi (Sterki, 1909); Figs. 1C, 8B

This member of the subgenus *Albinula* is a xerophile and calciphile that is found under rocks, around the base of grass tufts, and under sparse vegetation on xeric glades and grasslands.

Gastrocopta contracta (Say, 1822); Figs. 2A, 8C

Found in leaf litter and under logs in a wide range of habitats, ranging from mesic to wet, and forested to open. Although occurring in higher numbers in base-rich sites, it is also frequently present in base-poor locations.

Gastrocopta corticaria (Say, 1816); Figs. 2B, 8D

Large numbers of individuals can often be found on soil-covered ledges on wooded, calcareous bedrock outcrops. The species may also be frequent in deep leaf litter accumulations under red cedar, and is occasionally found in wooded wetlands. Pilsbry (1948) noted that this species may also be found crawling on trees 0.3-0.6 meters above the ground.

Gastrocopta cristata (Pilsbry and Vanatta, 1900);

Figs. 2N, 9A

In central and eastern Plains, individuals are largely limited to sandy floodplains. Farther west, they are reported from thin leaf litter accumulations on more xeric sites (Pilsbry 1948, Bequaert and Miller 1973, Hubricht 1985). They can also be common in disturbed, anthropogenic habitats, such as in Albuquerque, New Mexico where they commonly occur in yards under juniper plantings and in grass turf near irrigation sprinkler heads. The disjunct populations in the southern Delmarva Peninsula appear to be adventitious (Hubricht 1985).

Gastrocopta holzingeri (Sterki, 1889); Figs. 2G, 10A

Individuals are found in accumulations of grass thatch on dry grassland, soil covered ledges on bedrock outcrops, leaf litter accumulations under red cedar, and under rocks on forested talus slopes.

Gastrocopta pellucida (Pfeiffer, 1841); Figs. 2H, 9B

In the southern Plains, populations are most often found in leaf litter accumulations under juniper and among grass tufts on xeric bedrock outcrops and riparian sand deposits. Along the Gulf Coast, individuals occur in open woodlands, parklands, roadsides, and lawns. This is one of the most arid-tolerant snails of the desert southwest, being found throughout southern Arizona and New Mexico in litter accumulations under low juniper, palo verde, or mesquite scrub (Metcalf and Smartt 1997).

Gastrocopta pentodon (Say, 1821); Figs. 2E, 10B

(syn. *Gastrocopta carnegiei* (Sterki, 1916))

This cosmopolitan species occurs in leaf litter accumulations from base-rich to base-poor, xeric to mesic, and open to forested, including sites as diverse as sand savanna, carbonate cliffs, bedrock glades, and tallgrass prairie to high elevation heath balds and mesic upland forests. We fully agree with Pearce *et al.* (2007) that *Gastrocopta carnegiei* simply represents a somewhat wider than average *G. pentodon* individual for its height.

Gastrocopta pilsbryana (Sterki, 1890); Figs. 2F, 10C

In the southern Rockies, populations occur in leaf litter accumulations across a wide variety of dry-mesic and mesic forest sites from low to high elevation. In the far southwestern

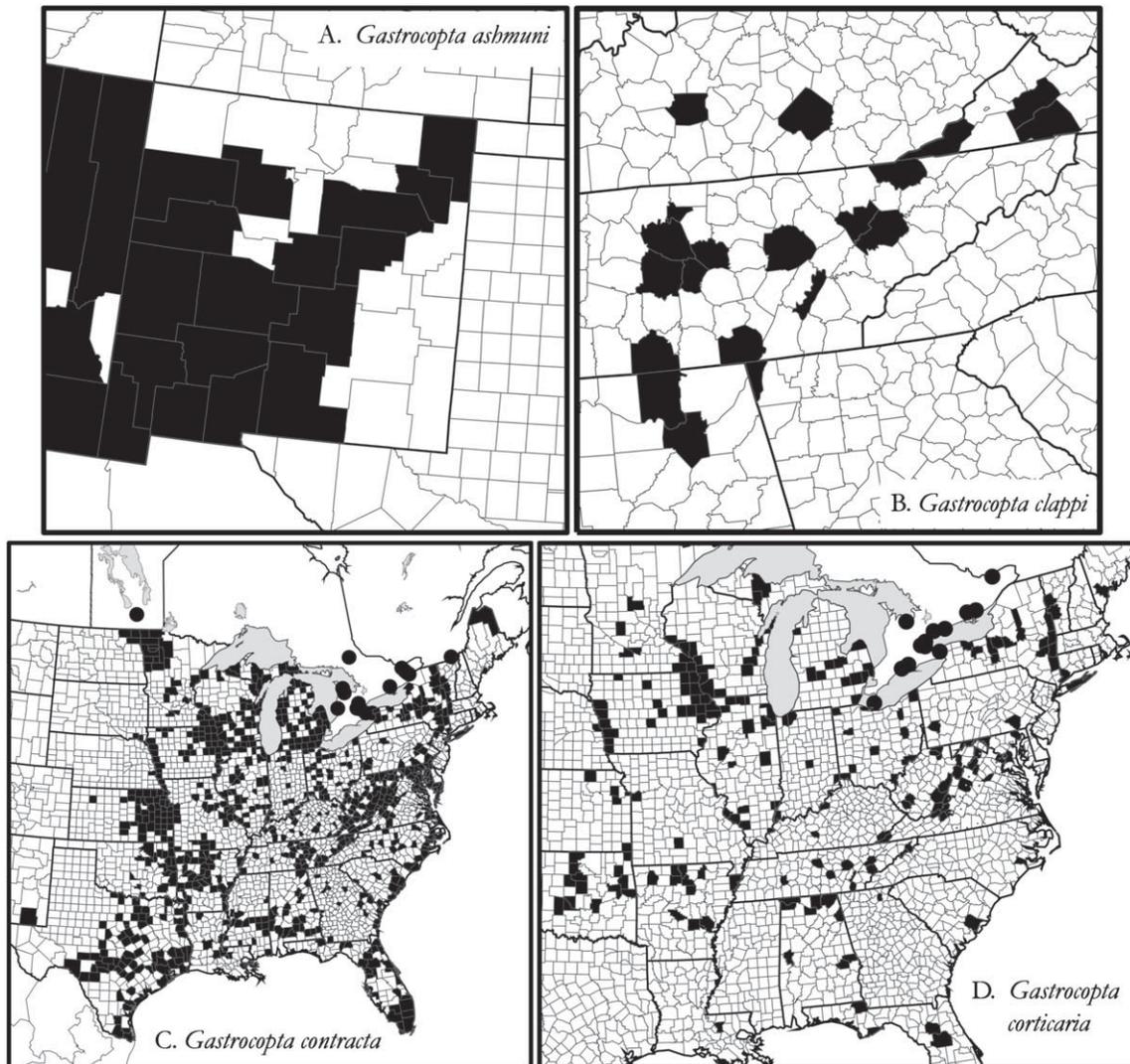


Figure 8. Range maps for *Gastrocopta ashmuni*, *Gastrocopta clappi*, *Gastrocopta contracta*, and *Gastrocopta corticaria*.

Plains, it is limited to forested pockets on shaded canyon sides. Individuals from eastern New Mexico are characterized by a thick apertural callus and distinct crest. While Pilsbry (1948) and Metcalf and Smartt (1997) indicate that *G. pilsbryana* lacks these features, these populations clearly represent this species due to their distinctly cylindrical shape, even in sites where it co-occurs with *G. pentodon*. The taxonomic status of this form is unclear.

Gastrocopta procera (Gould, 1840); Figs. 2J, 10D

This obligate calciphile is found under stones, in thatch, and in leaf litter accumulations on scrub-covered and exposed sites such as bedrock glades, dry prairie, and roadside verges. It also occurs in sandy river floodplain scrub and forest.

Gastrocopta riograndensis (Pilsbry and Vanatta, 1892);
Figs. 2L, 11A

We have found this species in thin soil accumulations on small ledges of xeric south-facing limestone cliffs in the Sacramento Mountains of New Mexico, where organic litter is generated from grasses and shrubs. It has also been reported from similar habitats in west Texas (Neck 1980). While much of the south Texas material at ANSP and CM represents flood wash debris, a number of these shells were also alive at time of collection, indicating the presence of extant populations in more mesic riparian habitats. This material differs from those observed in New Mexico by having a wider shell for a given height and a thinner palatal callus. In all other respects, however, these forms appear identical, suggesting that they are simply endpoints of environmentally driven clinal variation.

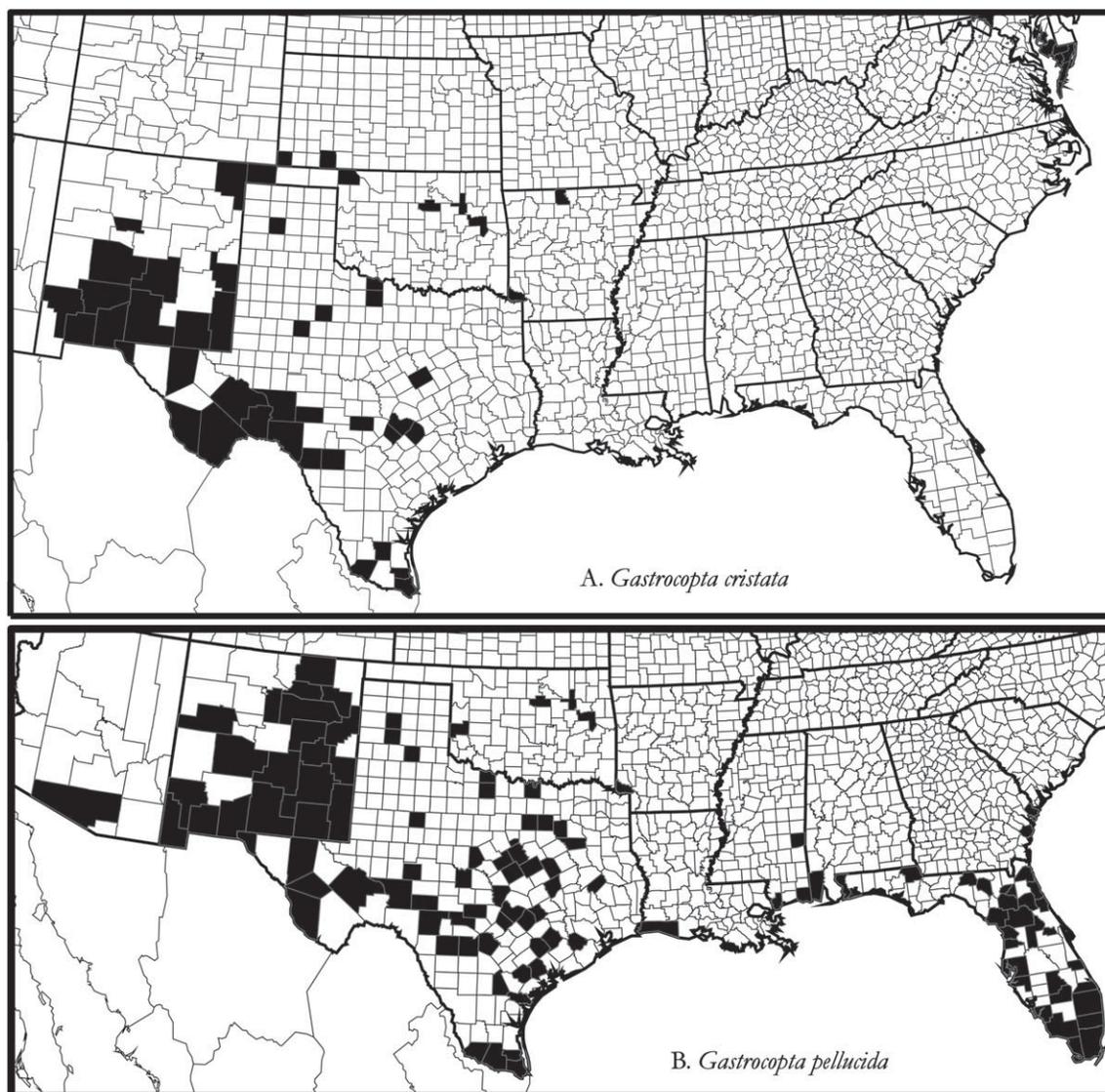


Figure 9. Range maps for *Gastrocopta cristata* and *Gastrocopta pellucida*.

Gastrocopta riparia Hubricht, 1978; Figs. 2K, 11B

Individuals are found in decomposed leaf litter accumulations, often under dense shrub or vine thicket cover in mesic, disturbed sites such as railroad rights-of-way, roadside verges, vacant lots, floodplains, and other scrubland habitats. It seems more tolerant of acidic conditions than *Gastrocopta procera*.

Gastrocopta rogersensis Nekola and Coles, 2001;

Figs. 2I, 11C

This calciphile is found on exposed soil, under stones and in thin accumulations of leaf litter and grass thatch on dry bedrock cliffs, xeric glades, and occasionally rocky, upland forest.

