Distribution and Ecology of *Vertigo cristata* (Sterki, 1919) in the Western Great Lakes Region

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Abstract: Vertigo cristata, previously unreported from the U. S. A., was located at 84 sites in northern Minnesota, northern and southwestern Wisconsin, the Upper Peninsula of Michigan, and also in Ontario on Manitoulin Island and the northern tip of the Bruce Peninsula. It was found in nine habitats (carbonate cliffs, lakeshore carbonate ledges, igneous cliffs, sandstone cliffs, rocky woodlands, igneous lakeshore outcrops, swamp forests, tamarack wetlands, and white cedar wetlands) and was essentially confined to areas north of 45°N. It was most frequently encountered on igneous rock outcrops, where it was observed in over 67% of surveyed sites. V. cristata individuals were easily separated from V. gouldi (A. Binney, 1843), with which it has often been lumped as a subspecies, as well as from other central U. S. Vertigo taxa, including V. modesta modesta, V. paradoxa, and V. meramecensis.

Key Words: Vertigo cristata, Great Lakes, biogeography, ecology

Vertigo cristata was first described (as V. gouldi cristata) by Sterki in 1919 from Quebec. Pilsbry (1948) considered it a 'strongly marked' race, and listed an additional site along the north shore of Lake Superior. Oughton (1948) reported it from 'probably the entire province' of Ontario, but expressed difficulty separating it from V. gouldi and V. paradoxa. Frest and Johannes (1991) treated V. cristata as a full species when comparing it to Black Hills V. paradoxa. V. cristata has not been reported from regions to the south (eastern U.S.: Hubricht, 1985), east (New Brunswick: Clarke et al. 1968), or west (Alberta: Platt, 1980; Van Es and Boag, 1981) of the Great Lakes.

In the course of analyzing land snail faunas in the western Great Lakes region, we encountered individuals referable to *Vertigo cristata* at 84 stations. Using these observations, a more thorough consideration can be made of its: (1) distribution; (2) shell morphology; (3) preferred habitats; and (4) molluscan associates.

METHODS AND MATERIALS

A total of 324 sites were surveyed for their terrestrial gastropod faunas within the states and provinces of Illinois, Iowa, Michigan, Minnesota, Ontario, New York, and Wisconsin. Sites were chosen for survey if they represented typical examples of their respective habitat, and

(except for anthropogenic sites) were undisturbed. Collections were made from 22 discrete habitat types, including carbonate cliffs, lakeshore carbonate ledges, igneous cliffs, algific talus slopes, fens, lakeshore alluvial banks, rocky woodlands, calcareous open meadows, low-land woods, alvars, cobble beaches, shale cliffs, carbonate glades, old fields, tallgrass prairie, aspen parklands, sand-stone cliffs, and open dunes. Descriptions of these habitat types are found in Nekola (1999). The location of each sample was marked on USGS (or equivalent) 7.5 minute topographic maps and digitized.

Documentation of terrestrial gastropods from each site was accomplished through standard soil litter sampling procedures, as outlined in Nekola (1999). All recovered, identifiable shells from each site were assigned to species (or subspecies) using the author's reference collection and the Hubricht collection at the Field Museum of Natural History. All specimens have been catalogued and are housed in collections maintained at the University of Wisconsin - Green Bay.

RESULTS AND DISCUSSION

Distribution

The 84 encountered Vertigo cristata populations were found in all four major political divisions of the western Great Lakes: 37 from northern Minnesota, 22 from the

Table 1. Vertigo cristata occurrences in the western Great Lakes region.

State / Province	# occurrences	# sampled	Coccurrence		
Minnesota	37	52	71.2		
Michigan	. 22	82	25.9		
Wisconsin	20	204	9.8		
Ontario	5	22	22.3		

Upper Peninsula of Michigan, 20 from northern and southwestern Wisconsin, and five from southern Ontario on Manitoulin Island and the Bruce Peninsula (Table 1; Fig. 1). The southernmost population occurs on a north-facing sandstone cliff at Camp Douglas in southwestern Wisconsin (43°55'N). The next most southern populations occur on wooded lakeshore carbonate outcrops at Toft Point (45°4'), Marshall's Point (45°8'N) and Peninsula State Park on the Door Peninsula in northeastern Wisconsin (45°9'N) and on the northern tip of the Bruce Peninsula in Ontario (45°14'N). The Michigan, Minnesota, and Wisconsin populations represent the first reported modern occurrences of this taxon from the U. S. A.

