Terrestrial gastropod fauna of Northeastern Wisconsin and the Southern Upper Peninsula of Michigan

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Abstract: The terrestrial gastropod fauna of eastern Wisconsin and the southern Upper Peninsula of Michigan is among the most poorly known in the eastern United States. To document this fauna, 242 sites were analyzed across 22 counties and 20 habitat types. A total of 82 taxa were encountered, or approximately half of those reported from the western Great Lakes region. Some of these are limited in the eastern USA to no more than 50 counties, including *Catinella exile, Catinella cf. gelida, Hendersonia occulta, Planogyra asteriscus, Strobilops affinis, Vallonia gracilicosta, Vertigo bollesiana, Vertigo cristata, Vertigo hubrichti, Vertigo modesta, Vertigo morsei, Vertigo nylanderi, Vertigo paradoxa,* and *Zoogenetes harpa*. Thirty-one taxa demonstrated significant variation in occurrence frequency across the landscape. Fourteen increased in frequency towards the southwest, another thirteen increased in frequency towards the northeast, two had their highest occurrence frequencies on the Door and Garden Peninsulas, and two taxa had their lowest occurrence frequencies on the Door and Garden Peninsulas. Fully 50% of the fauna also demonstrated significant differences in their occurrence frequencies between five broadly-defined habitat groupings (rock outcrops, upland forests, lowland forests, upland grasslands, and lowland grasslands). Fifteen taxa favored lowlands (either forest or grassland), thirteen favored rock outcrops, and nine favored both rock outcrop and upland forest sites. Because of these geographic and ecological trends, conservation of this fauna will likely require protection of a number of different habitats (particularly carbonate cliff, rocky forest, lowland forest, and fen sites) spread across the study area.

Key words: biodiversity, biogeography, Niagaran Escarpment, Midwestern U.S.A.

Thorough investigations into terrestrial gastropod biodiversity in the upper Midwest have been largely limited to Michigan (*e.g.*, Walker 1906, Burch and Jung 1988, Hubricht 1985, Pearce *et al.* 1992), the Paleozoic Plateau of northeastern Iowa, northwestern Illinois, southeastern Minnesota and southwestern Wisconsin (Frest 1981, 1982, 1987, 1990, 1991, Theler 1997), the Loess Hills of western Iowa (Frest and Dickson 1986), and the Black Hills of South Dakota and Wyoming (Frest and Johannes 1993). These regions have generally been found to support a diverse fauna including a number of rare taxa such as *Catinella* c.f. *gelida* (F. C. Baker, 1927); *Discus macclintocki* F. C. Baker, 1928; *Hendersonia occulta* (Say, 1831); *Vertigo arthuri* von Martens, 1882, *Vertigo hubrichti* (Pilsbry, 1934); *Vertigo meramecensis* Van Devender, 1979; *Vertigo morsei* Sterki, 1894; and *Vertigo paradoxa* Sterki, 1900.

However, over most of the region the modern land snail fauna is poorly known. In the six counties bordering Lakes Michigan and Huron in the Upper Peninsula of Michigan, only 62 species and 145 county occurrence records had been previously reported (Hubricht 1985). Prior investigations of modern northeastern Wisconsin land snails (Levi and Levi 1950, Solem 1952, Teskey 1954, Hubricht 1985) identified only 42 taxa and 122 county occurrence records across a 20-county region.

This paper summarizes findings of a land snail survey conducted from 1996-2001 in eastern Wisconsin and the southern Upper Peninsula of Michigan along the northern and western shores of Lakes Michigan and Huron, a region that straddles the boundary of the Northern and Interior Molluscan Provinces (Burch 1962), and harbors many unique natural habitats with uncommon plant species (Curtis 1959). Individual sites in this area are known to support land snail communities containing up to 34 taxa per 1000 m^2 (Nekola 1999). The data collected in this survey will be used to help better document: (1) the composition of the regional land snail fauna; (2) the geographic distribution of taxa within the region; and (3) the general habitat preferences of taxa.

MATERIALS AND METHODS

Study Area

This study was centered on 22 counties along the northern and western shores of Lakes Michigan and Huron (Fig. 1). Samples were collected from Chippewa, Delta, Luce, Mackinac, and Schoolcraft counties in Michigan and from Brown, Calumet, Dodge, Door, Fond du Lac, Green Lake, Kewaunee, Langlade, Manitowoc, Marinette, Oconto, Outagamie, Ozaukee, Sheboygan, Shawano, Washington, and Waushara counties in Wisconsin. Important geographic landmarks in this area that can be used to help describe species ranges include: Lake Winnebago, a large lake found south of Green Bay; the Door Peninsula, which separates Lake Michigan from Green Bay in northeastern Wisconsin; Sturgeon Bay, which almost bisects the center of the Door