Gastrocopta ruidosensis (Cockerell, 1909); Figs. 1D, 11D

This member of the subgenus *Albinula* is found on bare soil, under stones, and in thin accumulations of grass thatch and juniper litter on mid-elevation carbonate cliffs and xeric limestone grasslands along the eastern slopes of the Sangre de Cristo and Sacramento mountains in eastern New Mexico. Pleistocene fossil material has been found throughout the southern Plains (Hubricht 1985).

Gastrocopta rupicola (Say, 1821); Figs. 2O, 12A

Individuals are found in decomposed leaf litter, often under dense shrub or vine thicket cover in lowland forest, scrub, and disturbed habitats.

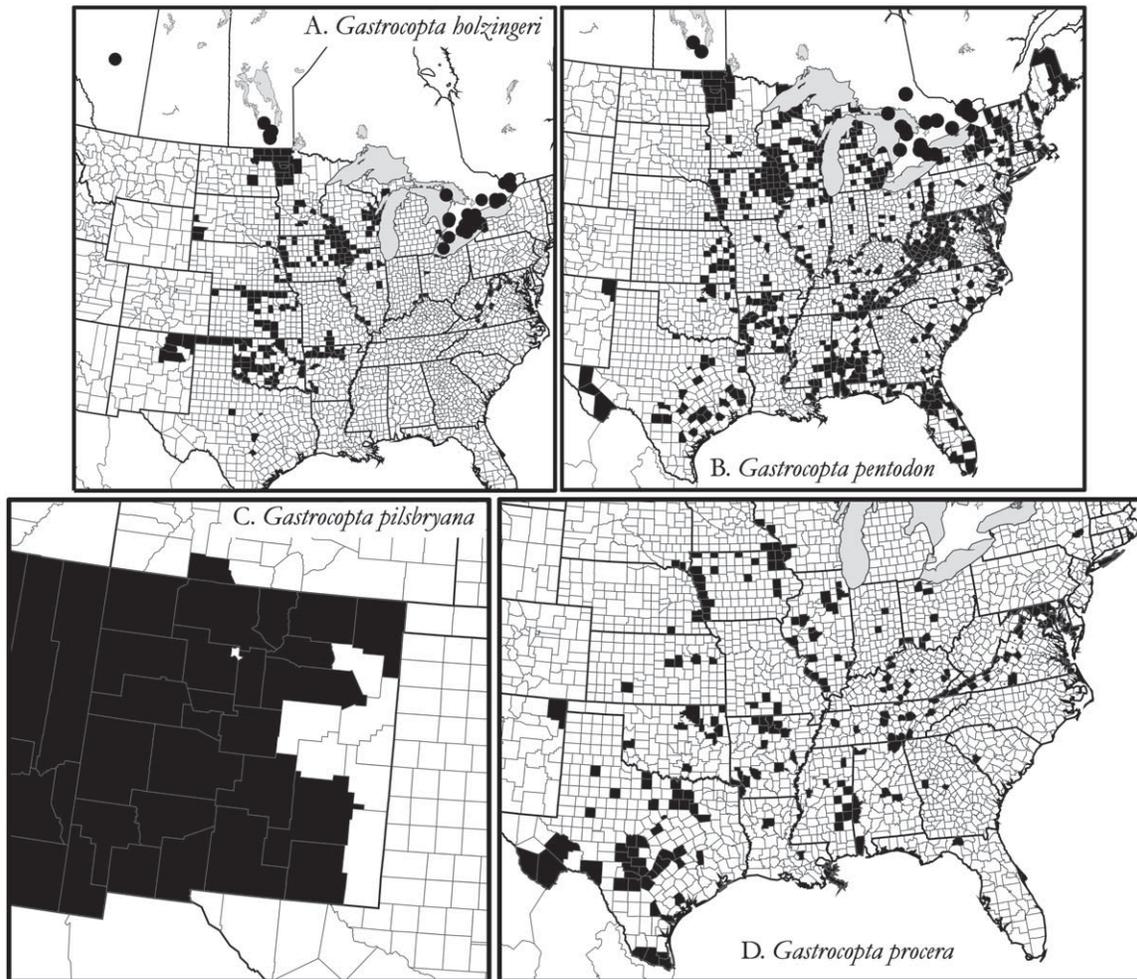


Figure 10. Range maps for *Gastrocopta holzingeri*, *Gastrocopta pentodon*, *Gastrocopta pilsbryana*, and *Gastrocopta procera*.

Gastrocopta servilis (Gould, 1843); Figs. 2P, 12B

This species appears to favor grass thatch and decomposed leaf litter in shoreline thickets and anthropogenically disturbed habitats such as roadsides, vacant lots, yards, and railroad rights-of-way.

Gastrocopta similis (Sterki, 1909); Figs. 1E, 12C

This obligate calciphile is the characteristic member of the genus *Albinula* in the upper Midwest, where it is found under stones, on bare soil, soil-covered cliff ledges, and in decomposed grass thatch and red cedar litter accumulations across a wide variety of habitats ranging from xeric grasslands to mesic forest and fens. However, it is most frequently encountered in dry, gravelly prairie and bedrock glades. *Gastrocopta similis* appears very similar to *Gastrocopta ruidosensis*, differing only by its slightly less massive apertural lamellae. The relationship between these two taxa requires further investigation.

Gastrocopta sterkiana Pilsbry, 1912; Figs. 2M, 12D

Found under stones, on bare soil, in thin grass thatch and juniper or litter accumulations on xeric grasslands such as bare limestone outcrops in the Flint Hills of northeastern Oklahoma and piñon-juniper parkland in northeastern New Mexico. On the western limit of its range, it may also occur in accumulations of cottonwood litter in riparian forest.

Gastrocopta tappaniana (C. B. Adams, 1842);
Figs. 2D, 13A

Found in accumulations of decomposing leaf litter in wooded and open wetland habitats such as riparian, floodplain and swamp woodlands, mesic and wet prairies, open shoreline bedrock outcrops, fens, pocosins, and *Sphagnum* bogs. While some have suggested that this taxon is an ecophenotypic variant of *Gastrocopta pentodon* (e.g., Bequaert and Miller 1973), multivariate morphometric

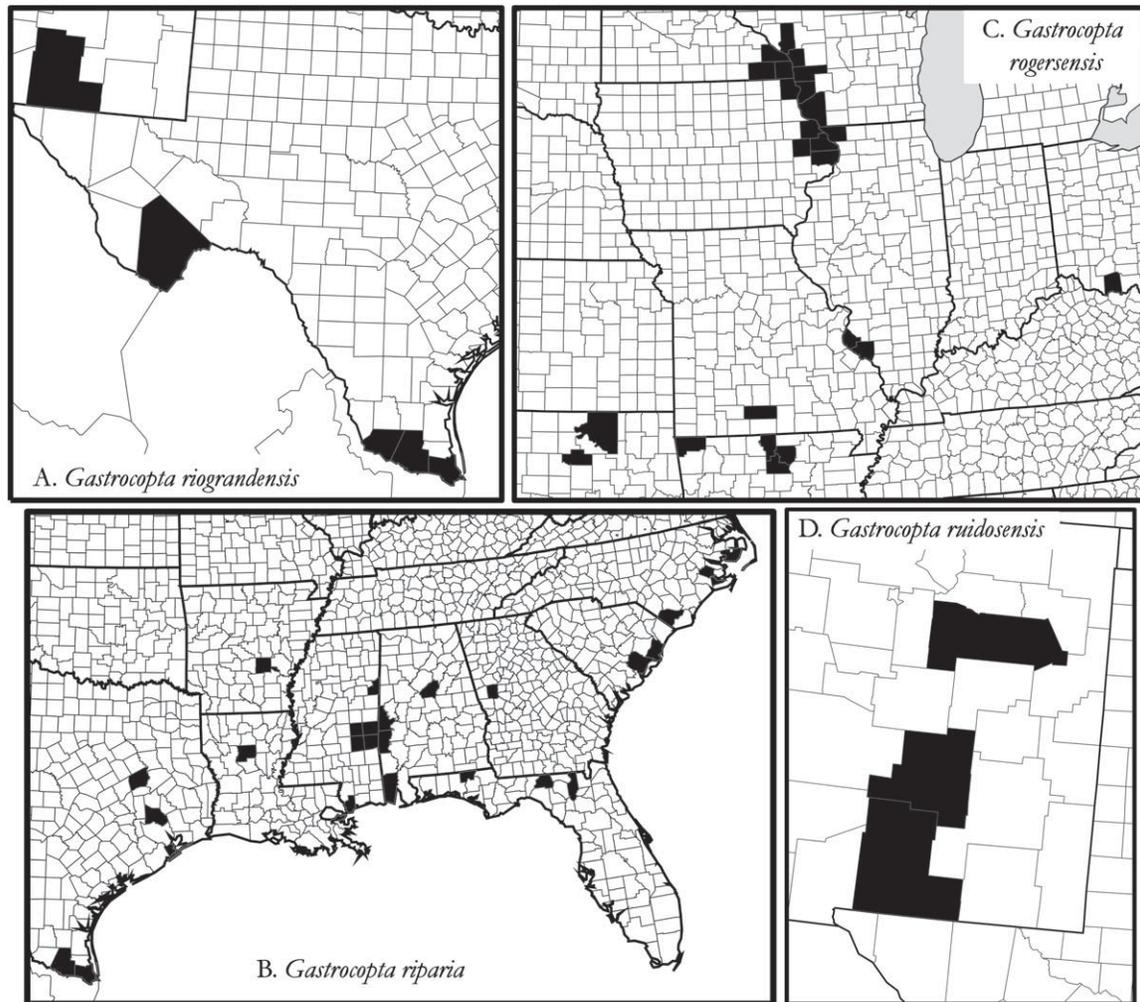


Figure 11. Range maps for *Gastrocopta riograndensis*, *Gastrocopta riparia*, *Gastrocopta rogersensis*, and *Gastrocopta ruidosensis*.

analyses of museum collections indicate that this species is clearly distinct (Pearce *et al.* 2007). Our field observations

from across the range of both species agree fully with this conclusion.

Pupilla Leach, 1828 (Figs. 3A-D):

1. Aperture with three well-developed lamellae; palatal lamella often longer than wide (Fig. 3D) *P. blandi*
 Aperture with two or fewer lamellae; palatal lamellae (if present) usually as wide as long (Figs. 3A-C) 2
2. Callus inserted into aperture; shell >3 mm tall (Figs. 3A-B) *P. muscorum*
 Massive callus at apertural margin; shell <2¾ mm tall (Fig. 3C) *P. muscorum xerobia*

Pupilla blandi Morse, 1865; Figs. 3D, 13B

East of the Rockies, populations of dwarfed individuals are occasionally found in xeric juniper savanna and mesic mixed conifer forest. In the mountains they occur in leaf litter accumulations in mid to high elevation oak, pine, fir, and spruce forest, becoming especially abundant in aspen groves.

Pupilla muscorum (Linné, 1758); Figs. 3A-C, 13C

East-central North American populations (Maine and Tennessee west to eastern Iowa) generally occur in disturbed anthropogenic habitats such as road verges, vacant lots, abandoned quarries, old fields, and concrete culverts (Hubricht 1985) although they may also occasionally inhabit less disturbed carbonate cliff, glade, and grassland sites. To