The occurrence frequency of *Vertigo cristata* among all sampled sites in these states and provinces ranged from almost 10% in Wisconsin to 71% in Minnesota. The high frequency of this taxon within Minnesota is likely due to the facts that: (1) all sites inventoried were north of 45°N;

and (2) the great majority of sampled habitats represented bedrock outcrops. The apparent limitation of *V. cristata* in this survey to areas near the Great Lakes is almost certainly an artifact of the sampling regime, which principally targeted sites with high-Ca bedrock exposures (carbonate or mafic/ultramafic igneous rock). In this region, such habitats are most commonly encountered within 40 km of the lakeshore.

The presence of Vertigo cristata at lower frequencies in other forested habitats (see below) suggests that it will eventually be found throughout a region bordered to the south by 45°N, to the east by the eastern border of the Province of Quebec, and to the west by the aspen parklands and tallgrass prairie of Manitoba and northwestern Minnesota. Current and historical data do not clearly indicate how far north and northwest this taxon will be found in Quebec, Ontario, and Manitoba, although it seems probable that it will occur north to forest-tundra border along the southern shore of Hudson Bay. Outlying populations at or south of 45°N are likely limited to areas that are microclimatically protected from warm summer temperatures. The southernmost Wisconsin and Ontario sites are limited to areas adjacent to the Great Lakes shore and/or north-facing cliffs. Maximum summer temperatures of lakeshore habitats are known to be depressed over areas farther inland due to their proximity to cold lake waters (Curtis, 1959).

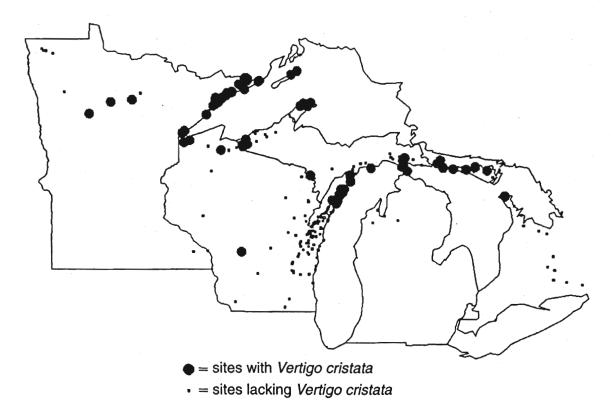


Fig. 1. Vertigo cristata distribution in the western Great Lakes.

Shell Morphology

Vertigo cristata was clearly marked and distinct. As such, I follow Frest and Johannes (1991) in considering it a full species. V. cristata is easily distinguished from V. gouldi (Fig. 2) by: (1) never possessing a basal lamella; (2) possessing a strong crest; (3) having the parietal lamella pointed towards the lower palatal, rather than the upper palatal (as in V. gouldi); and (4) having more closely spaced, regular, and sharp shell striations. Unlike Oughton (1948), I did not observe any individuals intermediate between V. cristata and V. gouldi, even at the 23 sites of cooccurrence. As I have not yet analyzed Oughton's material, the disposition of his intermediate individuals remains unclear. While Oughton reported V. cristata from 'probably the entire province,' I have been unable to locate it in Ontario south of the northernmost tip of the Bruce Peninsula. As such, his intermediate individuals may likely represent misidentified V. bollesiana, V. gouldi, or V. paradoxa, taxa that are more broadly distributed in southern Ontario.

Considerably more trouble was encountered in separating some of the largest Vertigo cristata individuals from the smallest V. modesta modesta. These two taxa were distinguished by the weaker crest (when present), more irregular shell striations, and more massive apertural lamellae of V. m. modesta as compared to V. cristata (Fig. 2). Additionally, a few individuals were found to approach V. paradoxa somewhat in appearance. These two taxa were distinguished using the more deeply set lower palatal lamella as compared to the upper, and lack of a crest in V. paradoxa. V. cristata, however, has a strong crest and lower and upper palatal lamellae set at equal depths into the aperture.

