Distribution and Ecology of *Vertigo nylanderi* Sterki, 1909 in the Western Great Lakes region

Jeffrey C. Nekola and Peter A. Massart

Department of Natural and Applied Sciences, University of Wisconsin — Green Bay, Green Bay, Wisconsin 54311, U. S. A.

Abstract: The land snail *Vertigo nylanderi*, previously reported from only 6 modern global sites, was located at 22 stations in north-central Minnesota, northern Michigan, and eastern Wisconsin. Its populations are limited to nutrient-rich, forested wetlands (typically dominated by Tamarack or Black Ash) that are underlain by calcareous substrates. Most sites are within 40 km of the Lake Michigan and Lake Huron shorelines. This species was found to be morphologically distinct from other conchologically similar taxa such as *V. arthuri* (von Martens, 1884), *V. hubrichti* (Pilsbry, 1934), and *V. paradoxa* Sterki, 1900. Although 54 other terrestrial gastropod taxa have been observed to coexist with *V. nylanderi*, only 12 of these occur in at least 50% of sites. The cool, wet, calcareous habitats that support *V. nylanderi* appear to be similar to late Pleistocene environments, and it is possible that this species represents a relict from that period.

Key Words: *Vertigo nylanderi*, Great Lakes, biogeography, ecology, glacial relict

Vertigo nylanderi is a minute and poorly known land snail of eastern North America. Until recently only 6 modern stations were known: the type location at Woodland in Aroostook County, Maine (Pilsbry, 1948), three sites in eastern Ontario (Onakawana, Cochrane District; Ottawa, Carleton County; Temagami Provincial Forest, Nipissing District; Oughton, 1948), Wilderness State Park in the northern Lower Peninsula of Michigan (Burch and Jung, 1988), and Lake Itasca State Park in Clearwater County, Minnesota (Dawley, 1955). Only one of these collections (Wilderness State Park) was made since 1949. Hubricht (1985) reported having never observed it in over 40 years of collecting within the eastern United States.

Little also has been reported of the preferred habitats for *Vertigo nylanderi*. No habitat information was provided for the Wilderness State Park, Lake Itasca or type stations. Oughton (1948) describes the region in the Temagami Provincial forest where *V. nylanderi* occurs (Olive Township) as having alkaline soils with pH values ranging from $6^1/_2$-7, but provided no other information regarding this, or any other, of the Ontario sites.

During a study of land snail communities within the Great Lakes region, 22 extant stations for *Vertigo nylanderi* were located. These allow for the first time a more thorough consideration of this species: (1) distribution in the Great Lakes region; (2) shell morphology; (3) habitats; (4) molluscan associates; and (5) Pleistocene history.

METHODS AND MATERIALS

A total of 424 sites were surveyed for their terrestrial gastropods across a 1300x1000 km region, including portions of Illinois, Michigan, Minnesota, New York, southern Ontario, and Wisconsin. Sites were chosen for survey if they represented typical examples of their respective habitat type, and (except for anthropogenic habitats) were undisturbed. Collections were made from 21 discrete habitat types including carbonate cliffs, lakeshore carbonate ledges, igneous cliffs, algific talus slopes, fens, lakeshore alluvial banks, rocky woodlands, calcareous open meadows, lowland woods, alvars, cobble beaches, shale cliffs, carbonate glades, aspen parkland, old fields, tallgrass prairie, and open dunes. Descriptions these habitat types are found in Nekola (1999). The location of each sample was marked on USGS 7.5 minute (or equivalent) topographic maps, and latitude-longitude coordinates determined through digitization of these maps using the ATLAS DRAW software package.

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

Although the 22 identified populations (Table 1) generally fall within the previously known range of *Verti nylanderi* (northern Maine to James Bay to northweste Minnesota), they verify for the first time its presence with Wisconsin and the Upper Peninsula of Michigan. All these populations are confined to sites underlain by calcar ous substrates (bedrock, glacial till, or lacustrine sec ments). In Michigan and Wisconsin, most sites are with 40 km of the Lake Michigan or Lake Huron shoreli

Table 1. Extant stations for *Vertigo nylanderi* in the western Great Lakes region.