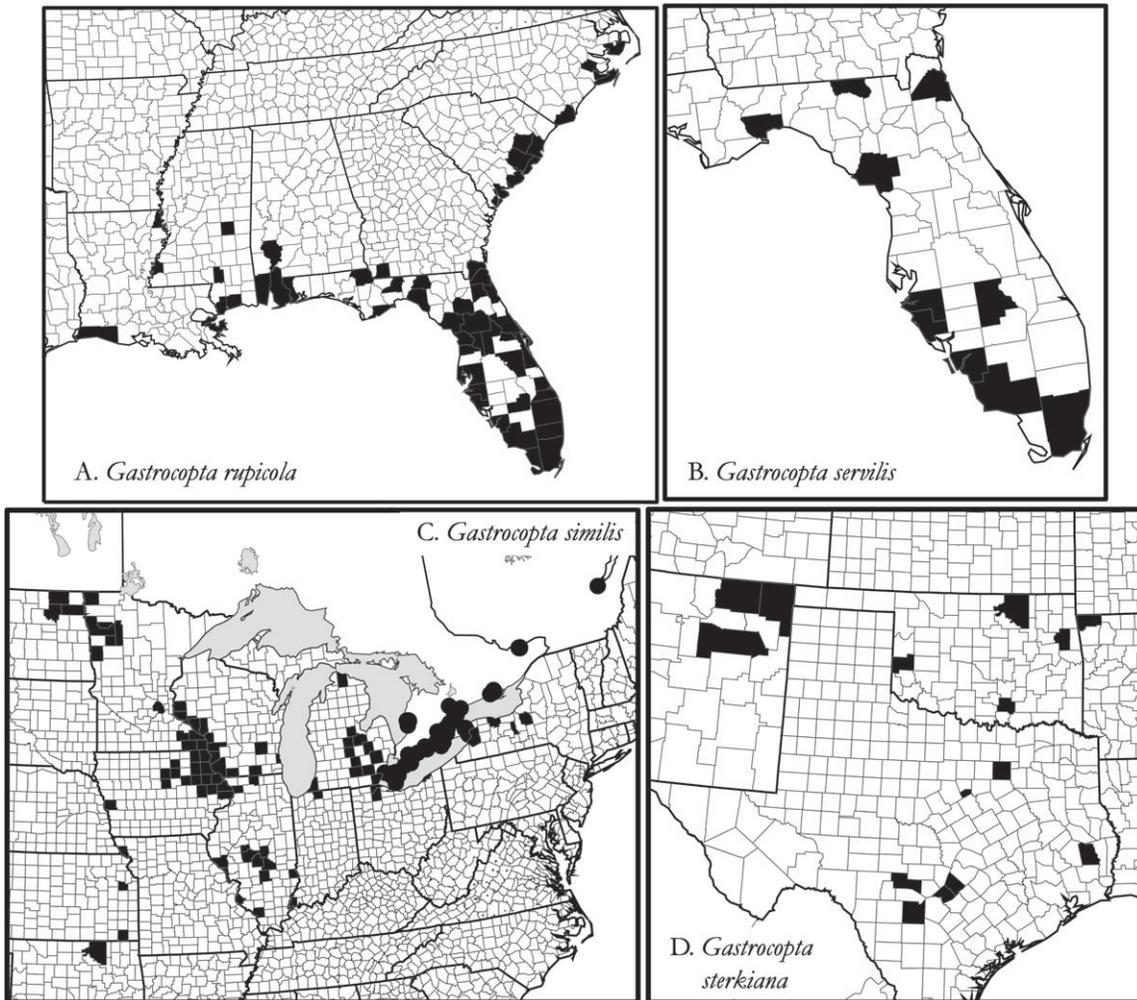


Figure 12. Range maps for *Gastrocopta rupicola*, *Gastrocopta servilis*, *Gastrocopta similis*, and *Gastrocopta sterkiana*.

the north (Newfoundland, the north shore of the St. Lawrence to northwestern Minnesota and the southern shore of Hudson’s Bay) populations occur on bare soil, under stones, on turf, and in thin leaf litter accumulations on sandy or rocky shorelines and in tundra. Recent mitochondrial DNA sequence analyses (Nekola *et al.* 2009, Von Proschwitz *et al.* 2009) indicate that throughout its Holarctic range this name has been applied to a species complex. Most of the populations in east-central North America (referable to *P. muscorum*) represent apparent European introductions, with Iowa roadside verge material being closest, for instance, to Swedish haplotypes. However, northern Plains populations represent an undescribed species distantly allied to *Pupilla hebes* and *Pupilla pratensis*. Given the morphologic variability noted

between northern Plains, southern Plains, and arctic populations, the presence of more than one native species also appears likely. The southern Plains form, limited to arid piñon-juniper forests, has been referred to as *Pupilla muscorum xerobia* (Pilsbry 1948). Metcalf and Smartt (1997) suggest that this taxon may be worthy of species status given its greatly thickened apertural lip, uniformly small size and height/width ratio, and divergent habitat and range. The native arctic populations differ from *P. hebes* only by the weak possession of a partial callus on the uppermost margin of the palatal wall, and appear quite similar to *Pupilla pratensis*. Additional sequence analysis will be required to make definitive taxonomic statements regarding this group not only in North America but also in Eurasia.

Pupisoma Stoliczka, 1873:

- Shell surface with minute spiral striae (Fig. 4D) *P. dioscoricola*
- Shell surface pitted-granulose, lacking striae (Fig. 4E) *P. macneilli*

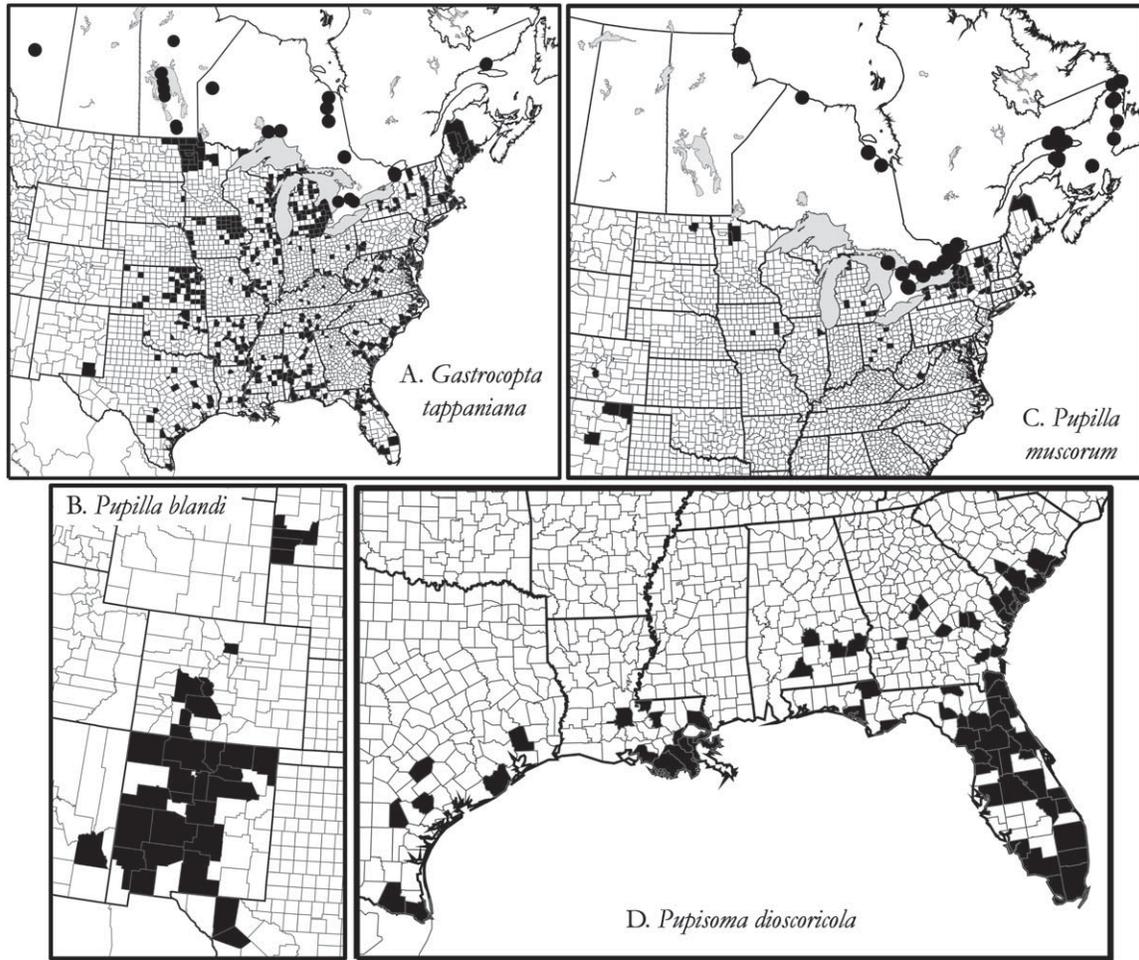


Figure 13. Range maps for *Gastrocopta tappaniana*, *Pupilla blandi*, *Pupilla muscorum*, and *Pupisoma dioscoricola*.

Pupisoma dioscoricola (C. B. Adams, 1845); Figs. 4D, 13D

Populations occur in sub-tropical forest and scrub, abandoned citrus orchards and carbonate rock outcrops. Individuals are principally arboreal on the undersides of leaves, with only a scattered few occurring in leaf litter. Hubricht (1985) reports that their mucus is especially adhesive, making them less likely to be dislodged by storms as compared to other arboreal taxa.

Pupisoma macneilli (Clapp, 1918); Figs. 4E, 14A

Populations occur in woodlands, scrub, and carbonate rock outcrops. Hubricht (1985) reports that individuals are most often found on the trunks of smooth-barked trees and shrubs, with only scattered shells occurring in leaf litter.

Pupoides Pfeiffer, 1854:

- 1. Shell conical (Figs. 3G-H) 2
- Shell cylindrical-ovoid (Figs. 3E-F) 3
- 2. Adult shell with calcified apertural margin (Fig. 3H) *P. albilabris*
- Adult shell with unthickened apertural margin (Fig. 3G) *P. modicus*
- 3. Shell surface with regular, widely-spaced ribs; aperture calcified (Fig. 3E) *P. hordaceus*
- Shell surface with irregular striations; aperture expanded but unthickened (Fig. 3F) *P. inornatus*

Pupoides albilabris (C. B. Adams, 1821); Figs. 3H, 14B

A calciphile found under stones, leaf litter under red cedar, in thin grass turf and thatch accumulations on rock

outcrops, bedrock glades, xeric prairie, and old fields. It is also occasionally found in riparian forests of the western plains.

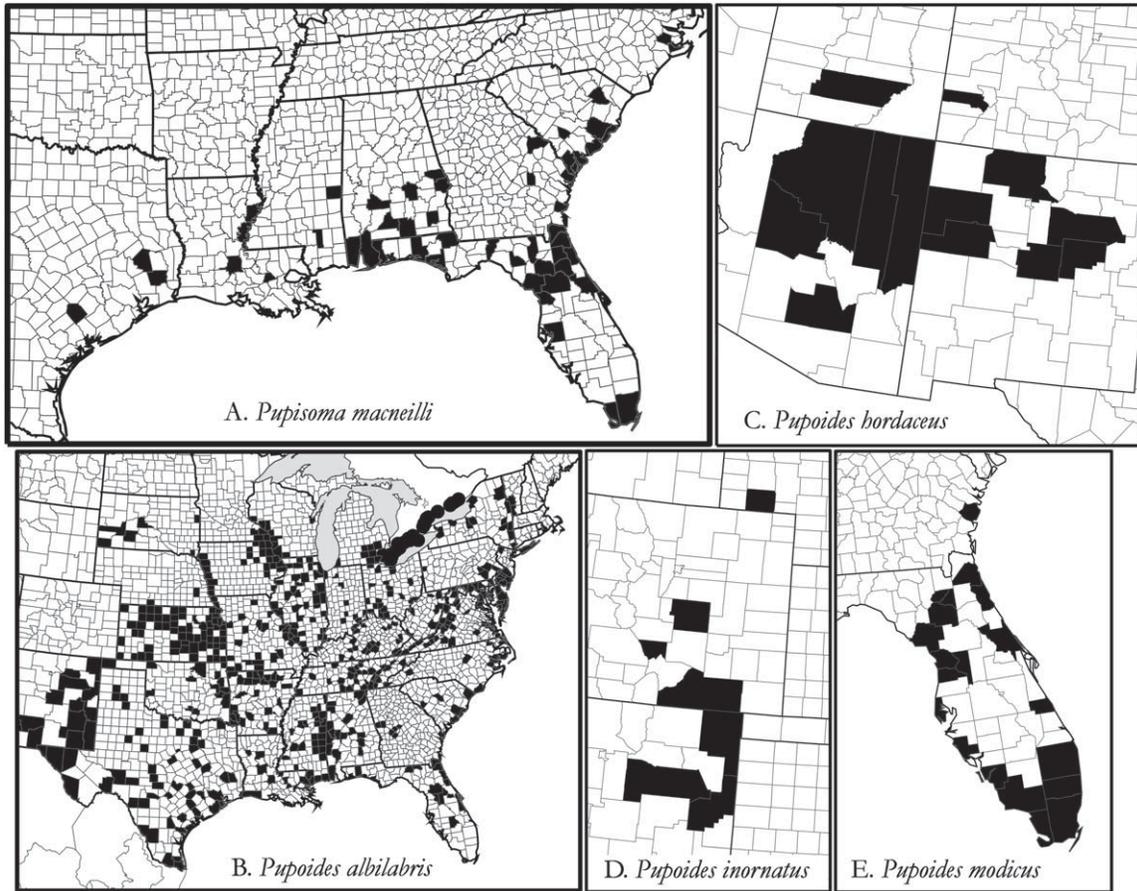


Figure 14. Range maps for *Pupisoma macneilli*, *Pupoides albilabris*, *Pupoides hordaceus*, *Pupoides inornatus*, and *Pupoides modicus*.

Pupoides hordaceus (Gabb, 1866); Figs. 3E, 14C

Individuals occur in deep juniper litter accumulations in xeric, low elevation juniper parkland where it is often the only species present.

Pupoides inornatus Vanatta, 1915; Figs. 3F, 14D

Populations occur in leaf litter accumulations under small shrubs and under rocks or in thin grass thatch in xeric grassland and parkland habitats (Metcalf and Smartt 1997). It also occurs in leaf litter accumulations in riparian forest.