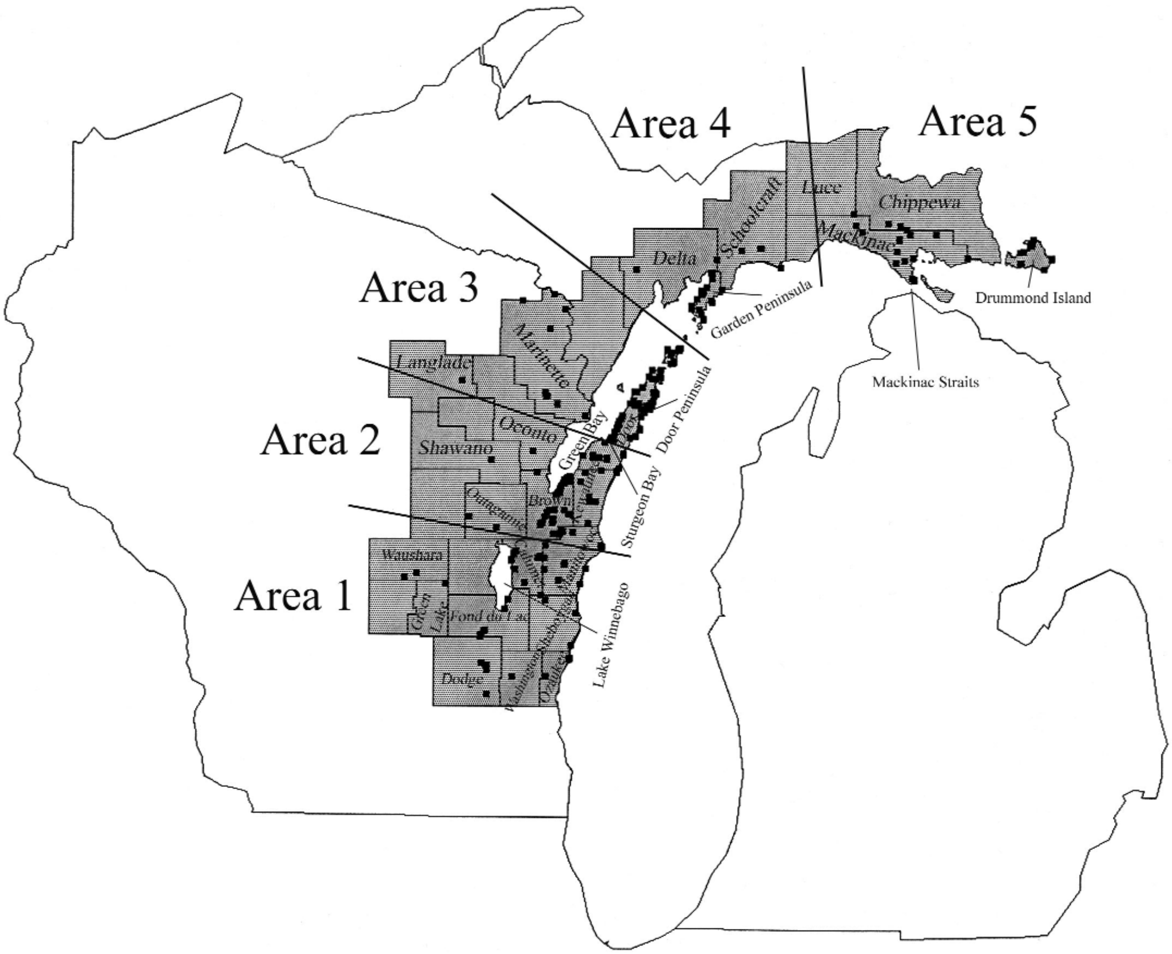

Figure 1. Map of the study area, showing outline of the states of Michigan and Wisconsin, and counties included in study region. Grey shading represents maximum extent of collected samples. Black squares represent the location of all 242 sample sites. Dark lines demarcate the five biogeographic areas used for statistical analysis of geographic trends in species occurrence frequency. Names and locations of the major geographic landmarks mentioned in text are also provided.

Peninsula; the Garden Peninsula, which separates Lake Michigan from Big Bay de Noc in the Upper Peninsula; the Straits of Mackinac, which join Lakes Michigan and Huron in the eastern Upper Peninsula; and Drummond Island, which is the eastern-most extension of the Upper Peninsula.

The bulk of this region is underlain by calcareous bedrock and tills associated with the Niagaran Escarpment, a band of outcropping Silurian limestones and dolomites that extend from western New York state to northeastern Iowa. In eastern Wisconsin the Niagaran Escarpment extends from Dodge County up the eastern shore of Lake Winnebago and the western side of the Door Peninsula to Rock Island. In the Upper Peninsula, the Niagaran Escarpment extends from the Garden Peninsula eastward through the Mackinac Straits to Drummond Island. Individual outcrop areas are isolated from one another in the region by glacial or lacustrine sediments, and are more widely spaced (up to 90 km) in Michigan.

The climate of this region is characterized by mean maximum summer temperatures ranging from 30°C in the southwest to 23°C in the northeast. Mean minimum January temperatures range from –5°C along the lakeshore in the south to –13°C in the north. Annual precipitation ranges from 710 mm in the Door Peninsula to 810 mm in the eastern Upper Peninsula. In proximity to the Great Lakes shore the climate is buffered, being warmer in the winter, cooler in the summer, and having a longer growing season as compared to inland areas of similar latitude (Eichenlaub *et al.* 1990).

During the late Pleistocene the entire area was covered by continental glaciers. Rapid retreat of this ice sheet, and partial removal of till by meltwaters, began 15,000 B.P. (Maher and Mickelson 1996). This period was followed by approximately 2000 years of severe cold that led to further till removal through periglacial erosion (Steiglitz *et al.* 1980). These processes have

Table 1. Habitat types sampled per county. The three sampled Rock Outcrop habitat types are Carbonate Cliff (RO1), Lakeshore Carbonate Ledge (RO2), and Igneous Cliff (RO3). The five sampled Upland Forest habitat types are Oak-Hickory (UF1), Maple-Basswood (UF2), Hemlock-Yellow Birch (UF3), Lakeshore (UF4), and Rocky (UF5). The five sampled Lowland Forest habitats types are Floodplain (LF1), Black Ash (LF2), Tamarack (LF3), White Cedar (LF4), and Shrub Carr (LF5). The three sampled Upland Grassland habitat types are Sand Dune (UG1), Alvar (UG2), and Old Field (UG3). The four sampled Lowland Grassland habitat types are Sedge Meadow (LG1), Fen (LG2), Calcareous Meadow (LG3), and Cobble Beach (LG4).