Site	Location	Wetland Habitat Type	Collection Date	# Adults
MICHIGAN				
Chippewa County				
Maxton Plains Center 2	84° 39' 24" W, 46° 4' 44" N	Tamarack - Sedge	June 17, 1998	4
Prentiss Bay	84° 13' 49" W, 46° 59' 25" N	Tamarack - Sedge	June 19, 1998	4
Delta County				
Garden Corners	87° 32' 4" W, 46° 53' 23" N	Tamarack - Sedge	June 27, 1998	1
Kalkaska County				
Angling Swamp	85° 1' 14" W, 45° 40' 14" N	Tamarack - Sedge	July 24, 1999	13
Mackinac County				
Townhall Road	85° 10' 28" W, 46° 8' 19" N	White Cedar - Tamarack	June 20, 1998	1
Schoolcraft County				
Birch Creek	86° 26' 35" W, 46° 47' 16" N	Tamarack - Sedge	July 14, 1999	4
MINNESOTA				
Beltrami County				
Pennington Bog	94° 28' 44" W, 47° 29' 59" N	White Cedar - Tamarack	July 29, 1999	4
Clearwater County				
Iron Springs	95° 15' 5" W, 47° 15' 11" N	Tamarack - Sedge	July 27, 1999	6
Bear Paw Point W	95° 11' 51" W, 47° 13' 23" N	Black Ash	July 27, 1999	1
Bear Paw Point E	95° 11' 41" W, 47° 13' 11" N	Black Ash - Tamarack	July 29, 1999	20
Itasca County				
Bowstring	94° 47' 43" W, 48° 33' 11" N	Tamarack - Sedge	July 29, 1999	3
WISCONSIN				
Brown County				
Lily Lake County Park	88° 51' 3" W, 44° 25' 19" N	Tamarack - Sedge	June 13, 1998	1
Lily Lake County Park	88° 51' 3" W, 44° 25' 22" N	White Cedar - Yellow Birch	June 13, 1998	1
Reforestation Camp	88° 5' 37" W, 45° 39' 36" N	White Cedar - Black Ash	December 11, 1999	2
Calumet County				
East River Road	88° 3' 42" W, 44° 8' 21" N	Tamarack - Sedge	November 15, 1998	1
Kiel Marsh	88° 3' 34" W, 44° 53' 52" N	Tamarack - Black Ash	October 29, 1998	12
Door County				
Corbisier Farm	88° 32' 57" W, 45° 45' 17" N	White Cedar Stonepile	October 25, 1998	26
Toft Point	87° 5' 52" W, 45° 4' 43" N	Tamarack - Sedge	October 11, 1997	2
Kewaunee County				
Tisch Mills 1	88° 38' 21" W, 44° 20' 46" N	Tamarack - Sedge	November 7, 1998	3
Tisch Mills 2	88° 38' 21" W, 44° 20' 50" N	White Cedar - Tamarack	November 7, 1998	1
Manitowoc County				
Zander Road	88° 52' 44" W, 44° 18' 32" N	Black Ash	October 4, 1998	1
Oconto County				
Morgan Marsh	88° 8' 10" W, 45° 47' 32" N	Alder - Tamarack	October 31, 1998	1