Pupoides modicus (Gould, 1848); Figs. 3G, 14E

Populations occur along roadsides and a variety of other open habitats.

Sterkia Pilsbry, 1898:

Sterkia eyriesi rhoadsi (Pilsbry, 1899); Figs. 4G, 15A

Pilsbry (1948, pp. 1016-1018) indicates that in eastern North America this species is limited to tropical hardwood hammocks in extreme southern Florida. He reported finding only two individuals in a “great amount of woodland debris” and indicated that George Clapp only located about a dozen shells from a “bushel of rubbish.” Based on our experience with other pupillids, these low numbers suggest to us that neither researcher deduced this taxon’s preferred microsites. Hubricht (1985) reported locating a single individual crawling on a log after a shower.

Vertigo Müller, 1774 (Figs. 5-6):

- 1. Body whorl strongly pustulose (Fig. 6F) *V. malleata*
- Body whorl lacking strong pustulose bumps (Figs. 5, 6A-E, 6G-T) 2
- 2. Upper palatal lamella short, low and straight, with long axis barely visible in apertural view (Figs. 5, 6A-Q) 3
- Upper palatal lamella long, tall and longitudinally curved, allowing long axis to be visible in apertural view (Figs. 6R-T) 4
- 3. Shell surface smooth or weakly striate (Fig. 5) 8
- Shell surface strongly striate (Figs. 6A, 6C-E, 6G-Q) 6

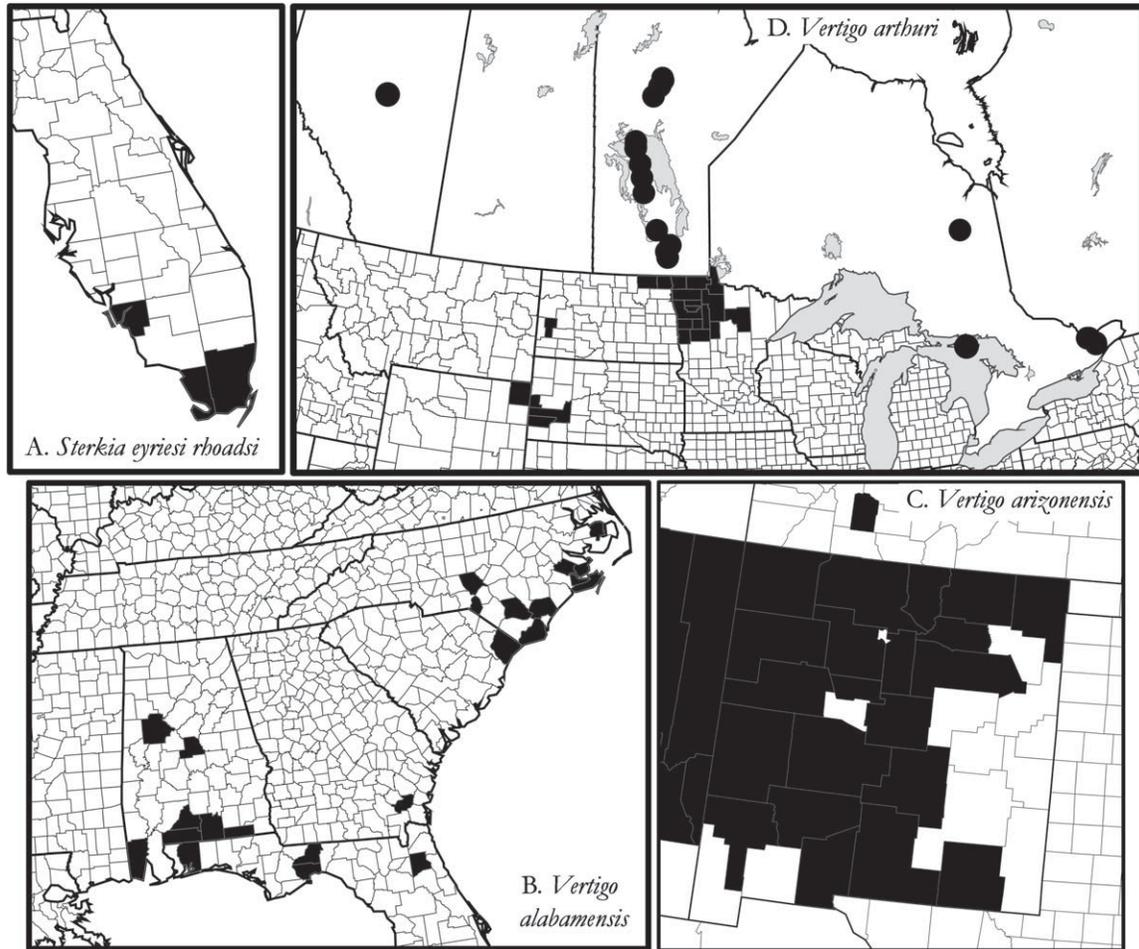


Figure 15. Range maps for *Sterkia eyriesi rhoadsi*, *Vertigo alabamensis*, *Vertigo arizonensis*, and *Vertigo arthuri*.

4.	Six or more apertural lamellae (Figs. 5A-E, 5O, 6B)	9
	Five or fewer apertural lamellae (Figs. 5F-R)	5
5.	Four or fewer apertural lamellae (Figs. 5F-N, 5R)	15
	Five apertural lamellae (Figs. 5D, 5P-O)	27
6.	Parietal lamella pointed directly at lower palatal lamella, so that parietal, lower palatal, and columellar lamellae form a cross (Figs. 5J, 6C-E, 6I)	33
	Parietal lamella pointed at upper palatal or space between the upper and lower palatals (Figs. 6A-B, 6G-H, 6J-M)	7
7.	Lower palatal lamella inserted near aperture margin so that only short axis is visible when seen in apertural view (Figs. 6A-E, 6G-M)	36
	Lower palatal lamella inserted more deeply into shell so that long axis is visible when seen in apertural view (Figs. 6N-Q)	43
8.	Aperture margin thickened; shell color deep yellow; imperforate (Figs. 6R-S)	<i>V. alabamensis</i>
	Aperture margin not thickened; shell color light yellow to horn; narrowly umbilicate (Fig. 6T)	<i>V. clappi</i>
9.	Angular lamella absent; palatal wall with callus and light-colored crest; shell dull (Fig. 5O)	<i>V. pygmaea</i>
	Angular lamella present; crest not light-colored (Figs. 5A-E, 6B)	10
10.	Shell weakly striate; dull; all lamellae short; shell with shallow suture and domed apex (Fig. 6B)	<i>V. oralis</i>
	Shell smooth, shiny; at least some of the lamella long and blade-like (Figs. 5A-E)	11
11.	Shell basally obese, with height less than 2 times width (Figs. 5B-C)	12
	Shell not basally obese, with height greater than 2 times width (Figs. 5A, 5D-E)	13
12.	Aperture wider than tall; columellar lip of aperture broad, more or less straight and angled away from palatal wall; infra-parietal lamella never present (Fig. 5B)	<i>V. teskeyae</i>
	Aperture as tall as wide; columellar lip of aperture rounded, not markedly broad; infra-parietal lamella often present (Fig. 5C)	<i>V. ovata</i>
13.	Shell height >2½ mm; ~6 whorls; aperture less than ½ of shell height (Fig. 5A)	<i>V. morsei</i>
	Shell height <2½ mm; ~4 whorls; aperture more than ½ of shell height (Figs. 5D-E)	14
14.	Lower palatal lamella straight and not deeply entering aperture; shell height >1.9 mm (Fig. 5D)	<i>V. binneyana</i>
	Lower palatal lamella curved and deeply entering aperture; shell height <1.9 mm (Fig. 5E)	<i>V. milium</i>

15. No apertural lamellae; note that juvenile *Vertigo* species lack lamellae and may key out here; see also *Columella* species which are somewhat similar in form to *Vertigo* (Figs. 5F, 5K) 16
 2-4 apertural lamellae (Figs. 5G-J, 5L-N, 5Q-R) 18
16. Crest absent; dull surface luster (Fig. 5F) *V. aff. genesii* 17
 Crest present; glassy surface luster (Figs. 5H, 5K) 17
17. Shell <2½ mm tall, shell ovoid-conical (Fig. 5H) *V. modesta hoppi*
 Shell >2½ mm tall, shell ovate (Fig. 5K) *V. modesta ultima* 19
18. One or two apertural lamellae (Figs. 5G-H) 19
 Three or four apertural lamellae (Figs. 5L-O, 5Q-R) 20
19. Shell lacking palatal lamellae; ovoid-conical; crest present (Fig. 5H) *V. modesta hoppi*
 At least one strong palatal lamellae present; shell cylindrical; crest absent (Fig. 5G) *V. oughtoni* 21
20. Shell >2 mm tall, ovoid-cylindrical (Figs. 5G, 5I-J) 21
 Shell 2 mm or less tall, ovoid-conical (Figs. 5L-N, 5Q-R) 23
21. Four apertural lamellae, lower and upper palatal lamellae of similar size (Fig. 5J) *V. modesta*
 Three or four lamellae, upper palatal lamella weak or absent (Figs. 5G, 5I) 22
22. Shell ovoid; >2¼ mm tall; lower palatal lamella a short peg (Fig. 5I) *V. modesta form arctica*
 Shell cylindrical; 2¼ mm or less tall; lower palatal lamella longer than wide (Fig. 5G) *V. oughtoni* 23
23. Body whorl narrower than penultimate whorl, making shell bluntly pointed at both top and bottom; four lamellae, with an elongate vertical columellar (Fig. 5L) *V. oscariana*
 Body whorl at least as wide as the penultimate whorl; columellar lamella peg-shaped (Figs. 5M-N, 5Q-R) 24
24. Body whorl inflated, making shell height less than twice the width (Figs. 5Q-R) 25
 Body whorl not greatly inflated, making shell height approximately twice the width (Figs. 5M-N) 26
25. Moderately strong sinus; shell color red-brown; weak spiral striation on body whorl; aperture margin pale (Fig. 5Q) *V. ventricosa*
 Weak sinus; shell color with slight greenish cast; distinct spiral striation on body whorl; aperture margin usually dark olive-brown to black (Fig. 5R) *V. perryi* 26
26. Shell height >1¾ mm; a weak upper palatal lamella often present (Fig. 5N) *V. tridentata*
 Shell height <1¾ mm; upper palatal lamella absent (Fig. 5M) *V. parvula* 27
27. Shell >2¼ mm tall; angular lamella present (Fig. 5J) but with angular *V. modesta form parietalis*
 Shell <2¼ mm tall; angular lamella absent (Figs. 5C-D, 5O-Q, 6J) 28
28. Shell height less than twice the width, with marked basal inflation (Figs. 5C, 5Q) 29
 Shell height twice the width or more, ovoid (Figs. 5D, 5O-Q, 6J) 30
29. Strong apertural lamellae and sinus; shell translucent (Fig. 5C, but lacking infraparietal) *V. ovata*
 Moderate apertural lamellae and sinus; shell glassy and transparent (Fig. 5Q) *V. ventricosa* 30
30. Shell weakly striate; single depression behind aperture over both palatal lamellae (Fig. 6J) *V. bollesiana*
 Shell smooth; separate slight depressions under each palatal lamella, or none (Figs. 5D, 5O-P) 31
31. Shell surface dull; strong crest; light-colored callus on palatal wall (Fig. 5O) *V. pygmaea*
 Shell surface shiny; crest less prominent; callus of same color as shell (Figs. 5D, 5P) 32
32. Lower palatal lamella inserted more deeply than upper palatal; upper palatal lamella thickened towards aperture; shell shape ovoid (Fig. 5D) *V. binneyana*
 Lower palatal lamella inserted as deeply as upper; upper palatal lamella not thickened towards aperture; shell apex elongate and somewhat conical; strong callus often present in base-rich habitats (Fig. 5P) *V. elatior* 33
33. Shell >2.3 mm tall, shiny with weak striae (Fig. 5J) *V. modesta*
 Shell <2.3 mm tall, shell dull with distinct striae (Fig. 6) 34
34. Shell shape conical with body whorl much wider than the penultimate; color deep cinnamon-red; crest absent; shell striation irregular in strength and spacing. (Fig. 6I) *V. meramecensis*
 Shell shape ovate with body whorl approximately the same width as the penultimate; color yellow-red brown; crest present; shell striation uniform (Figs. 6C-E) 35
35. Upper and lower palatal lamellae short and of same length; shell striation fine, regular; crest weak to moderate (Figs. 6D-E) *V. cristata*
 Lower palatal lamella longer than upper palatal; shell striation coarse, irregular; very strong crest (Fig. 6C) *V. concinnula* 36
36. Angular lamella present (Figs. 6A-B, 6G-H, 6M) 37
 Angular lamella absent (Figs. 6G, 6J-L) 41
37. Basal lamella absent (Figs. 6G, 6M) 38
 Basal lamella present (Figs. 6A-B, 6H) 39
38. Shell ovoid, <1½ mm tall; angular lamella weak/vestigial (Fig. 6G) *V. hebarði*
 Shell cylindrical, >1½ mm tall; angular lamella strong (Fig. 6M) *V. arizonensis* 39
39. Shell cylindrical with bottom two whorls of same width; no callus on palatal wall (Fig. 6H) *V. hamai*
 Shell ovate, body whorl larger than penultimate whorl; weak callus present on palatal wall (Figs. 6A-B) 40
40. Shell narrowly ovate; coarsely striate; usually >1.8 mm tall; apex tapered (Fig. 6A) *V. rugosula*
 Shell broadly ovate; weakly striate; usually <1.8 mm tall; apex domed (Fig. 6B) *V. oralis* 41
41. Basal lamella absent; shell height <1½ mm (Fig. 6G) *V. hebarði*
 Basal lamella present; shell height >1½ mm (Figs. 6J-L) 42
42. Striae indistinct, with shell often appearing smooth under low (×10) magnification; single deep depression over both palatal lamellae; ~1¾ mm tall (Fig. 6J) *V. bollesiana*
 Striae distinct, with shell not appearing smooth under low (×10) magnification; palatal depression weak or absent; most forms >1¾ mm tall (Fig. 6L), with small southern Appalachian forms being ~1¾ mm tall (Fig. 6K) *V. gouldii* 43
43. Callus surrounding at least the upper palatal and often the entire palatal wall; ranging from eastern Ontario to Alaska and south to New Mexico (Fig. 6N) *V. arthuri*
 Callus absent on palatal wall (Figs. 6O-Q) 44