State/County	Habitat Code																				
	RO1	RO2	RO3	UF1	UF2	UF3	UF4	UF5	LF1	LF2	LF3	LF4	LF5	UG1	UG2	UG3	LG1	LG2	LG3	LG4	Total
Michigan																					
Chippewa	9	1						2			2				1		1			2	18
Delta	6	1					1	2			1				3				2	1	17
Luce								1													1
Mackinac	1							3				4					1	2			11
Schoolcraft	1	1						2			1									1	6
Wisconsin																					
Brown	14			1		1		3		1	2	2			2			1	1		28
Calumet	5			1				1			2						1				10
Dodge	5																				5
Door	30	19			1		5	6		1	4		1					4	1	2	74
Fond du Lac	7																				7
Green Lake																		1			1
Kewaunee		1					1	1			4	2	1				1	1	1		13
Langlade								1													1
Manitowoc	2				1		5	1	2	3	5			1		1		1	1		23
Marinette			2							1	2	2						1	3		11
Oconto											1										1
Outagamie	1											1									2
Ozaukee							1	1			1					1		1			5
Shawano	1																				1
Sheboygan							2				1					1					4
Washington																		1			1
Waushara											1							1			2
Total	82	23	2	2	2	1	15	24	2	6	27	11	2	1	6	3	4	14	9	6	242

allowed for a more frequent exposure of bedrock in the study region as compared to surrounding landscapes.

Study Sites

A total of 242 sites were surveyed for terrestrial gastropods (Fig. 1; Table 1). The number of samples per county ranged from 74 (Door) to 1 (Green Lake, Langlade, Luce, Oconto, Shawano, and Washington). Sites were selected if they represented typical examples of their respective habitat, and (except for anthropogenic habitats) were undisturbed. Most surveyed sites were within 60 km of the shore.

Collections were made from 20 habitat types known or suspected to support diverse and/or interesting land snail communities (Nekola 1999: Table 1). These habitats can be broadly grouped into five categories: rock outcrops, upland forests, lowland forests, upland grasslands, and lowland grasslands.

Three types of rock outcrop sites were surveyed. Carbonate cliffs (82 sites) are 3-20 m tall, wooded limestone or dolomite outcrops that typically support moss, fern, and soil-covered ledges. Lakeshore carbonate ledges (23 sites) are <3 m tall, wooded limestone or dolomite outcrops that are within 4 km of the Lake Michigan or Lake Huron shore. Sampling of igneous cliffs in the region was restricted (2 sites) to 2-8 m tall ultramafic Precambrian outcrops located along the Menominee River on the Wisconsin-Michigan border in Marinette County, one of the few places in the study region where igneous rocks are exposed.

Five types of upland forest habitats were surveyed. Three of these had deep, non-rocky soils, and were characterized by their canopy composition, including oak-hickory (2 sites), maple-basswood (2 sites), and hemlock-yellow birch (1 site) forests. Lakeshore forests (15 sites) were found on steep slopes of unconsolidated lacustrine material adjacent to the Great Lakes shoreline. Rocky woodlands (24 sites) were upland tracts with rocky soils derived from either local bedrock or glacial till.

Five types of lowland forests were surveyed. Floodplain forests (2 sites) occur on silty or sandy soils adjacent to streams. Black ash (6 sites), tamarack (27 sites), and white cedar (11 sites) forests were typically found in areas underlain by calcareous bedrock or till. While surficial soil chemistry on these sites can vary from acidic (where *Sphagnum* moss is abundant) to neutral or alkaline (where *Sphagnum* is largely absent), litter collection was generally limited to the latter microsites. Shrub-carr habitats (wetland areas dominated by shrub thickets, see Curtis, 1959; 2 sites) had a canopy of alder, willow, and dogwood, with a ground layer consisting primarily of sedges.

Only three types of upland grasslands were surveyed, as the regional climate generally favors development of forest communities in most upland situations. Sand dunes (1 site) are xeric grasslands found along the Great Lakes shore. Alvars (6 sites) are treeless areas developed on flat expanses of carbonate bedrock that are covered by little (or no) soil. While such sites are typically xeric by mid-summer, shallow pools are common in the spring. Old fields (3 sites) are early successional grasslands that have developed following agricultural abandonment.

Four types of lowland grassland habitats were surveyed. Sedge meadows (4 sites) are composed of a variety of wetland sedge and grass species, and often support scattered clumps of willows and dogwood. Fens (14 sites) are peatland areas found at sites of ground water discharge. They maintain higher soil moisture and cooler soil temperatures than are otherwise found in the surrounding landscape (Nekola 1994). Sampling was conducted only from sites in which Sphagnum was either uncommon or lacking. Calcareous meadows (9 sites) are often sparsely vegetated wetlands found on mineral (rather than organic) soils. Cobble beaches (6 sites) are constantly wet grasslands developed on limestone or dolomite pavement along the Great Lakes shore. Little or no soil development exists on these sites except along bedrock fractures.

Field Methods

Documentation of terrestrial gastropods from each site was accomplished by hand collection of larger shells and litter sampling for smaller taxa from representative 100-1000 m≤ areas. Soil litter sampling was primary used as it provides the most complete assessment of site faunas (Oggier *et al.* 1998). As suggested by Emberton *et al.* (1996), collections were made at places of high micro-mollusc density, with a constant volume of soil litter (approximately 4 l) being gathered from each site. For woodland sites, sampling was concentrated: (1) along the bases of rocks or trees; (2) on soil-covered bedrock ledges; and/or (3) at other places found to have an abundance of shells. For grassland sites, samples consisted of: (1) small blocks (ca. 125 cm3) of turf; (2) loose soil and organic litter accumulations under or adjacent to shrubs, cobbles, boulders, and/or hummocks; and (3) other locations observed to have an abundance of shells.