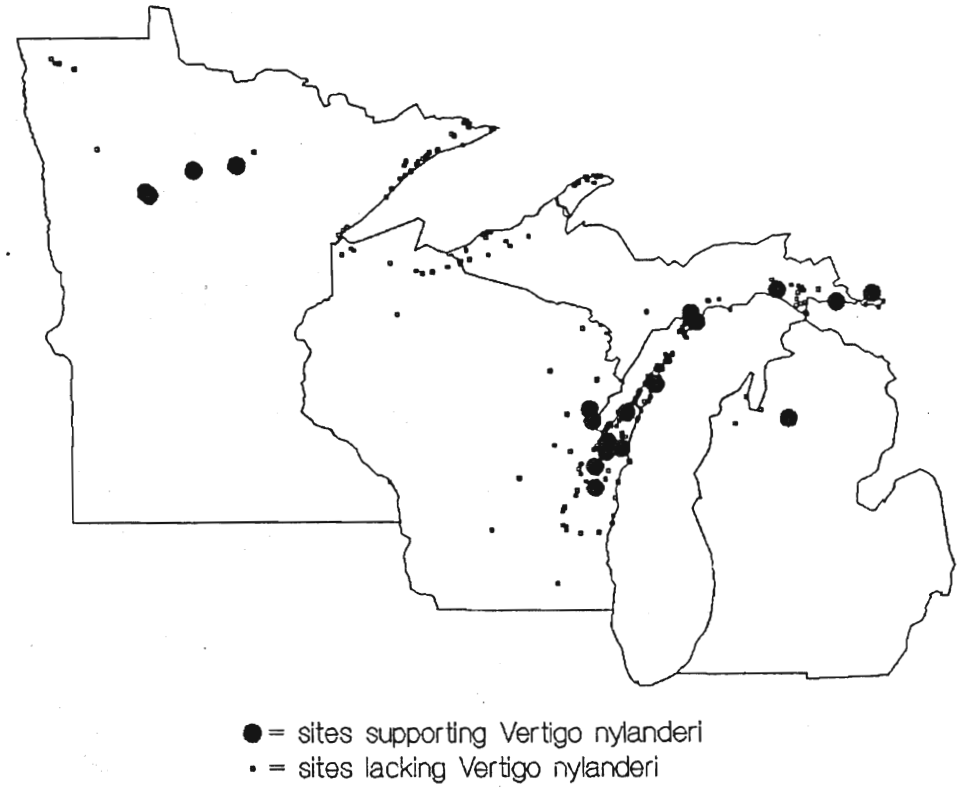

Fig. 1. *Vertigo nylanderi* distribution in the western Great Lakes. As some stations are close together (Lily Lake 1 and 2, Tisch Mills 1 and 2, and Bear Paw Point E, Bear Paw Pt W, and Iron Springs), their occurrence dots overlap. As such, only 18 separate occurrences are apparent at this map scale.

(Fig. 1).

The previously documented populations are also apparently confined to areas underlain by calcareous bedrock or till. The type location in Aroostook County, Maine rests atop Silurian and Ordovician limestones (Osberg *et al.*, 1985). The Ottawa and Onakawana sites in Ontario rest above limestone, while the Temagami Provincial Forest site has calcareous soils (Oughton, 1948). The Lake Itasca area is covered by tills from the Des Moines lobe, which is largely composed of limestone and shale (Ojakangas and Matsch, 1982).

While Levi & Levi (1950) listed *Vertigo nylanderi* from Peninsula State Park in Door County, Wisconsin, these data suggest that this report is almost certainly in error. No appropriate habitats for *V. nylanderi* are known from the park, and we have not been able to locate it there. It seems likely that their report was based on the closely related *V. hubrichti*, which is frequent on limestone cliffs in the park (Nekola, *unpublished data*). Unfortunately, verification of Levi & Levi's specimens was not possible as their repository is unknown.

Shell Morphology

As only roughly a dozen shells had been previously collected (Oughton, 1948; Pilsbry, 1948; Dawley, 1955), the 112 adult individuals secured in these analyses (Table 1) represent the first time a series of *Vertigo nylanderi* has been available. These shells ranged from 1.3-1.8 mm in height and 0.75-1.0 mm in width. Thus, some individuals were both shorter and more narrow than the previously published size range (1.55-1.8 mm tall, 0.9-1.0 mm wide; Pilsbry 1948).

The shape and appearance of these specimens (Fig. 2i-l) agree well with the descriptions and figure from Pilsbry (1948). In particular, the width of the body and penultimate whorls are similar; the outer margin of the aperture has a strong sinulus; a strong angular lamella exists in the aperture; the basal lamella is weak; and the lower palatal lamella is very deeply inserted, with its outer edge coincident with the inner end of the upper palatal. A deep, groove-like indentation on the outside of the shell over the lower palatal lamella is also present. However, unlike the description from Pilsbry (1948) few (if any) shells were noted to be of a cinnamon color, with most being a much lighter shade of yellow-brown.