44. Columellar lamella more massive than the parietal; angular lamella strong; lower palatal lamella so deeply inserted that most of it is obscured by the columellar wall; striation fine and sharp (Fig. 6Q) *V. nylanderi*
 Parietal lamella more massive than the columellar; angular lamella weak or absent; lower palatal lamella less deeply inserted so that most is observable in apertural view; striae somewhat rounded (Figs. 6O-P) 45
45. Basal and weak angular lamellae often present; ranging from the Upper Mississippi River valley to eastern Ontario (Fig. 6O) *V. hubrichti*
 Basal and angular lamellae often absent; ranging from Newfoundland and central Manitoba to northern Minnesota, northern Wisconsin, and the New England states; also in Alaska and the Yukon (Fig. 6P) *V. paradoxa*

Vertigo alabamensis Clapp, 1915; Figs. 6R-S, 15B
 (syn. *V. alabamensis conecuhensis* in Pilsbry, 1948 and
V. conecuhensis in Hubricht, 1985)

An obligate acidophile occurring in well-decomposed leaf litter typically caught among low growing shrubs and vines in mesic pineland, pine-wiregrass savanna, and bay forest. This species displays a high degree of seasonality, with all individuals hatching in early spring and coming to adult age from late April to early June. Because they rapidly erode in their acidic habitats, surveys outside this period document few (if any) shells. Populations are readily eliminated by fire management, and the species is now absent from many seemingly appropriate sites which are subjected to high return frequency prescribed burning. Obese individuals with less massive lamellae, equating to *V. conecuhensis* as understood by Hubricht (1985), are found within populations throughout the range of *V. alabamensis*. As populations demonstrate complete intergradation between both morphotypes, we relegate this form to a synonym of *V. alabamensis*.

Vertigo arizonensis (Pilsbry and Vanatta, 1900);
 Figs. 6M, 15C

(syn. *V. gouldii arizonensis* in Pilsbry, 1948)

Individuals favor accumulations of highly decomposed leaf litter, often under maple or Douglas fir, in mid to low elevation forests in the southern Rockies. In the caprock canyons of far northeastern New Mexico, it is limited to mesic forest pockets. While considered a subspecies of *V. gouldii* by Pilsbry (1948), and of no taxonomic merit by Bequaert and Miller (1973) and Metcalf and Smartt (1997), shells of this taxon never intergrade with other sympatric *V. gouldii* subspecies. DNA sequence analysis confirms its status as a full species (Nekola *et al.* 2009).

Vertigo arthuri (von Martens, 1884); Figs. 6N, 15D
 (syn. *V. gouldii basidens* Pilsbry and Vanatta, 1900
 in Pilsbry 1948)

Populations occur in well-decomposed leaf litter in aspen parkland, jack pine forest, and taiga, as well as mesic mixed conifer and aspen groves in the Black Hills and southern Rockies. Long known from two individuals collected in 1882 (Pilsbry 1948, Hubricht 1985), this species is now known to be the most abundant *Vertigo* in aspen forests at the northern limit of the Great Plains (Nekola

2002), ranging as far east as Ottawa, Ontario and as far west as Anchorage, Alaska. Observation of material from across this range demonstrates that *V. arthuri* encompasses the entire morphological range of *Vertigo gouldii basidens*, including populations at the type locality in the Jemez Mountains of northern New Mexico.

Vertigo binneyana Sterki, 1890; Figs. 5D, 16A

Individuals occur in grass thatch and leaf litter in mesic grasslands and adjacent oak-aspen woodlands. Reports of this species from the central plains and to the west of the continental divide appear to be based on misidentified material.

Vertigo bollesiana (Morse, 1865); Figs. 6J, 16B

Found in leaf litter often under shrubs, on cliff-face ledges and boulder tops in mesic upland forest, and mesic microsites in northern white cedar wetlands. This species always shows a strong depression on the outside of the shell over both palatal lamellae. All purported southern Appalachian material seen by the authors lacks this feature and represents misidentified small individuals of *Vertigo gouldii*. As a result, all records of *V. bollesiana* south of Pennsylvania should be considered questionable and be critically reexamined.

Vertigo clappi Brooks and Hunt, 1936; Figs. 6T, 16C

Individuals favor well-decomposed leaf litter and fine soil on shaded boulders, talus, ledges and bases of forested bedrock outcrops.

Vertigo concinnula Cockerell, 1897; Figs. 6C, 16D

East of the Rockies this species is restricted to mesic limestone forest in the Black Hills (Hubricht 1985). To the west, it occurs in well-decomposed leaf litter in mid to high-elevation Douglas fir, aspen, and spruce-fir forests in the Rockies where it often demonstrates considerable tolerance for acidic conditions. While Bequaert and Miller (1973) indicate that this taxon is simply a subspecies of *Vertigo modesta*, both shell morphology and DNA sequence data suggest that it is worthy of species-level distinction (Nekola *et al.* 2009). We retain the use of *concinnula* as the specific epithet for this taxon on the basis of Pilsbry (1948: 979) who considered the prior name of *Vertigo ingersolli* to be "absurdly inadequate."

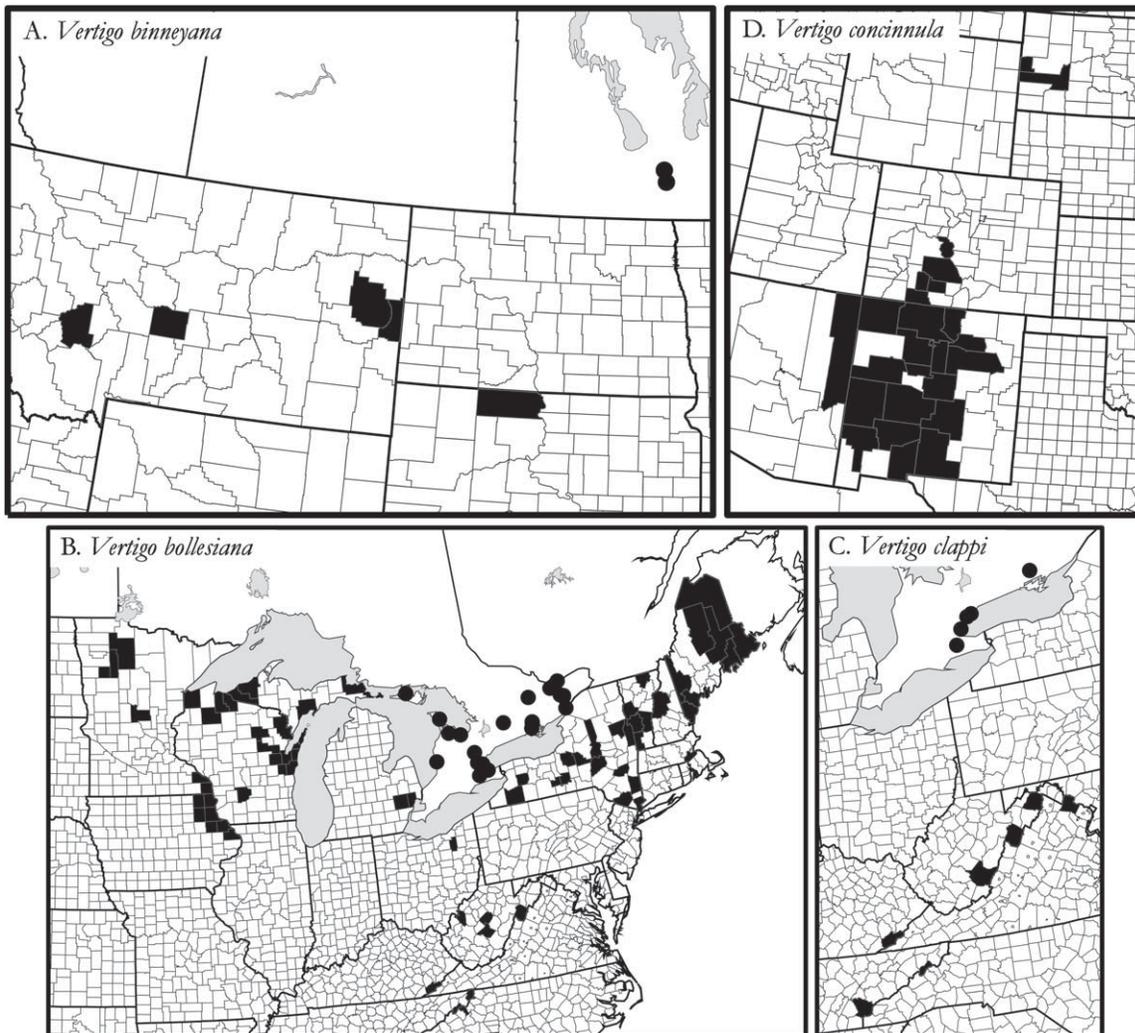


Figure 16. Range maps for *Vertigo binneyana*, *Vertigo bollesiana*, *Vertigo clappi*, and *Vertigo concinnula*.

Vertigo cristata Sterki, 1919; Figs. 6D-E, 17A

Found in well-decomposed leaf litter in a wide variety of northern forest habitats, ranging from wetlands to dry upland rock outcrops. It is particularly common in base-poor sites such as pine and spruce forest, heaths, and *Sphagnum*-dominated peatlands. Throughout its range, two size morphs are present, one with mature shells <1.9 mm tall, and a second with shell heights ranging from 2 to 2¼ mm (Nekola 2001). The holotype at ANSP represents the latter morph. Both morphs often co-occur in sites without presence of intermediates. However, DNA sequence analyses do not support them as being distinct (Nekola *et al.* 2009). Shells of the large morph are similar in size to small *Vertigo modesta* from which they are most readily distinguished by their strong striation and sharper crest. All prior records for *Ver-*

tigo modesta from the New England states (*e.g.*, Pilsbry 1948) likely represent the large morph of *Vertigo cristata*, which we have seen throughout the high mountains of this region. However, we have not seen *Vertigo modesta* south of the Gulf of St. Lawrence.

Vertigo elatior Sterki, 1894; Figs. 5P, 17B

Individuals occur in well-decomposed humid leaf litter and graminoid thatch in a variety of open and wooded wetland habitats, including coastal alvar, wet prairie, fens, wet meadows, tundra, and black ash, tamarack, northern white cedar, and black spruce swamp forests. Although predominately a calciphile in the east, it tolerates acidic conditions in the upper Midwest. After rains or on dewy mornings, individuals commonly adhere to a hand run through damp leaves.