Laboratory Procedures

The location of each sample was marked on USGS 7.5' topographic maps. The latitude-longitude coordinates for each was then determined through digitization of these maps using the ATLAS DRAW software package.

Samples were slowly and completely dried in either a low-temperature soil oven (ca. 80-95ºC) or in full sun in a greenhouse. Dried samples were then soaked in water for 3-24 h, and subjected to careful but vigorous water disaggregation through a standard sieve series (ASTME 3/8" [9.5 mm], 10 [2.0 mm], 20 [0.85], and 40 [0.425 mm] mesh screens). Sieved sample fractions were then dried and passed again through the same sieve series. These dry, resorted fractions were hand-picked against a neutral-brown background. All shells and shell fragments were removed.

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 (FMNH). Some additional specimens representing Holarctic taxa were verified by Robert Cameron of the University of Sheffield. All specimens have been catalogued and are housed in the author's collection at the University of Wisconsin - Green Bay. Nomenclature generally follows that of Turgeon *et al.* (1998). Where these differ from Hubricht (1985), the latter has been provided in brackets. The few exceptions to this are detailed more fully below in the annotated list under the entry for that taxon.

Given the diversity in the region within the genera Vertigo and Gastrocopta, and the few published images of these taxa, a plate of SEM micrographs representing a selection of these taxa has been provided to aid in their future identification (Figure 2). These images are based on representative specimens from the UWGB collection that were located in or adjacent to the study region, and hence do not represent paratypes or topotypes. 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.

Statistical Tests

Contingency table analyses were used to assess which taxa differed in their occurrence frequencies between five similar-sized biogeographic areas within the region (Fig. 1). Area 1 (51 sites) ranged south of Lake Winnebago. Area 2 (64 sites) ranged from Sturgeon Bay and central Oconto County to the north side of Lake Winnebago. Area 3 (74 sites) ranged from Rock Island and Marinette County to Sturgeon Bay and central Oconto County. Area 4 (23 sites) ranged across Delta and Schoolcraft counties, including all of the Garden Peninsula. Area 5 (30 sites) ranged from Drummond Island west to central Mackinac counties.

The number of occurrences and absences for each taxon within each area was calculated. Because observed frequencies of taxa were often sparse (< 5) in more than one-fifth of the areas, a log-likelihood ratio test (Zar 1984) was used to identify significant differences in occurrence frequencies. Because this test was repeated on each of the 82 encountered taxa, a Bonferroni correction was used to adjust the significance threshold to 0.000610.

A similar procedure was used to identify which taxa differed

Table 2. Number of sites at which taxon occurred in each county; an "x" represents species reported by Hubricht (1985) from a given county, but which were not observed in that county during this study.