In eastern North America, Vertigo cristata appears

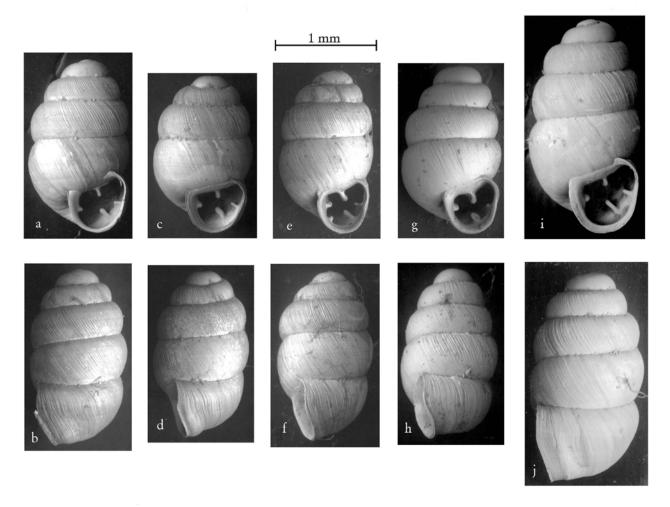


Fig. 2. Scanning electron micrographs of Vertigo cristata and related taxa. a, b: V. cristata, Mt. Josephine, Cook County, Minnesota, U. S. A. (89°39'14" W, 47°58'50" N), #4559. c.d. V. cristata, Toft Point, Door County, Wisconsin, U. S. A. (87°5'5" W, 45°4'40" N), #1061. e.f.: V. gouldi, Toft Point, Door County, Wisconsin, U. S. A. (87°5'5" W, 45°4'40" N), #1062. g.h.: V. meramecensis, Dark Hollow, Linn County, Iowa, U. S. A. (91°30' W, 41°53'54" N), #376. i.j.: V. modesta modesta, Metcalf Rock, Grey County, Ontario, Canada (80°26'31" W, 44°25'3" N), #2543. Micrographs were taken with a Hitachi S-2460N Scanning Electron Microscope in N-SEM Mode (10 Pa; 22 kV) with a backscatter detector and #2 Gamma Correction.

most similar to V. meramecensis VanDevender, 1979, which occurs in the Ozark Plateau of Missouri and Arkansas (Hubricht, 1985, Brian Coles, pers. comm.) and the Paleozoic Plateau of northeastern Iowa, southeastern Minnesota, and northwestern Illinois (Frest, 1986, 1991). Both of these taxa range from 1.7-2.2 mm in size, have strong shell striations, and possess four principle apertural lamellae, with the parietal being pointed at the lower palatal (Fig. 2). However, V. meramecensis differs from V. cristata in: (1) lacking a crest; (2) having a dark cinnamon-red shell color (rather than yellowish); (3) occasionally possessing a weak basal lamella; and (4) having the body whorl being wider than the penultimate (Frest and Fay, 1981). While no co-occurring populations of V. cristata and V. meramecensis were found, both taxa occur on cool cliffs in the Paleozoic Plateau, and such sites may eventually be located in southeastern Minnesota or southwestern Wisconsin.

Shells of *Vertigo cristata* fell into two size classes, with one ranging from 1.7-1.9 mm, and another from 2.1-2.2 mm (Fig. 2). The larger form appeared limited to northeastern Minnesota and the Keweenaw Peninsula of Michigan. As shells in these two groups appeared to be otherwise identical, these races were not considered separate taxonomic entities. However, further morphometric and genetic analyses may be warranted to help elucidate their true status.

Habitat Preferences

Vertigo cristata populations were located from 9 different habitats (Table 2), with a preference being shown for wooded outcrops of igneous rock: 67% of surveyed igneous bedrock outcrop sites supported populations, followed by igneous lakeshore outcrops (50%), sandstone cliffs (50%), carbonate lakeshore ledges (43.5%), white cedar wetlands (13.3%), carbonate cliffs (12.6%), tamarack wetlands (10.3%), rocky woodlands (8%), and swamp forest (6.3%). Most sites were wooded, with eastern white cedar (Thuja occidentalis L.) being commonly present. On bedrock outcrops, V. cristata was most often found on soil-

Table 2. Habitats of Vertigo cristata in the western Great Lakes region.