As noted by Sterki (Pilsbry, 1948), the deeper insertion of the lower palatal lamella as compared to the upper, and the depression on the outside of the shell over the

palatals, suggests closer affinity of *Vertigo nylanderi* to *V. paradoxa* and *V. hubrichti* than other eastern North American *Vertigo*. Comparisons can also be drawn with a putative, undescribed, new taxon which (if valid) is closely related to *V. hubrichti* (Frest, 1991). *V. nylanderi* can be distinguished from these taxa (Figure 2a-f) because it possesses a columellar lamella of greater volume than the parietal, a strong angular lamella, a very weak basal lamella, and a very deeply set lower palatal. This last feature is most easily seen by looking at the outside of the shell with the aperture facing down. In *V. nylanderi*, the lower palatal is so deeply set that the depression over it runs parallel to the aperture on the very back of the shell. In *V. paradoxa* and *V. hubrichti* the less deep insertion of the lower palatal places this depression at an acute angle from the aperture on the side of the shell.

While individuals intermediate between *Vertigo nylanderi* and *V. paradoxa* do not exist (even at sites of co-occurrence), some slightly intermediate individuals between *V. nylanderi* and *V. hubrichti* were located at the Corbisier Farm site. These were the tallest shells encountered (1.7-1.8 mm), had the strongest basal lamellae, and had a columellar lamella only slightly larger in volume as compared to the parietal. However, in all other regards these individuals appeared identical to other *V. nylanderi* specimens. These differences in shell morphology at the Corbisier Farm are likely due to ecotypic variation rather than to genetic introgression, as these were the only individuals not found in a wetland environment.

Vertigo nylanderi also bears some resemblance to *V. arthuri* by possessing an angular lamella, a columellar lamella of greater volume as compared to the parietal, and a lower palatal lamella more deeply set as compared to the upper. However, *V. arthuri* is easily distinguished from *V. nylanderi* by having a thickened callus adjacent to the palatal lamellae, a less deeply inserted and shorter lower palatal lamella, and a distinct crest in back of the aperture (Fig. 2g-h).

Habitat Preferences

Except for the Corbisier Farm, *Vertigo nylanderi* was limited to wooded wetlands. Tamarack (*Larix laracina* (DuRoi) K.Koch) and/or Black Ash (*Fraxinus nugra* Marsh.) were usually present, and either (or both) of these species dominated the tree canopy tree at all but 3 sites. At Townhall Road and Tisch Mills 2, White Cedar (*Thuja occidentalis* L.) was the dominant tree. At Lily Lake 2, White Cedar, Yellow Birch (*Betula lutea* Mich.), and Hemlock (*Tsuga canadensis* (L.) Carr.) were co-dominant. All sites had a ground layer harboring nutrient-rich wetland bryophytes (e.g. *Cratoneuron filicinum* (Hedw.) Spruce, *Mnium cuspidatum* Hedw., *M. punctatum* Hedw., *Thuidium delicatulum* (Hedw.) BSG), various sedges (e.g. *Carex lacustris* Willd., *C. leptalea* Wahlenb.) and small shrubs (e.g. *Ribes lacustris* (Pers.) Poiret and *Rhamnus alnifolia* L'Her). *Sphagnum* mosses were generally rare or absent. Some of the Minnesota sites are also known to harbor *Malaxis paludosa* (L.) Sw., one of North America's rarest boreal orchids.

The Corbisier Farm population was found in a very different situation: a White Cedar grove growing on top of an anthropogenic stone pile. According to the Corbisier family, this stone pile dates back almost 100 years. Although seemingly very different, some similarities were noted between this and other *Vertigo nylanderi* sites. First, the stone pile was constructed on top of a spring next to a cold stream, which makes its soil cool and wet. Second, the stone pile rests within a wetland matrix, which before agricultural conversion was likely dominated by White Cedar, Tamarack, and Black Ash. The history and ecological conditions of the Corbisier Farm stone pile appear unique, as none of the other anthropogenic stone piles in the region which have been analyzed support *V. nylanderi* or other species (e.g. *Euconulus alderi, V. bollesiana*) which occur here.

Associated Species

A total of 54 terrestrial gastropod taxa were sympatric with *Vertigo nylanderi* (Table 2). Twelve of these (*Carychium exiguum, Nesovitrea electrina, Euconulus alderi, Striatura milium, Zonitoides arboreus, Gastrocopta tappaniana, Striatura exigua, Strobilops labyrinthica, Vertigo elatior, Punctum minutissimum, Carychium exile,* and *Columella simplex*; 22% of total) were found in 50% or more of sites. Of the remaining, 36 (over 66% of the total) taxa were found in less than 25% of sites.