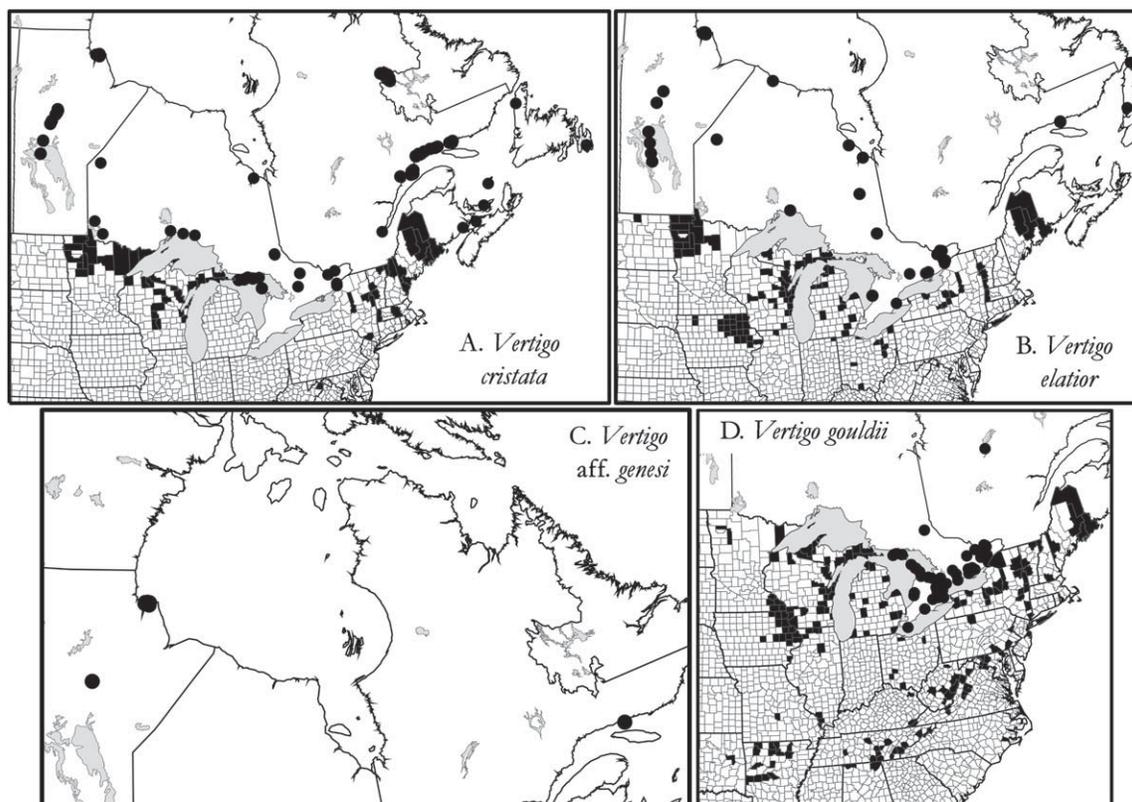


Figure 17. Range maps for *Vertigo cristata*, *Vertigo elatior*, *Vertigo aff. genesii*, and *Vertigo gouldii*.

Vertigo aff. genesii (Gredler, 1856); Fig. 5F, 17C

Found in accumulations of graminoid leaf litter in sedge meadows, turf, and shrub carr in tundra and taiga districts, where it extends as far west as Alaska. This taxon has previously been confused with *Vertigo oughtoni* (see below). However, it appears closest to the European *Vertigo genesii* (see Kerney and Cameron 1979) due to its ovate-conical shell, simple apertural lip without reflexion, indentation or crest, and total lack of apertural lamellae. Whether the North American populations represent *V. genesii* or distinct species remains to be determined.

Vertigo gouldii (A. Binney, 1843); Figs. 6K-L, 17D

Individuals are most abundantly encountered in well-decomposed leaf litter on shaded cliff ledges and bases and on the top of large rocks. They also occur in lower numbers throughout upland and lowland forest, and may be occasionally seen crawling on cliff faces. Small shells <math><1\frac{3}{4}</math> mm in height with reduced striation and dentition from the southern Appalachians and Ozarks have often been misidentified as *Vertigo bollesiana* (see above). The reported populations from Jamaica represent a taxon allied with *Vertigo hebardii* (Gary Rosenberg, pers. comm.).

Vertigo hannai Pilsbry, 1919; Figs. 6H, 18A

In Churchill, Manitoba, individuals are found in well-decomposed thatch and leaf litter of upland tundra, short turf, fens, and wooded wetlands. In northern Alaska, this species also habits upland and riparian forest and parklands. Reports of this species from eastern Ontario alvars are based on a misidentified shell of *Vertigo hubrichti*.

Vertigo hebardii Vanatta, 1912; Figs. 6G, 18B

This species has not been seen alive in over 75 years. Pilsbry (1948) reported it from a series of Keys off the southern Florida coast, with no associated habitat information. Presumably, populations occur in tropical hardwood forest. Hubricht (1985) suggested that it is arboreal because all museum specimens were dead when collected.

Vertigo hubrichti (Pilsbry, 1934); Figs. 6O, 18C

(syn. *V. brierensis* Leonard, 1972 in Frest 1991,

V. hubrichti variabilis Frest, 1991, *V. iowaensis* Frest, 1991)

Found in leaf litter pockets supporting a cool summer microclimate, in particular northern white cedar groves on carbonate bedrock ledges (and occasionally uplands) near the Lake Michigan and Lake Huron shores (Nekola 2004), eastern

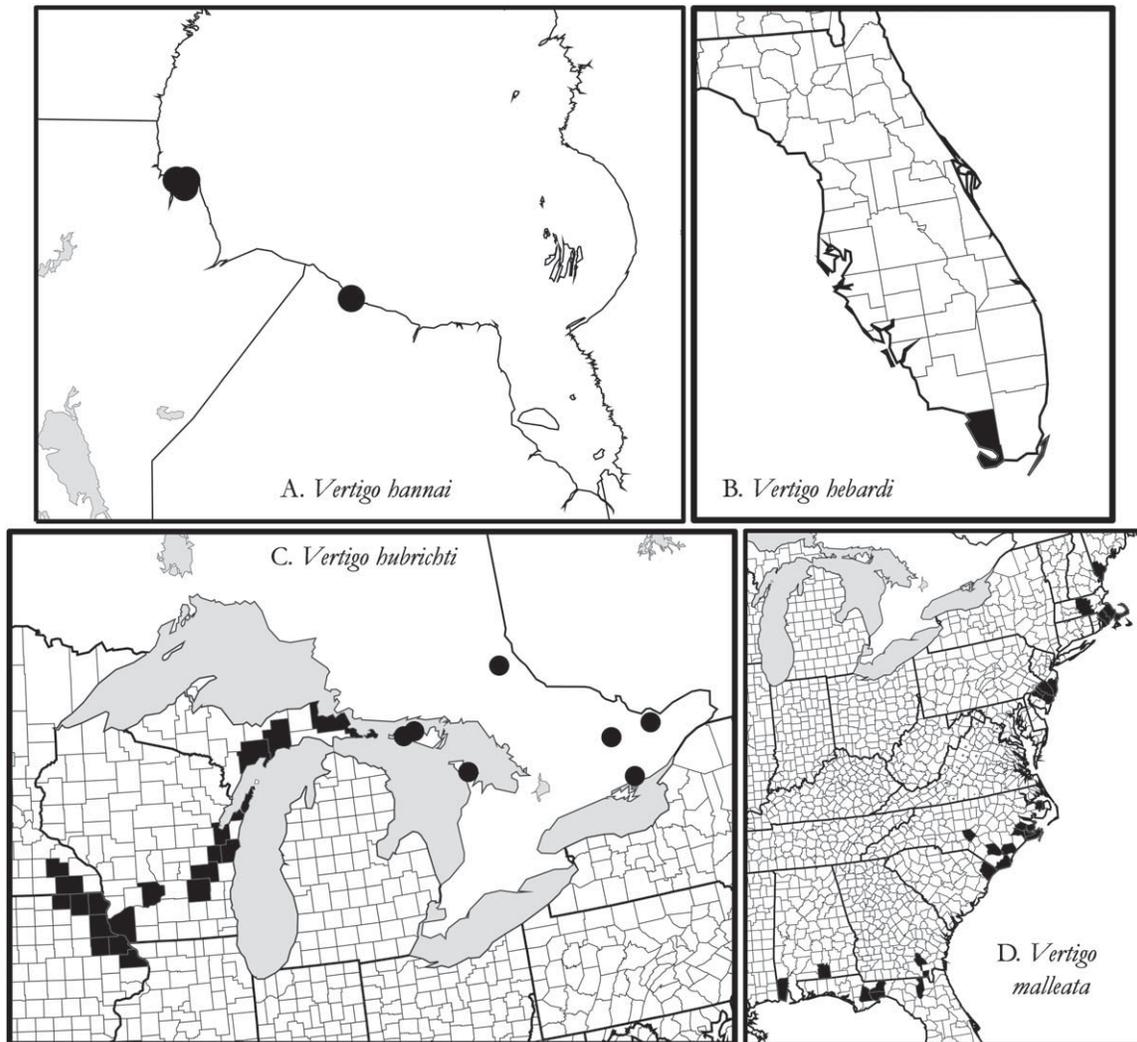


Figure 18. Range maps for *Vertigo hannai*, *Vertigo hebardei*, *Vertigo hubrichti*, and *Vertigo malleata*.

Ontario alvars, and algific talus slopes along the upper Mississippi River valley (Frest 1991). Observations of populations across its range indicate that its normal morphologic variation completely encompasses *Vertigo brierensis*, *Vertigo hubrichti variabilis*, and *Vertigo iowaensis* of Frest (1991). As such, we reduce these forms to synonyms. Although treated as a specific taxon by Hubricht (1985), Frest (1991), and Nekola (2004), we have also noted complete intergradation of *V. hubrichti* with *Vertigo paradoxa* from northeastern Wisconsin through northern Maine.

Vertigo malleata Coles and Nekola, 2007; Figs. 6F, 18D

This obligatory acidophile is primarily found in humid accumulations of ericaceous and pine leaf litter in mesic to wet base-poor habitats along the eastern seaboard such as longleaf pine forest and savanna, bay and Atlantic white cedar forest, heaths, pocosins, and other acid peatlands.

Vertigo meramecensis Van Devender, 1979; Figs. 6I, 19A

A strict calciphile found in decomposed leaf litter on fern and moss-covered ledges and open rock and lichen-covered surfaces of mesic, shaded carbonate cliffs.

Vertigo milium (Gould, 1840); Figs. 5E, 19B

Individuals are found in humid, well-decomposed thatch and leaf litter across a wide variety of mesic to wet sites including rocky woodland, riparian woodland, cliffs, wet prairie, sedge meadows, roadside verges, fens, and swamps.

Vertigo modesta (Say, 1824)

Vertigo modesta appears to be a species complex (Pilsbry 1948). Our own experience with this aggregate in boreal and arctic North America shows the presence of at least three forms that possess consistent morphology and habitat preferences over wide geographical ranges. Their ecology and distribution

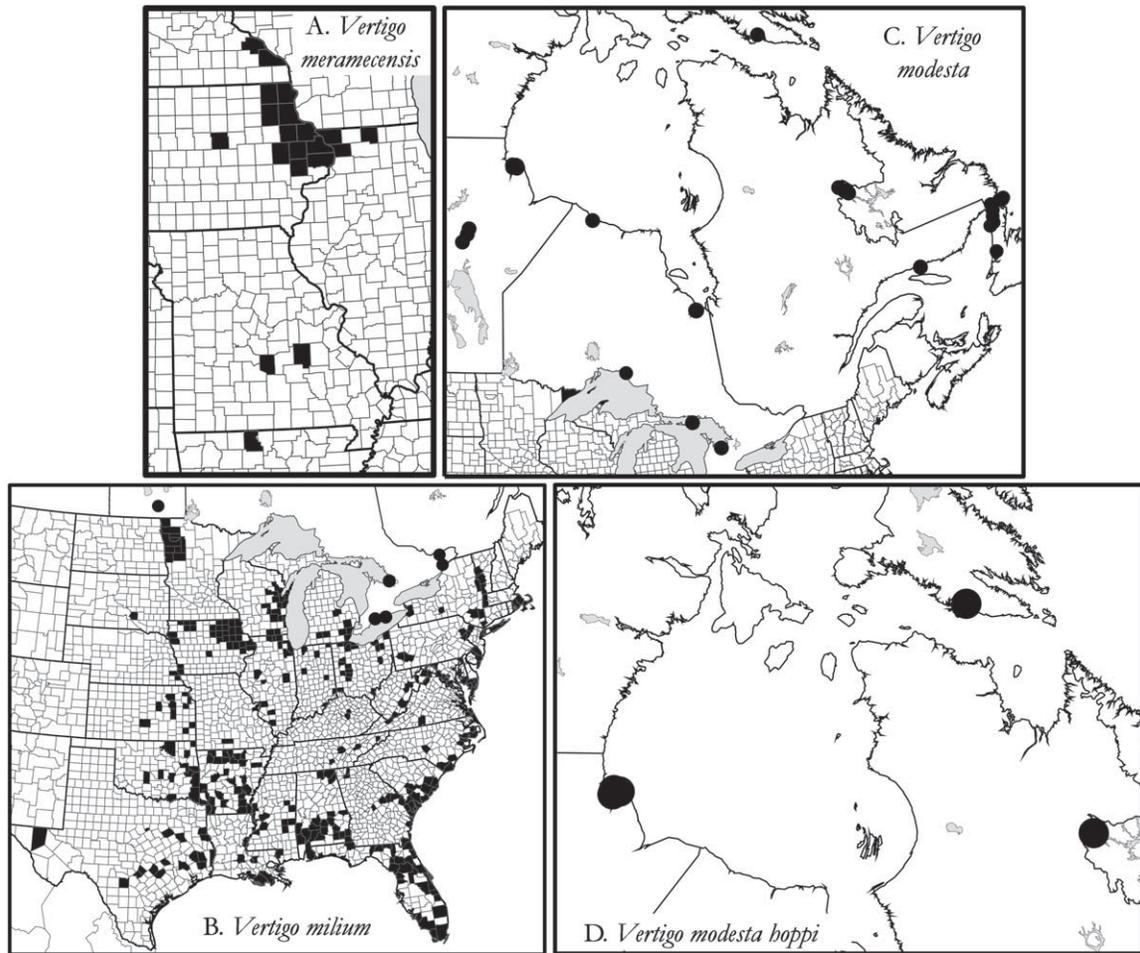


Figure 19. Range maps for *Vertigo meramecensis*, *Vertigo milium*, *Vertigo modesta hoppii*, and *Vertigo modesta modesta*.

are summarized below using a sub-specific nomenclature based on the names used by Pilsbry (1948). Whether they represent distinct species or merely consistent ecophenotypes is not clear, although we have never noted intermediate individuals, even in sites of co-occurrence. Note also that the large *Vertigo cristata* morph has often been confused with *Vertigo modesta modesta* by previous researchers (see above).