Taxon	State and County																						
	Michigan					Wisconsin																	
	Chippewa	Delta	Luce	Mackinac	Schoolcraft	Brown	Calumet	Dodge	Door	Fond du Lac	Green Lake	Kewaunee	Langlade	Manitowoc	Marinette	Oconto	Outagamie	Ozaukee	Shawano	Sheboygan	Washington	Waushara	Total
Allogonia profunda		1			x	4	4	3	8	6		x		1	x	x	x	x	x				27
Anguispira alternata	11	11	1	4	2	16	7	4	50	7		2	x	5	2	x	1	2	1	1			128
Carychium exiguum	4	3		5	2	8	4		16		1	10		5	7	1	1	2		1	1	2	73
Carychium exile	4	8		3	4	19	6	5	28	7		7		8	4			2	1				107
Catinella avara	1	2	x	x	1	3	3		3			3		2	x		x			1			19
Catinella exile	1	1		1					2		1										1	1	8
Catinella cf. *gelida*						4	4	5		5									1				19
Catinella cf. *vermeta*	1																						1
Cochlicopa lubrica	3	2	1	3	2	17	5	2	13	3		4		8				3	x	3		1	70
Cochlicopa lubricella		2		2	1	11	2	2	7	1		3		2	3		1					1	38
Cochlicopa morseana	5	4	1	1			1		5			2	1				1		1				22
Columella simplex	14	12	1	7	4	8	2	1	56	2		5		9	4		2		1	1		1	129
Deroceras spp.	2	5		1	1	12	6	5	7	7	1	5	1	5	5		1	1			1	1	67
Discus catskillensis	13	11	1	6	4	11	5	5	54	7		4	1	5	4	x	1		1				133
Discus whitneyi	3	1		1	2	7	3		3	1	1	4	1	3	1			1		1	1		34
Discus patulus						x																	
Euchemotrema fraternum	5	3	1	3	1	4	5	4	22	6		x	x		x	x			1				55
Euchemotrema leai	1	1		x	1	4	2		5		1	5		2	2	1					1	2	28
Euconulus alderi	2	2		4	2	3	3		7		1	7		2	4	1		1		1	1	2	43
Euconulus fulvus	11	8	1	3	3	11	3	3	40	5			1	11	4		2	1					107
Euconulus polygyratus	5	4	1	4	2	6	3	1	24	1		2		2									55
Gastrocopta armifera						6		3	2	2				1			1						15
Gastrocopta contracta	4	6	1	1		18	7	5	30	7	1	4		7	2		2	1	1		1	1	99
Gastrocopta corticaria						8	5	5	6	7													31
Gastrocopta holzingeri		2				15	6	5	8	7		1		4		1	1		1				51
Gastrocopta pentodon	4	8			2	16	5	3	38	6		2		6	2		2		1				95
Gastrocopta similis								1															1
Gastrocopta tappaniana	5	4		4	1	9	4		11		1	9		7	2	1	2	2		2	1	2	67
Glyphyalinia indentata	7	7	1	3	x	11	2	2	23			2		1	1	1	1		1				63
Glyphyalinia rhoadsi	3	2	1	1	x	1			5										1				14
Glyphyalinia wheatleyi	x	x		1					1														2
Guppya sterkii		1				2			1														4
Haplotrema concavum	1					1								3									5
Hawaiia minuscula	3	4			1	18	7	5	8	7	1	2		3	2	1	2	1	1		1	2	69
Helicodiscus parallelus	8	4	1	4	1	9	5	2	4	2	1	5		5	3	1	2	1			1	1	60
Helicodiscus shimeki	6	10	1	5	3	16	8	4	53	7		5		7	2		1	1	1				130
Hendersonia occulta		x				15	1		20			2		9				1		2			50
Mesodon thyroidus						x			4						x	x			x				4
Neohelix albolabris	1	x	x	x	x				9	x			x	x		x		1	x				11
Nesovitrea binneyana	10	6	1	7	x	3	2		15	1			1	2	2								50
Nesovitrea electrina	3	5	x	3	2	8	3		18		1	10		6	7	1		2		2	1	2	74
Novisuccinea ovalis		1		x		13	5	1	20	6		5		2	1	x		2		1	1		58
Oxychilus cellarius									1														1
Oxychilus draparnaudi									1														1
Oxyloma retusa	1	2	x	1	1	5	1	x	1		1	4		3	3	1	x				1	1	26
Paravitrea multidentata	8	7	1	3	1	8	2		36			2											68
Planogyra asteriscus	1	1		4	2										1					x			9
Pomatiopsis lapidaria						1						x		2	1								4
Punctum minutissimum	17	14	1	7	6	9			64			6		1	5		1		1	1			133
Punctum n.sp.							2		1		1				2						1	1	9
Punctum vitreum						12	6	5	1	7		2		13			1	1		1			49
Pupilla muscorum				2																			2
Pupoides albilabris						1																	1
Stenotrema barbatum														x				2			1		3
Striatura exigua	10	4	1	10	2	4			21	x		8		2	6	1						1	70
Striatura ferrea	6	4	1	6	1	2			14			2		2	2	1							41
Striatura milium	13	12	1	8	5	7	2		44	1		10		8	9	1	1	2				1	125
Strobilops aenea									1														1
Strobilops affinis				1		4	1		1		1	4		2	2		x				1	2	19
Strobilops labyrinthica	14	14	1	9	4	20	6	5	62	7		9		9	10	1	1	2	1			1	176
Vallonia costata	x	2	x	x	2	12	2	1	7	1		2		6	3			1		1		1	41
Vallonia excentrica						1												1		1			3
Vallonia gracilicosta	5	3				7	1	1	12	3													32
Vallonia perspectiva							5	1		6													12
Vallonia pulchella	x	2		x	x	9		1	2	1		2		5	4	1		1	x	1			29
Vertigo bollesiana	3	5				8	3		45			2	1	2	1		2		1				73
Vertigo cristata	4	2		3	1				12						3								25
Vertigo elatior	5	5		4	2	4	1		11		1	5		7	5	1	1	2	x	1	1	2	58
Vertigo gouldi	10	9	1	4	3	15	8	5	48	7		2		6	2		2		1				123
Vertigo hubrichti	5	8			3	8		1	41	6				1									73
Vertigo milium						13	3	3	5	1	1	2		3	1	1	2	2	x		1	2	40
Vertigo modesta													1										1
Vertigo morsei	x			2					3													1	6
Vertigo nylanderi	2	1		1	1	3	2		2			2		1		1						1	17
Vertigo ovata	1	1			1	1	2		5		1	2		2	5	1	x			1			23
Vertigo paradoxa	7	1		1	3				4						2								18
Vertigo pygmaea	1					16	1	1	2	1		2		5	2	1		1		2			35
Vertigo tridentata						1		2		2													5
Vitrina limpida	3	2	1	4	2				2			1		1						1			17
Webbhelix multilineata						1	4		1						x	x			x				6
Zonitoides arboreus	16	9	1	7	4	18	8	5	59	7		9	1	12	9	1	2	2	1		1	1	173
Zonitoides limatulus									x														
Zonitoides nitidus	1	1		x		7	3		6			1		5				1		3		1	29
Zoogenetes harpa	4	3		2	1				1														11
Total richness	55	57	28	50	46	63	51	36	70	38	17	49	12	53	47	29	31	30	27	22	19	27	84

Table 3. Number of taxon occurrences per habitat type. The three sampled Rock Outcrop habitat types are Carbonate Cliff (RO1), Lakeshore Carbonate Ledge (RO2), and Igneous Cliff (RO3). The five sampled Upland Forest habitat types are Oak-Hickory (UF1), Maple-Basswood (UF2), Hemlock-Yellow Birch (UF3), Lakeshore (UF4), and Rocky (UF5). The five sampled Lowland Forest habitats types are Floodplain (LF1), Black Ash (LF2), Tamarack (LF3), White Cedar (LF4), and Shrub Carr (LF5). The three sampled Upland Grassland habitat types are Sand Dune (UG1), Alvar (UG2), and Old Field (UG3). The four sampled Lowland Grassland habitat types are Sedge Meadow (LG1), Fen (LG2), Calcareous Meadow (LG3), and Cobble Beach (LG4).