Two general associations were noted. Tamarack-dominated sites in eastern Wisconsin and northern Michigan (Angling Swamp, Birch Creek, East River Road, Garden Corners, Lily Lake County Park 1, Maxton Plains Center 2, Prentiss Bay, Tisch Mills 1, Toft Point) supported a very consistent fauna essentially limited to the 9 most common taxa. Average species richness of these sites is 11.9. Tamarack-dominated sites in Minnesota (Bowstring, Iron Springs) had a similar, though richer, fauna (16-18 species). These associates are consistent with those listed by Oughton (1948) for the 3 Ontario sites. Olaf Nylander also collected *Vertigo elatior* from the type station (Pilsbry, 1948).

Black Ash, White Cedar, and/or Alder dominated sites (Bear Paw Point E, Bear Paw Point W, Corbisier Farm, Keil Marsh, Lily Lake 2, Morgan Marsh, Pennington Bog, Reforestation Camp, Tisch Mills 2, Townhall Road, Zander Road) were found to harbor not only the common

Table 2. Species associated with *Vertigo nylanderi* in Michigan, Minnesota, and Wisconsin. Nomenclature is based on Hubricht (1985).

Species	Site																					Total
	Michigan						Minnesota					Wisconsin										
	1	2	3	4	5	6	1	2	3	4	5	1	2	3	4	5	6	7	8	9	10	11	
Carychium exiguum (Say, 1822)	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	22
Nesovitrea electrina (Gould, 1841)	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	21
Euconulus alderi (Gray, 1840)	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x			x	19
Striatura milium (Morse, 1859)		x	x	x	x	x	x	x	x	x	x	x	x	x		x		x	x	x	x	x	19
Zonitoides arboreus (Say, 1816)	x	x	x		x	x	x	x	x	x	x		x	x	x	x	x	x	x		x	x	19
Gastrocopta tappaniana (C. B. Adams, 1842)	x	x	x	x			x	x	x	x	x	x		x	x	x	x	x	x		x	x	18
Striatura exigua (Stimpson, 1847)	x		x	x	x		x	x	x	x	x	x	x	x				x	x	x	x	x	17
Strobilops labyrinthica (Say, 1817)	x		x	x	x		x	x	x	x	x		x	x		x		x	x	x	x	x	17
Vertigo elatior Sterki, 1894	x	x	x	x	x	x	x	x	x	x	x	x		x	(x)			x			x	x	17
Punctum minutissimum (I. Lea, 1841)	x	x		x	x	x	x	x	x	x	x	x	x							x			13
Carychium exile H. C. Lea, 1842				x	x		x		x	x	x		x	x					x	x	x		11
Columella simplex (Gould, 1841)		x		x	x	x	x	x		x	x		x				x				x		11
Deroceras laeve (Müller, 1774)				x				x		x		x			x				x		x		7
Gastrocopta contracta (Say, 1822)									x	x			x	x		x	x				x		7
Helicodiscus parallelus (Say, 1817)									x	x						x	x		x		x	x	7
Helicodiscus shimeki Hubricht, 1962					x						x		x	x		x				x	x		7
Discus catskillensis (Pilsbry, 1898)					x	x	x			x	x										x		6
Discus cronkhitei (Newcomb, 1865)				x			x	x	x								x	x					6
Gastrocopta pentodon (Say, 1821)										x			x	x		x					x		5
Hawaiia minuscula (A. Binney, 1840)									x	x							x	x				x	5
Catinella avara (Say, 1824)								x		x					x	x							4
Cochlicopa lubrica (Müller, 1774)									x		x						x	x					4
Euconulus fulvus (Müller, 1774)													x	x			x				x		4
Nesovitrea binneyana (Morse, 1864)					x			x			x	x											4
Punctum vitreum H. B. Baker, 1930														x		x	x				x		4
Striatura ferrea Morse, 1864					x								x								x	x	4
Vertigo gouldi (A. Binney, 1843)					x								x				x				x		4
Vertigo milium (Gould, 1840)														x				x			x	x	4
Vertigo ovata Say, 1822									x	x						x						x	4
Cochlicopa lubricella (Porro, 1838)										x	x							x					3
Euconulus polygyratus (Pilsbry, 1899)					x								x								x		3
Glyphyalinia indentata (Say, 1823)			x											x								x	3
Punctum n. sp.											x					x	x						3
Stenotrema leai leai (A. Binney)																x		x				x	3
Succinea ovalis Say, 1817				x												x	x						3
Vallonia pulchella (Müller, 1774)							x											x				x	3
Vertigo bollesiana (Morse, 1865)																	x	x			x		3
Vertigo cristata (Sterki, 1919)							x			x	x												3
Zonitoides nitidus (Müller, 1774)													x				x	x					3
Anguispira alternata (Say, 1817)					x													x					2
Gastrocopta holzingeri (Sterki, 1889)														x								x	2
Haplotrema concavum (Say, 1821)														x							x		2
Hendersonia occulta (Say, 1831)														x							x		2
Oxyloma retusa (I. Lea, 1834)									x													x	2
Strobilops affinis Pilsbry, 1893															x		x						2
Vallonia gracilicosta Reinhardt, 1883							x			x													2
Vertigo arthuri (von Martens, 1884)							x		x														2
Vertigo paradoxa Sterki, 1900			x				x																2
Planogyra asteriscus (Morse, 1857)					x																		1
Pupilla muscorum (Linné, 1758)					x																		1
Stenotrema fraternum fraternum (Say, 1824)					x																		1
Vallonia costata (Müller, 1774)																		x					1
Vertigo pygmaea (Draparnaud, 1801)																						x	1
Vitrina limpida Gould, 1850																		x					1
Immature *Cochlicopa*																					x		
Immature *Discus*		x																					
Immature Polygyrinae													x		x								
Immature Succineidae													x								x		
Immature *Vallonia*			x		x																		
Total Richness (including *V. nylanderi*)	8	13	11	14	22	13	21	16	21	25	18	13	20	20	12	24	22	11	12	9	28	21	