Habitat type	# occurrences	# sampled	% occurrence
Igneous Cliff	50	74	67.6
Carbonate Cliff	13	103	13.7
Carbonate Lakeshore Ledge	10	23	31.6
Tamarack Wetland	3	29	5.0
Rocky Woodland	2	26	9.1
White Cedar Wetland	2	15	20.0
Igneous Shoreline	2	4	50.0
Sandstone Cliff	1	2	50.0
Swamp Forest	l	16	6.3

covered ledges, while in wetland sites it was most frequently encountered in deciduous leaf accumulations above the high-water line.

Associated Species

Across all habitats, 54 land snail species were found to co-occur with Vertigo cristata (Table 3). Eight of these (Discus catskillensis, Zonitoides arboreus, Striatura milium, Nesovitrea binneyana, Punctum minutissimum, Euconulus fulvus, V. paradoxa, and Strobilops labyrinthica) were found in 50% or more of the V. cristata sites. Of the remaining, 39 (over 70% of the total) were found in fewer than 25% of V. cristata sites. None of these associated taxa was found only with V. cristata.

The number of co-occurring taxa ranged from 41 in carbonate cliffs to 12 in igneous lakeshore outcrops (Table 3). Mean richness for sites supporting *Vertigo cristata* varied from 25 in swamp forest and 18.5 on carbonate cliffs to 9.5 and 9.4 on igneous lakeshore outcrops and cliffs. Thus, the sites where *V. cristata* is most frequently encountered are also, on average, the most species-poor.

The habitats supporting Vertigo cristata have two general assemblages (Table 3). Wooded rock outcrop sites (carbonate cliffs, carbonate lakeshore ledges, igneous cliffs, sandstone cliffs, rocky woodlands, and igneous lakeshore outcrops) support not only the most common associates, but also typical western Great Lakes region wooded bedrock outcrop taxa such as Anguispira alternata, Carychium exile, Helicodiscus shimeki, Paravitrea multidentata, Stenotrema fraternum, V. bollesiana, V. gouldi, V. hubrichti, and Zoogenetes harpa. Wooded wetland habitats for V. cristata (swamp forest, tamarack wetland, and white cedar wetland), harbored the most common associates as well as typical western Great Lakes region wooded wetland taxa such as C. exiguum, Euconulus alderi, Gastrocopta tappaniana, V. elatior, and V. nylanderi.

Most of the associated species have northeastern or cosmopolitan modern ranges (Hubricht, 1985). However, seven (Hendersonia occulta, Vallonia gracilicosta, Vertigo hubrichti, V. modesta modesta, V. modesta parietalis, Vertigo n.sp. sensu Frest, 1991, and V. paradoxa) had extensive eastern U.S. ranges during the late Pleistocene, even though they are largely limited in modern times to the Great Lakes region (Frest, 1991; Frest and Johannes, 1991). Given that almost 15% of V. cristata's associates represent such potential glacial relicts, it is surprising that it is not more strongly represented in the Pleistocene record. Neither Hubricht (1985) nor Frest and Dickson (1986) report Pleistocene fossil sites. The only published fossil occurrence is from Illinoian-age sediments in southern Illinois (Miller et al., 1994). This situation is reminiscent of V. meramecensis, which also regularly occurs with glacial

Table 3. Species associated with Vertigo cristata in the western Great Lakes region. Nomenclature follows Hubricht (1985). Attable 3. Species associated with Vertigo cristata in the western Great Lakes region. Nomenclature follows Hubricht (1985).