Taxon	Habitat Code																				
	RO1	RO2	RO3	UF1	UF2	UF3	UF4	UF5	LF1	LF2	LF3	LF4	LF5	UG1	UG2	UG3	LG1	LG2	LG3	LG4	Total
Allogona profunda	19	3						5													27
Anguispira alternata	79	18	2	1	1		8	15			1	2								1	128
Carychium exiguum	4					1		2		4	24	10	2		1		3	13	5	4	73
Carychium exile	52	11	1			1	8	10	1	4	3	6			3	2		2	3		107
Catinella avara	1										6				4		1	1	3	3	19
Catinella exile																		5		3	8
Catinella cf. *gelida*	19																				19
Catinella cf. *vermeta*															1						1
Cochlicopa lubrica	25	3		2			9	15			3	3			2	2	2	2	1	1	70
Cochlicopa lubricella	17	2		1			1	8		1		1			1		1	2	3		38
Cochlicopa morseana	9	2					2	6			1	1							1		22
Columella simplex	53	21	1		1	1	12	13		2	5	6	1		2		2	3	2	5	130
Deroceras spp.	34	1	1	1			1	3	1	3	6	2						8	4	2	67
Discus catskillensis	73	21	2		1		5	16		2	3	4	1			1	1		2	1	133
Discus whitneyi	8	2					1	6		1	5	3				1	2	2	1	2	34
Euchemotrema fraternum	42	7						5				1									55
Euchemotrema leai	1							1			6	2	2		1		2	7	3	3	28
Euconulus alderi								1		3	17	3	1				2	11	3	2	43
Euconulus fulvus	48	17	2		1	1	6	12	1	3	2	4		1	1			3	4	1	107
Euconulus polygyratus	24	9			1	1	3	11		1		2				1		1	1		55
Gastrocopta armifera	13						1								1						15
Gastrocopta contracta	57	8				1	1	6		3	6	3			1			6	6	1	99
Gastrocopta corticaria	30	1																			31
Gastrocopta holzingeri	42	2				1	1	1		1	1			1	1						51
Gastrocopta pentodon	61	8			1	1	1	5		5	6	2			2	1			1	1	95
Gastrocopta similis	1																				1
Gastrocopta tappaniana	3						2	3		3	21	4	1		5		3	12	6	4	67
Glyphyalinia indentata	34	7			1		1	8		1	2	2			2	1		1	2	1	63
Glyphyalinia rhoadsi	8	1					1	4													14
Glyphyalinia wheatleyi		1						1													2
Guppya sterkii	3							1													4
Haplotrema concavum	1					1				2	1										5
Hawaiia minuscula	38	1					2	5		1	5	3			1			4	5	4	69
Helicodiscus parallelus	21	4						11		1	12	4			2			4	2		60
Helicodiscus shimeki	66	19	1	1	1	1	7	14		3	4	6			2			2	2	1	130
Hendersonia occulta	28	3				1	8	4	2	1	1	1						1			50
Mesodon thyroidus	3	1																			4
Neohelix albolabris	3	3			1		1	3													11
Nesovitrea binneyana	24	9	1				2	4				5			1	1		1	1	1	50
Nesovitrea electrina	5	3				1	1	1		4	25	7	2		3	1	2	13	4	2	74
Novisuccinea ovalis	26	5		1			8	7			2	2	1			1	1	1	3		58
Oxychilus cellarius								1													1
Oxychilus draparnaudi		1																			1
Oxyloma retusa	1								1	1	2	2			1		2	7	5	4	26
Paravitrea multidentata	44	12			1		1	10													68
Planogyra asteriscus		2	1				1	1				3						1			9
Pomatiopsis lapidaria									1			1						1	1		4
Punctum minutissimum	51	22	1		1	1	8	16		2	9	5	1		4		1	3	4	4	133
Punctum n.sp.											3							5	1		9
Punctum vitreum	28	1					5	4	2	3	3	2						1			49
Pupilla muscorum								1				1									2
Pupoides albilabris																			1		1
Stenotrema barbatum											1							2			3
Striatura exigua	14	8			1	1	3	8		3	15	9	1				1	4	2		70

Table 3. (continued)

Taxon	Habitat Code																				
	RO1	RO2	RO3	UF1	UF2	UF3	UF4	UF5	LF1	LF2	LF3	LF4	LF5	UG1	UG2	UG3	LG1	LG2	LG3	LG4	Total
Striatura ferrea	11	7				1	2	7		3	2	6	1					1			41
Striatura milium	31	20	1		1	1	7	13		5	22	10	2		1		1	6	4		125
Strobilops aenea	1																				1
Strobilops affinis										2	5	2			1		1	5	3		19
Strobilops labyrinthica	76	22	2		1	1	8	13		5	17	9	1	1	3	1	1	7	4	4	176
Vallonia costata	18	2					1	4		1	1	2			1	3	1	2	4	1	41
Vallonia excentrica								1								2					3
Vallonia gracilicosta	31	1																			32
Vallonia perspectiva	11							1													12
Vallonia pulchella	8							4		1	2				1	2	1	3	7		29
Vertigo bollesiana	41	18	1				4	4		2	1	2									73
Vertigo cristata	9	10	2					2			1	1									25
Vertigo elatior					1		1	1		4	20	4	1		2		1	12	6	5	58
Vertigo gouldi	81	20	2	1		1	2	10	1	2	1	2									123
Vertigo hubrichti	54	15					1	2							1						73
Vertigo milium	19							2		2	6	3				1		4	3		40
Vertigo modesta								1													1
Vertigo morsei																		6			6
Vertigo nylanderi						1		1		2	11	2									17
Vertigo ovata										1	4	1					1	4	7	5	23
Vertigo paradoxa	10	3	2					2			1										18
Vertigo pygmaea	15			1			2	3			1				1	2	2	2	6		35
Vertigo tridentata	5																				5
Vitrina limpida	4						2	5				1			2	2				1	17
Webbhelix multilineata	3							1			1						1				6
Zonitoides arboreus	73	21	2		1	1	7	16		6	24	8	2	1	1			4	4	2	173
Zonitoides nitidus	5	1					4	3			6	2				1	3	1		3	29
Zoogenetes harpa	6	2						3													11
Species Richness	63	48	16	8	16	20	42	61	8	38	48	49	15	4	32	18	25	44	40	28	

in their occurrence frequencies among the five major habitat groups (rock outcrop, upland forest, lowland forest, upland grassland, lowland grassland). The number of occurrences and absences for each taxon within each habitat group was calculated, with the resultant contingency table being analyzed via a log-likelihood ratio test. Again, a Bonferroni correction was used to adjust the significance threshold to 0.000610.