Site Code Legend for Table 2:

Michigan:
1. Maxton Plains Center 2
2. Prentiss Bay
3. Garden Corners
4. Angling Swamp
5. Townhall Road
6. Birch Creek

Minnesota:
1. Pennington Bog
2. Iron Springs
3. Bear Paw Point W
4. Bear Paw Point E
5. Bowstring

Wisconsin:
1. Lily Lake Tamarack
2. Lily Lake White Cedar
3. Reforestation Camp
4. East River Road
5. Kiel Marsh
6. Corbisier Farm
7. Toft Point
8. Tisch Mills 1
9. Tisch Mills 2
10. Zander Road
11. Morgan Marsh

associates, but the bulk of the rarer ones as well. Most of these additional species are characteristic of mesic, calcareous woodlands. The Morgan Marsh site is located along a road, and a number of the additional species found there are typical of disturbed situations (e.g. *Vallonia pulchella, Vertigo pygmaea*). Species richness of these sites was also considerably higher, with a mean of 22.4 being observed. Minimum richness never fell below 20, with a maximum of 28 being recorded from a ca. 100 m^2 area at Zander Road. These sites represent the richest land snail communities not associated with carbonate bedrock outcrops in the region.

Pleistocene History

Vertigo nylanderi has been identified from 20,000 B.P. (Frest 1991) and 750,000 B.P. (Miller *et al.*, 1994) deposits in Illinois. During the late Pleistocene, nutrient-rich wetlands of Tamarack and Black Ash (Miller, 1980; Baker *et al.*, 1996; Jackson *et. al.*, 1997) were common in the landscape. Regional climates of this period were also less extreme than today, having similar winter temperatures, but cooler summers and more constant precipitation (Prior, 1991). Roughly similar climatic conditions persist in modern Tamarack and Black Ash dominated wetlands, especially those along the shores of Lakes Huron and Michigan where the buffering effect of lake waters lowers summer temperatures, creates warmer winter temperatures, and allows for more constant precipitation than is otherwise present in the continental interior (Curtis, 1959; Eichenlaub, 1979). Tamarack and Black-Ash wetlands in the western Great Lakes may thus represent close edaphic and microclimatic analogues to Pleistocene wetland habitats. Given the almost complete limitation of modern *V. nylanderi* to such sites, it may be best to consider this species a glacial relict. A similar argument has been advanced by Miller (1980, 1987) to suggest that disjunct populations of western calciphile plant species in the northeastern U.S. and southeastern Canada represent glacial relicts.