Species	Number of Occurrences in Habitat:										
		1		3	4	5	6	7	8	9	Total
Discus catskillensis (Pilsbry, 1898)		13	9	43	1	2	2	1	3	2	76
Zonitoides arboreus (Say, 1816)	-	12 .	9	44	1	2		1	2	. 2	73
Striatura milium (Morse, 1859)		10	10	31	1	2	2	1	3	1	61
Nesovitrea binneyana (Morse, 1864)		8	6	40	1		I	1	2	1	60
Punctum minutissimum (ILea, 1841)		13	10	24	1	2	2	1	3	2	58
Euconulus fulvus (Müller, 1774)		11	9	25	1	1	1		1		49
Vertigo paradoxa Sterki, 1900		9	2	29		1	1		1		43
Strobilops labyrinthica (Say, 1817)		12	8	13	1	2	1	1	2	2	42
Anguispira alternata (Say, 1817)		13	9	18		1					41
Columella simplex (Gould, 1841)		10	9	12	1	2	1	1	2	1	39
Zoogenetes harpa (Say, 1824)		1	1	29		. 2	2				35
Striatura exigua (Stimpson, 1847)		3	4	20		1	1	1	3	1	34
Vertigo gouldi (A. Binney, 1843)		13	8	5		î	•	•		-	27
Helicodiscus shimeki Hubricht, 1962		7	8	8		•			1	1	25
Carychium exile H.C.Lea, 1842		5	5	9				1	2	1	23
Discus cronkhitei (Newcomb, 1865))		5	2	10				•	2	•	19
Vertigo bollesiana (Morse, 1865)		6	6						2		17
- · · · · · · · · · · · · · · · · · · ·			2	5 4	1	2	2	1			
Helicodiscus parallelus (Say, 1817)		3	. 7	4	1	2	2	1			15
Vertigo hubrichti (Pilsbry, 1934)		8		,				,	•		15
Nesovitrea electrina (Gould, 1841)		ı	1	6		,		1	3	1	13
Paravitrea multidentata (A. Binney, 1840)		6	2	3		1					12
Succinea ovalis Say, 1817		2	1	9							12
Vallonia gracilicosta Reinhardt, 1883		9	1					1	1		12
Vertigo n.sp. sensu Frest, 1991		7	.5								12
Cochlicopa lubrica (Müller, 1774)	•	1 .	1	5	1	1			1	1	11
Gastrocopta pentodon (Say, 1821)		5	1	3	I			1			11
Glyphyalinia indentata (Say, 1823)		5	1	1	1	1					9
Planogyra asteriscus (Morse, 1857)			3	3					1	2	9
Striatura ferrea Morse, 1864			3	3	2					1	9
Stenotrema fraternum fraternum (Say, 1824)		5	2	1							. 8
Carychium exiguum (Say, 1822)								1	3	2	6
Cochlicopa lubricella (Porro, 1838)				2	1	1		1			6
Gastrocopta contracta (Say, 1822)		4			1			1			6
Vitrina limpida Gould, 1850		3		1		1	1				6
Euconulus polygyratus (Pilsbry, 1899)		2	2			1					5
Vertigo modesta modesta (Say, 1824)		1		4							5
Deroceras laeve (Müler, 1774)		2		1				1			4
Euconulus alderi (Gray, 1840)		_		-				î	2	1.	4
Gastrocopta tappaniana (C.B. Adams, 1842)								1	3	-	4
Triodopsis albolabris (Say, 1816)		2	2					-	-		4
Vallonia costata (Müller, 1774)		ĩ	2								3
Vertigo elatior Sterki, 1894		•	-					1	2		3
Vertigo modesta parietalis (Ancey, 1887)				3				•	~		3
Vertigo modesia parteians (Ancey, 1887) Vertigo nylanderi Sterki, 1909				3				1	2		3
Cochlicopa morseana (Doherty, 1878)		1		1					4		2
Glyphyalinia rhoadsi (Pilsbry, 1899)		i I	1	1							2
		1	1		,						
Hawaiia minuscula (A. Binney, 1840)					1			1			2
Catinella avara (Say, 1824)								1			1
Gastrocopta holzingeri (Sterki, 1889)		1									I .
Guppya sterkii (Dall, 1888)		1							,		1
Hendersonia occulta (Say, 1831)		1									1
Punctum n.sp. sensu Frest, 1990								1			1
Vallonia pulchella (Müller, 1774)									1		1
Vertigo arthuri (von Martens, 1884)									1		1
Total Number of Associates		41	34	32	15	19	12	24	24	16	
Average Species Richness per Site		18.5	16.9	9.4	16	14.5	9.5	25	16.7	12	

^{1 =} Carbonate Cliff, 2 = Carbonate Lakeshore Ledge, 3 = Igneous Cliff, 4 = Sandstone Cliff, 5 = Rocky Woods, 6 = Igneous Lakeshore Outcrop, 7 = Swamp

Forest, 8 = Tamarack Wetland, 9 = White Cedar Wetland.

relict taxa, but is unknown from Pleistocene sediments (Frest and Fay, 1981).

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