RESULTS

Enumeration of fauna

A total of 82 taxa were identified from the 242 sampled sites. An additional two taxa (*Discus patulus* [Deshayes, 1830] and *Zonitoides limatulus* [W. G. Binney, 1840]) have been previously reported from this region (Levi and Levi 1950, Teskey 1954), but were not relocated during this survey. The total known fauna known from the region is thus 84. The distribution (Table 2), habitat associations (Table 3), and taxonomic considerations (when appropriate) for each of the 82 encountered taxa are detailed in the following alphabetical list. Distribution maps for each (also alphabetically arranged) are found in Appendix I.

Allogona profunda **(Say, 1821)**

Twenty-seven stations for this species were encountered south and east from the Garden Peninsula. Populations were limited to rock outcrops and upland forests. Complete shells were often difficult to find due to high levels of shrew and rodent predation.

Anguispira alternata **(Say, 1816)**

This was the most abundant large land snail in the study area (128 sites), being found throughout the region. The great majority of sites occurred on rock outcrops and upland woods. Over 95% of carbonate cliff sites supported populations of this species.

Carychium exiguum **(Say, 1822)**

Seventy-three stations for this species were encountered throughout the region, with most populations occurring in lowland forests and grasslands. This species is easily distinguished from the following taxon, being consistently wider for a given shell height, even at sites of co-occurrence (Nekola and Barthel 2002).

Carychium exile **(H. C.Lea, 1842)**

One hundred seven stations were encountered, with occurrence frequencies being highest in the southwest and on the Garden Peninsula. Most populations were found in rock outcrops and upland forests, although it was also found in almost 30% of lowland forests. Morphometric analysis of these populations documented continual variation from small individuals in the southwest to large individuals in the northeast. These data indicate that *Carychium exile canadense* Clapp, 1906 simply represents an endpoint of continuous clinal variation, and does not warrant subspecies designation (Nekola and Barthel 2002).

Catinella avara **(Say, 1824)**

Nineteen stations for this species were found throughout the region in grasslands and lowland forests. While its shell appeared larger and darker than other members of the genus, the taxonomy of this group (as it true for most Succineids) is made difficult due to extreme plasticity in shell and anatomical morphology. Although Turgeon *et al.* (1998) lump *Catinella avara* into *Catinella vermeta* (Say, 1829), I have chosen to retain *C. avara* due to its long-standing use by North American malacologists (*e.g.*, Baker 1939, Pilsbry 1948, Hubricht 1985), and the use of *C. vermeta* by Frest and Dickson (1986) to designate a different xerophile *Catinella* taxon (see below).

Catinella exile **(Leonard, 1972)**

Eight stations for this taxon were located throughout the region from lowland grasslands (especially calcareous fens). Diagnostic characteristics are based on Frest (1990), who noted that its shell is smaller, has a higher spire, and is more orange-colored than *Catinella avara*. Described from Pleistocene material, this taxon was previously reported extant only from Iowa fens (Frest, 1990).

Catinella **cf. *gelida*** **(F. C. Baker, 1927)**

Nineteen populations for this taxon were found south from Green Bay, with all being limited to rock outcrops. Its shell is smaller than *Catinella avara*, has stronger growth lines, and is of yellowish-green color (Frest 1991). However, it appears essentially identical to *Catinella wandae* (Webb, 1953), which is found in dry, rocky woodlands from eastern Iowa to eastern Oklahoma (Hubricht 1985). No distinguishing features have been provided in the literature (Webb 1953, Frest 1991) to allow separation of these two taxa . Anatomical comparison of *C. wandae* with the type of *Catinella gelida* is not possible, as the latter is a Pleistocene fossil. More anatomical and genetic analysis will be necessary to determine the relationship between these taxa. If valid, *C. gelida* represents a rare Pleistocene relict that was previously reported from only a dozen very small populations in northeastern Iowa and the Black Hills of South Dakota (Frest 1991, Frest and Johannes 1993).

Catinella **cf. *vermeta*** **(Say, 1829)**

A single population of this taxon was located on the Maxton Plains Alvar of Drummond Island. It is smaller (< 5 mm tall) and has a deeper suture than *Catinella avara*. I have followed the taxonomic treatment of Frest and Dickson (1986) for these specimens. They reported a similar small, deep-sutured *Catinella* from xeric prairies in western Iowa as *C. vermeta*. Seemingly identical individuals also occur in xeric carbonate glades of northeastern Iowa and southeastern Minnesota (Nekola in press).

Cochlicopa lubrica **(Müller, 1774)**

Seventy stations for this taxon were located, with occurrence frequencies being highest in the southwest. Populations were most frequently encountered in upland forests and grasslands. It was especially characteristic of anthropogenically modified habitats such as field-edge stone piles, road verges, and old fields. Following the morphometric analyses of Preece (1992), I have used this name to demarcate individuals with shell heights > 6 mm and widths > 2.3 mm. I have also chosen the European convention (*e.g.*, Kerney and Cameron 1979, Preece 1992, Armbruster 1995) in using *Cochlicopa*, rather than *Cionella* (Turgeon *et al.* 1998), as the generic name for this and the following two taxa.