ACKNOWLEDGEMENTS

The authors wish to thant Robert Wise and the University of Wisconsin - Oshkosh for use of their SEM facilities. Matt Barthel was responsible for the SEM imaging of specimens. Funding for the SEM imaging was received from the Minnesota Nongame Wildlife Tax Checkoff and Minnesota State Park Nature Store Sales through the Minnesota Department of Natural Resources Natural Heritage and Nongame Research Program. Assistance in Minnesota field collection was provided by Brian Coles. Assistance in litter sample processing was provided by students participating in the Land Snail Ecology Practicum at the University of Wisconsin — Green Bay. Funding was provided by the Door County Office of the Wisconsin Chapter of The Nature Conservancy, a Cofrin Arboretum grant (administered by the Cofrin Biodiversity Center at the University of Wisconsin - Green Bay), the U.S. Fish and Wildlife Service, and the Small Grants Program of the Michigan Department of Natural Resources. Work at the Hubricht Collection was supported in part by the Prince Visiting Scholar Fund from the Field Museum of Natural History.

LITERATURE CITED

Baker, R. G., E. A. Bettis III, D. P. Schwert, D. G. Horton, C. A. Chumbley, L. A. Gonzalez, and M. K. Reagan. 1996. Holocene paleoenvironments of northeastern Iowa. *Ecological Monographs.* 66:203-234.

Burch, J. B., and Y. Jung. 1988. Land snails of the University Michigan Biological Station Area. *Walkerana* 3(9)1-177.

Curtis, J. T. 1959. The Vegetation of Wisconsin. University of Wisconsin Press, Madison. 657 pp

Dawley, C. 1955. Minnesota land snails. *The Nautilus* 69:56-62.

Eichenlaub, V. L. 1979. Weather and Climate of the Great Lakes Region. University of Notre Dame Press, Notre Dame, Indiana. 271

Frest, T. J. 1991. Summary Status Reports on Eight Species of Candidate Land Snails from the Driftless Area (Paleozoic Plateau), Upper Midwest. Final Report, Contract #301-01366, USFWS Region 3, Ft. Snelling, Minnesota.

Hubricht, L. 1985. The distributions of the native land mollusks of the eastern United States. *Fieldiana* n.s. 24:1-191.

Jackson, S. T., J. T. Overpeck, T. Webb III, S. E. Keattch, and K. H. Anderson. 1997. Mapped plant-macrofossil and pollen records of late Quaternary vegetation change in eastern North America. *Quaternary Science Reviews* 16:1-70.

Levi, L. R. & H. W. Levi. 1950. New records of land snails from Wisconsin. *The Nautilus* 63:131-138.

Miller, B. B., R. W. Graham, A. V. Morgan, N. G. Miller, W. D. McCoy, D. F. Palmer, A. J. Smith, and J. J. Pilny. 1994. A biota associated with Matuyama-age sediments in west-central Illinois. *Quaternary Research* 41:350-365.

Miller, N. G. 1980. Mosses as paleoecological indicators of lateglacial terrestrial environments: some North American studies. *Bulletin of the Torrey Botanical Club* 107:373-391.

Miller, N. G. 1987. Phytogeography and paleoecology of a late Pleistocene moss assemblage from northern Vermont. *Memoirs of the New York Botanical Garden* 45:242-258.

Nekola, J. C. 1999. Terrestrial gastropod richness of carbonate cliff and associated habitats in the Great Lakes region of North America. *Malacologia* 41:231-240.

Ojakangas, R. and C. Matsch. 1982. Minnesota's Geology. University of Minnesota Press, Minneapolis.

Osberg, P. H., A. M. Husey II and G. M. Boone. 1985. Bedrock Geologic Map of Maine. Maine Geological Survey, Department of Conservation, Augusta.

Oughton, J. 1948. A Zoogeographical Study of the Land Snails of Ontario. University of Toronto Studies: Biological Series #57.

Pilsbry, H. A. 1948. Land Mollusca of North America (North of Mexico). Academy of Natural Sciences of Philadelphia, Monograph #3. 1113 pp.

Prior, J. C. 1991. Landforms of Iowa. University of Iowa Press, Iowa City. 153 pp

Date of manuscript acceptance: 21 March 2000