Vertigo modesta (Say, 1824); Figs. 5I-J, 19C

Individuals occur in accumulations of humid leaf litter in mesic to wet taiga, notably shrub carr dominated by willow, alder, or birch, and in willow and birch litter accumulations across the entire moisture gradient in tundra. Populations at the extreme southern margin of the range along the Lake Superior shore are limited to cool, mesic lower margins of open talus slopes. Throughout its range, we have noted the presence of individuals with an angular lamella which Pilsbry (1948) termed *V. modesta* form *parietalis*. A marked clinal

reduction in palatal lamellae development is noted towards the north, with the upper palatal being absent from many tundra locations. These shells often also possess a distinctly more red color than their southern counterparts. This form, referred to as *Vertigo modesta arctica* in Europe (Kerney and Cameron 1979), is dominant along the southern shore of Hudson's Bay, southern Baffin Island, and from limestone pavements along the northern shore of the St. Lawrence. It also represents the western Newfoundland material identified as *Vertigo modesta castanea* by Brooks and Brooks (1940).

Vertigo modesta hoppii (Möller, 1842); Figs. 5H, 19D

Populations occur in leaf litter and thatch accumulations in base-poor tundra, sedge meadows, and peatlands. This form has a smaller and more conical shell than is typical for *V. modesta*, with the palatal lamellae being absent. We have noted some populations from Alaska which also lack parietal and columellar lamellae. These individuals can be most

readily separated from *V. aff. genesi* by their larger volume, apertural crest, and shiny luster.

Vertigo modesta ultima Pilsbry, 1948; Figs. 5K, 20A

Individuals occur in wet shrub carr and sedge meadow in northern taiga and tundra. This entity not only differs from *V. modesta* by lacking parietal and palatal lamellae (though a vestigial columellar may be present), but also in its larger size, more inflated whorls, more open umbilicus, and possession of a broadly reflected lip on the columellar wall of the aperture. This form may be identical to *V. extima* from far northern Eurasia (Pilsbry 1948, Pokryszko 2003). DNA sequence analysis will be required to determine their exact relationship.

Vertigo morsei Sterki, 1894; Figs. 5A, 20B

Populations occur in humid, aerated, well-decomposed leaf litter often overlying marl or carbonate bedrock in highly calcareous open wetlands including fens, alvars, and wet prairie. They may also be occasionally found crawling on *Juncus* stems.

Vertigo nylanderi Sterki, 1909; Figs. 6Q, 20C

Individuals occur in sedge and grass thatch and stick-filled depressions in a variety of wooded wetland habitats across the base-status spectrum including northern white cedar (Maine), black ash, tamarack, black spruce (upper Midwest), and shrub carr (Ontario, Manitoba), as well as fens.

Vertigo oralis Sterki, 1898; Figs. 6B, 20D

Populations reside in broadleaf and graminoid leaf litter accumulations, and under logs, in wet woodlands including pool margins in oak-sweetgum forest, red maple swamp, cypress swamp, and riparian and pocosin scrub.

Vertigo oscariana (Sterki, 1890); Figs. 5L, 21A

Individuals occur in well-decomposed accumulations of broadleaf and pine litter in mesic-wet woodlands and shaded rock outcrops. Habitats range from montane hardwood forest in the Appalachians to oak-pine-bay bottomland woodland along the Gulf Coast to acid pine forest in Arkansas, Louisiana, and Texas. Hubricht (1985) reported it from the undersides of palmetto leaves.

Vertigo oughtoni (Pilsbry, 1948); Figs. 5G, 21B

(syn. *Vertigo alpestris oughtoni* in Pilsbry, 1948)

An arctic calciphile which occurs in thin grass and sedge thatch in flushes, calcareous fens, seeps, and shrub carr. Pilsbry (1948) described *V. oughtoni* as a subspecies of the Eurasian *Vertigo alpestris* Alder, 1838, but the two taxa share little in common in terms of shell morphology or habitat preferences (Kerney and Cameron 1979). It appears most closely allied to *V. parcedentata* (A. Braun, 1847), with which it shares a columnar shell with a blade-like lower palatal lamella, a reduced (or absent) columellar and upper palatal lamella, a simple apertural lip without reflection and marked

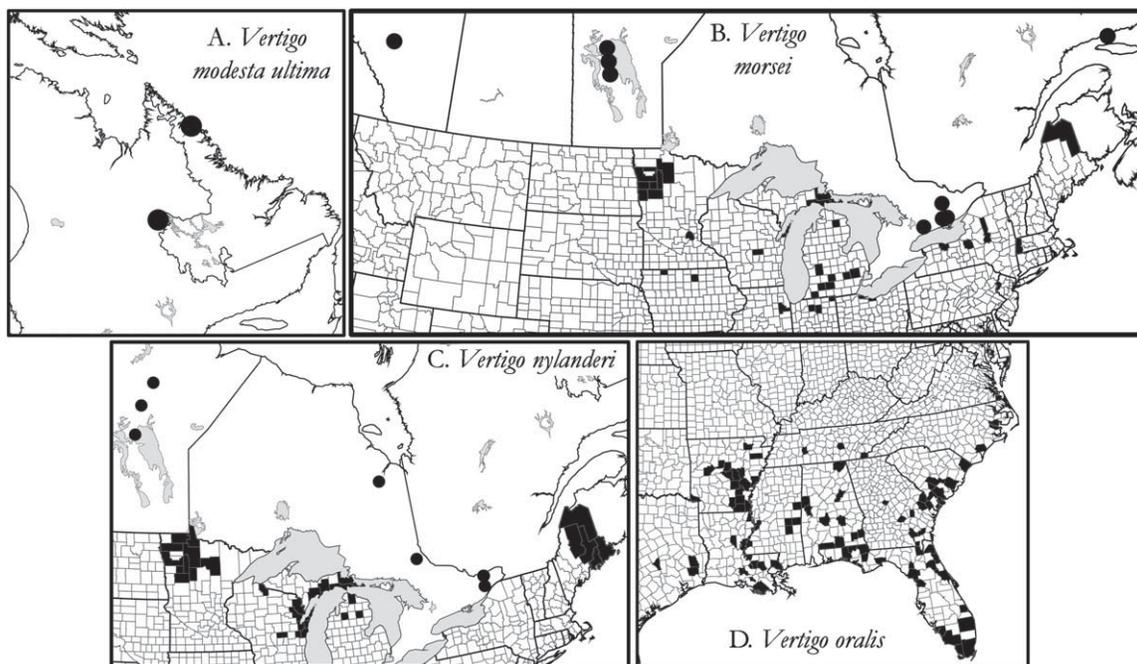


Figure 20. Range maps for *Vertigo modesta ultima*, *Vertigo morsei*, *Vertigo nylanderi*, and *Vertigo oralis*.

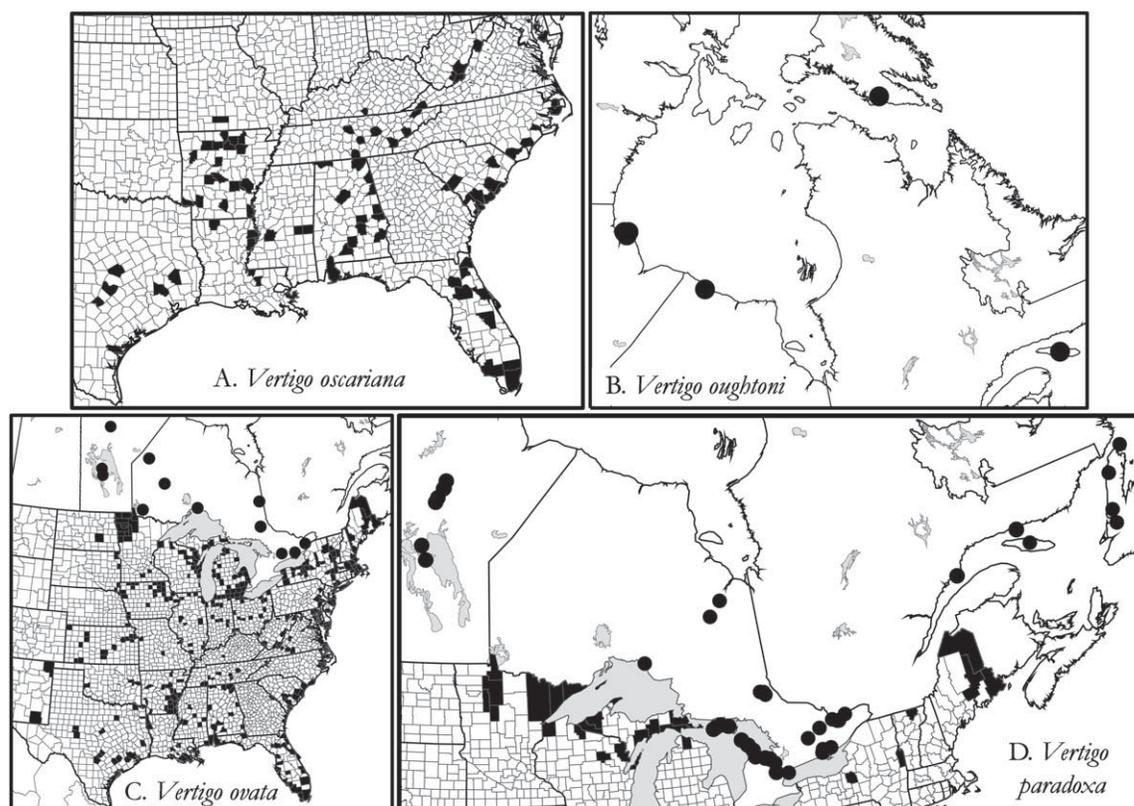


Figure 21. Range maps for *Vertigo oscariana*, *Vertigo oughtoni*, *Vertigo ovata*, and *Vertigo paradoxa*.

preference for moist, base-rich meadows. While *V. oughtoni* differs from *V. parcedentata* by having a glassy shell luster and lacking any trace of a depression over the lower palatal, it is unknown how much these features are under environmental control. Determination of the status of these two taxa will require additional DNA sequence analysis.

Vertigo ovata Say, 1822; Figs. 5C, 21C

Populations are primarily found in graminoid litter and on cattail leaves in swamps, sedge meadows, wet and mesic prairie, low calcareous meadows, river banks, lakeshores, roadside ditches, and wooded wetlands. It is also occasionally found on bedrock outcrops, upland forest, and upland grassland habitats. It can ascend vegetation to approach 1 m off the ground.

Vertigo paradoxa (Sterki, 1900); Figs. 6P, 21D

Most frequently found in white cedar litter pockets on calcareous bedrock ledges, dry microsites in white cedar wetlands, and in thatch on calcareous alvars, seaside turf, and shoreline bedrock outcrops. This taxon introgresses with both *Vertigo arthuri* and *Vertigo hubrichti* in regions of range overlap (see above). Reports from the Black Hills (Frest and Johannes 1993) are based on *V. arthuri* with a poorly developed apertural callus.

Vertigo parvula Sterki, 1890; Figs. 5M, 22A

Individuals occur in accumulations of well-decomposed leaf litter in base-rich cove forests, rock outcrops, and talus slopes at mid-low elevations in the central Appalachians and adjacent Piedmont.

Vertigo perryi Sterki, 1905; Figs. 5R, 22B

Populations reside in humid accumulations of sedge leaf litter on hummock sides in base-poor wet meadows and *Sphagnum* peatlands as well as in deciduous leaf litter in base-poor red maple, Atlantic white cedar, and northern white cedar wetland forests. Pilsbry (1948) reported that in wet weather individuals will crawl on living vegetation over a third of a meter above the ground; we have observed this behavior to be most pronounced on dead sedge leaves.

Vertigo pygmaea (Draparnaud, 1801); Figs. 5O, 22C

Individuals occur in graminoid thatch and leaf litter accumulations in a variety of anthropogenically disturbed grasslands including roadsides, old fields, yards, and abandoned quarries. It may also occur in more undisturbed habitats such as upland forest, bedrock cliffs, tallgrass prairie, sedge meadows, and acid bogs. We suspect that these

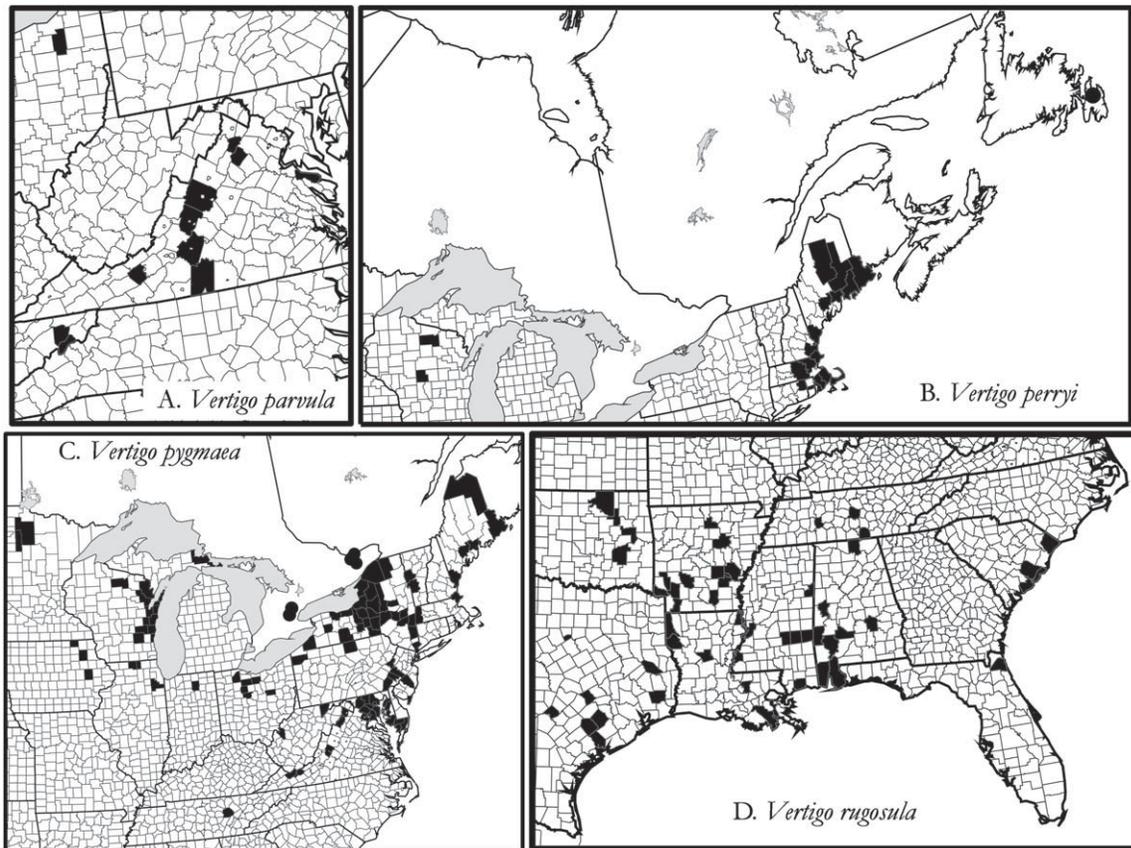


Figure 22. Range maps for *Vertigo parvula*, *Vertigo perryi*, *Vertigo pygmaea*, and *Vertigo rugosula*.

populations represent Eurasian waifs which were brought to North America over a century ago.

Vertigo rugosula Sterki, 1890; Fig. 6A, Fig. 22D
(syn. *Vertigo wheeleri* Pilsbry, 1928)

Found primarily in graminoid thatch in short turf and scrub such as prairie, mown roadsides, yards, and riparian corridors. It also occasionally occurs in rocky forest. After observing types at ANSP, we agree with Hubricht (1974) that *V. wheeleri* simply represents a population of small *V. rugosula* individuals.

Vertigo teskeyae Hubricht, 1961; Figs. 5B, 23A

Individuals are most commonly seen crawling on open mud and water-saturated logs in floodplain forests and along river, pond, and lake shores following water level drawdown in mid to late summer. They are also occasional in leaf or grass litter adjacent to boggy pools and streams.

Vertigo tridentata Wolf, 1870; Figs. 5N, 23B

Populations are found in graminoid thatch on calcareous prairie and bedrock glades, in well-decomposed leaf litter

accumulations on shaded cliff ledges and talus, and occasionally in upland forest. Hubricht (1985) reported it crawling on mints, while Pilsbry (1948) mentioned it foraging over a meter off the ground on “weeds”. We have seen it crawling on *Sedum* spp. on limestone cliff ledges in the Ozark Mountains of Arkansas.

Vertigo ventricosa (Morse, 1865); Fig. 5Q, 23C

Individuals occur in accumulations of humid, well-decomposed graminoid and broadleaf plant litter in moderately to highly acidic wooded and open wetlands, in particular lowland northern white cedar and red maple forest, sedge meadows, *Sphagnum* peatlands, and poor fens. Although reported from as far west as central Iowa (Hubricht 1985), we have observed no specimens referable to it west of central New York state and eastern Ontario in either the field or from museum collections. All of this western material represents immature *Vertigo elatior* with incompletely formed apertural lamellae. The two species do co-occur in some New England sites. While distinguishing them can be quite challenging, *V. elatior* possesses a taller

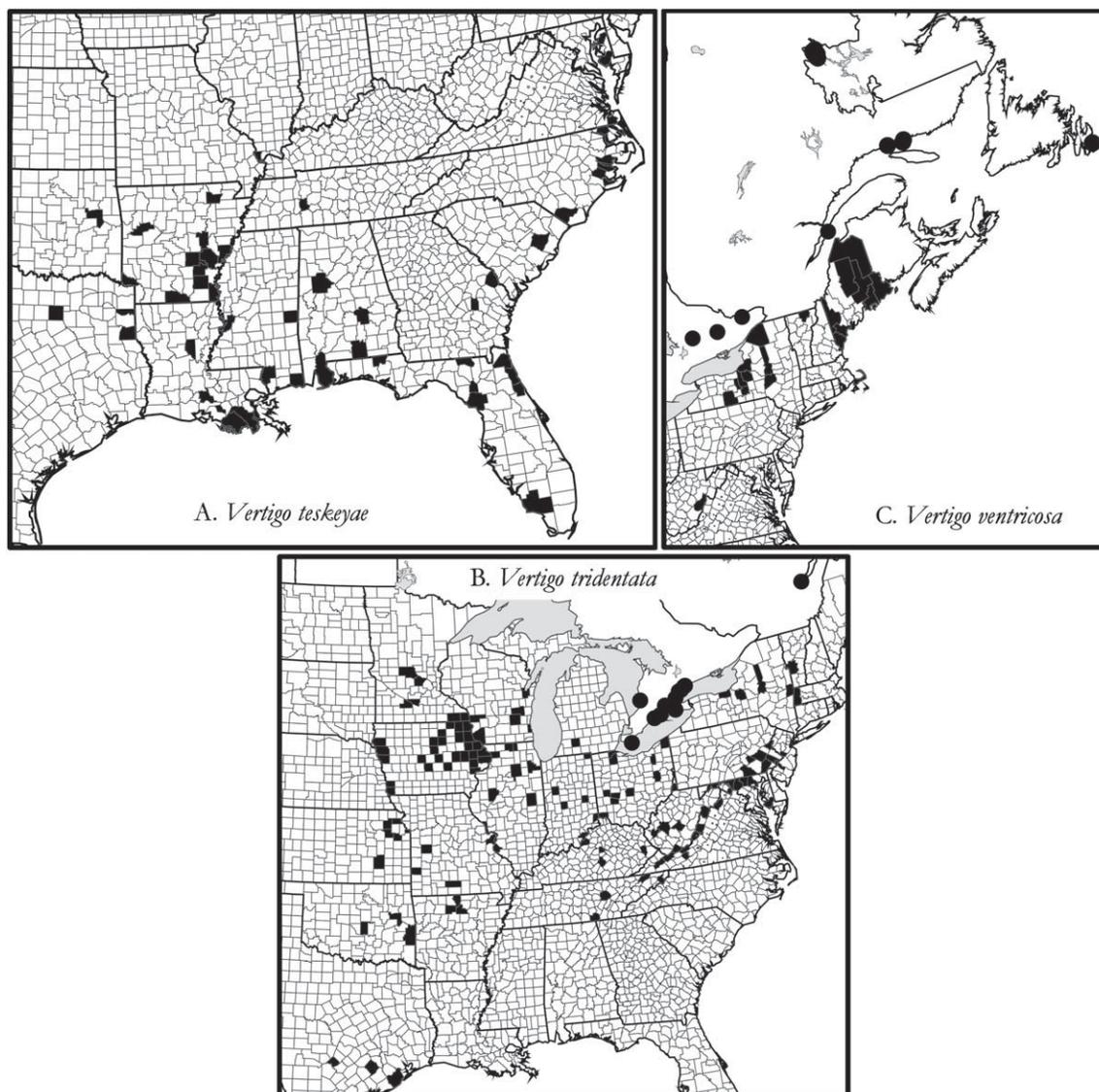


Figure 23. Range maps for *Vertigo teskeyae*, *Vertigo tridentata*, and *Vertigo ventricosa*.

and somewhat more conical upper half of the shell, whereas *V. ventricosa* is ovate in outline. The apertural lamellae and sinulus are also more weakly developed in *V. ventricosa*. Future investigations of these two taxa should be initiated to determine whether they represent ecophenotypes of the same species.

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APPENDIX 1. Illustrated glossary of important terms.

Many of the terms used in the keys are common to the descriptions of most land snail shells. We have chosen to not define all these here as many good sources for this information exist. Interested readers are referred in particular to the excellent illustrated glossary in Kerney and Cameron (1979). However, the use of some of these terms is essentially limited to pupillids, and a review of them is essential for successful use of the taxonomic keys:

Alvar: a grassland community residing on a limestone plain with thin or no soil.

Angular lamella: the tooth on the parietal wall of the aperture to the right of the parietal lamella in dextral shells (Fig. 24).

Apex: the uppermost 2-3 whorls of the shell (Fig. 25).

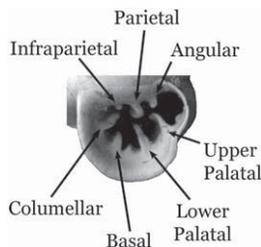


Figure 24. Location of the major apertural lamellae used in pupillid identification, illustrated through use of a *Vertigo ovata* SEM image.

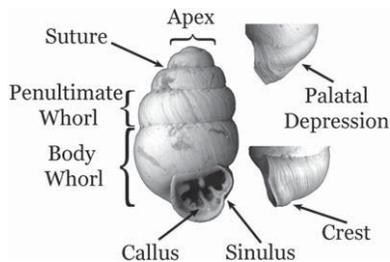


Figure 25. Major shell features used to identify pupillid taxa, illustrated through use of SEM images of *Vertigo elatior* (left), *Vertigo bollesiana* (upper right), and *Vertigo cristata* (lower right).

Basal lamella: the tooth on the bottom left side (in dextral shells) of the aperture below the columellar lamella (Fig. 24).

Body whorl: the final full whorl in an adult shell (Fig. 25).

Callus: calcified thickening of the palatal wall of the aperture, often deposited between lamellae (Fig. 25).

Columellar lamella: tooth on the columellar wall of the aperture (Fig. 24).

Columellar wall: the left side of the aperture in dextral shells.

Crest: a bowing out of the shell immediately in back of the aperture as seen in side view (Fig. 25).

Ericaceous: plants within the Ericaceae, or heath family.

Infra-parietal lamella: the tooth on the parietal wall to the left of the parietal lamella in dextral shells (Fig. 24).

Lower palatal lamella: lowermost of the two major teeth often found on the palatal wall (Fig. 24).

Palatal depression: indentation of the shell surface at the location of the palatal lamellae (Fig. 25).

Palatal wall: the right side of the aperture in dextral shells.

Parietal lamella: major tooth in the middle of the parietal wall of the aperture (Fig. 24).

Parietal wall: upper side of the aperture.

Penultimate whorl: the next to the last whorl in an adult shell (Fig. 25).

Pocosin: a peatland of the southeastern U.S.A. with acid soils and semitropical vegetation.

Shrub carr: a wetland community dominated by tall shrubs.

Sinulus: indentation of the aperture margin along the palatal wall (Fig. 25).

Suture: indentation of the shell surface where two whorls meet (Fig. 25).

Upper palatal lamella: uppermost of the of the two major teeth often found on the palatal wall (Fig. 24).