Cochlicopa lubricella **(Porro, 1838)**

Thirty-eight stations for this taxon were found throughout the region in a wide variety of habitats. It was most frequently observed in upland forest sites. Kerney and Cameron (1979), Hubricht (1985), and Preece (1992) are followed in using this name to demarcate those mature individuals with shells < 2.3 mm wide and < 6 mm tall. Unlike European populations that are most characteristic of xeric grasslands, the smallest shells were consistently observed from open, calcareous wetlands. Members of this species often co-occurred with *Cochlicopa lubrica*, with intermediate individuals being observed from a number of sites. Additional morphometric and genetic analysis is needed to determine if these taxa are distinct in eastern North America, and if North American populations should be considered synonymous with Eurasian populations.

Cochlicopa morseana **(Doherty, 1878)**

Twenty-two stations for this taxon were encountered, with occurrence frequencies being highest in the east. Populations were largely limited to cool, mesic rock outcrops and upland forests. This taxon differed from other Cochlicopa in the region by possessing tall (> 6 mm) and narrow (< 2.3 mm) shells with flattened whorls (Pilsbry 1948).

***Columella simplex* (Gould, 1841)**

This taxon was found at 130 stations. Populations were most common north and east from Sturgeon Bay. Although observed in almost all habitat types, populations were most often encountered on rock outcrops and upland forests. Live individuals were often observed on low-growing herbs and shrubs, and could be most easily collected through sweep-netting of vegetation. While most populations appeared identical to those figured in Pilsbry (1948), some taller individuals were also found that approached *Columella columella alticola* (Ingerson, 1875) in size, although not in shape. Additional investigations will be necessary to determine the taxonomic status of these populations.

***Deroceras* spp.**

Due to the nature of field collection techniques, live slugs were only infrequently observed. However, internal plates with conspicuous calcareous granules representing *Deroceras* spp. were encountered 67 times from a variety of habitats, particularly to the south of Green Bay. Observations of living individuals suggested that many of the lowland populations represent the native *Deroceras laeve* (Müller, 1774), while upland populations are the introduced *Deroceras reticulatum* (Müller, 1774). The introduced *Arion hortensis* Férussac, 1819 was also frequently observed in upland, wooded sites.

***Discus catskillensis* (Pilsbry, 1898)**

This taxon was observed at 133 stations. It tended to be most frequent northeast of Sturgeon Bay, and showed a strong preference for rock outcrops and upland forests. It also appeared relatively tolerant of anthropogenic disturbance, being frequently present in old fields and field-edge stone piles. Individuals from the far east of the study region (particularly Drummond Island) appeared intermediate with *Discus whitneyi* (Newcomb, 1864). I have also frequently encountered such intermediate individuals in southern Ontario, the Keweenaw Peninsula, and northern Minnesota, suggesting that Pilsbry (1948) may be correct in considering *Discus catskillensis* a subspecies of *D. whitneyi*.

***Discus whitneyi* (Newcomb, 1864) [*Discus cronkhitei*]**

Thirty-four stations for this taxon were encountered throughout the region. Although found in a variety of habitats, populations tended to most frequently occur in lowland grasslands, lowland forests, and upland forests.

***Euchemotrema fraternum* (Say, 1824) [*Stenotrema fraternum*]**

Fifty-five stations for this taxon were found throughout the region. It was most frequently encountered on rock outcrops.

***Euchemotrema leai* (A. Binney, 1841) [*Stenotrema leai*]**

Twenty-eight stations for this taxon were encountered throughout the region. It was most frequently found in lowland grasslands and forests.

***Euconulus alderi* (Gray, 1840)**

Forty-three stations for this taxon were encountered throughout the region, principally from lowland grasslands and forests. Live material was verified as representing this taxon in 1999 by Robert Cameron (pers. comm.). Mature shells were most easily distinguished from *Euconulus fulvus* (Müller, 1774) by being < 2.8 mm in diameter, having a darker-orange color, more glassy luster, and possessing spiral lines on the ventral surface that were more distinct than the transverse lines (Kerney and Cameron 1979). The diameter of the nuclear whorl for *Euconulus alderi* also appeared slightly larger than that of *E. fulvus*. However, in this region *E. alderi* and *E. fulvus* were less distinct than western European populations. The frequency of intermediate individuals appeared low enough, however, to merit maintaining these taxa as separate. Further morphometric and genetic work will be necessary to verify this hypothesis.

***Euconulus fulvus* (Müller, 1774)**

This taxon was observed at 107 stations. Populations tended to be more frequent to the northeast of Sturgeon Bay, and were most often encountered on rock outcrops and upland forests.

***Euconulus polygyratus* (Pilsbry, 1899)**

Fifty-five stations for this taxon were encountered throughout the region. Populations were most often observed in upland forests and rock outcrops. I have opted to consider *Euconulus polygyratus* as separate from *Euconulus fulvus* due to its slower and more constant rate of increase in whorl width, allowing the body whorl thickness to be less than that of the initial whorls. This species also has pitted transverse lines on the protoconch, giving it a silky luster.

***Gastrocopta armifera* (Say, 1821)**

Fifteen stations for this taxon were encountered principally to the south of Green Bay. Populations were largely limited to rock outcrops and upland grasslands. It differed from the closely related *Gastrocopta similis* (Sterki, 1909) by possessing a wider adult shell, a pyramidal columellar lamella, and a taller and thinner lower palatal lamella (Hubricht 1972).

***Gastrocopta contracta* (Say, 1822)**

Ninety-nine stations for this taxon were encountered

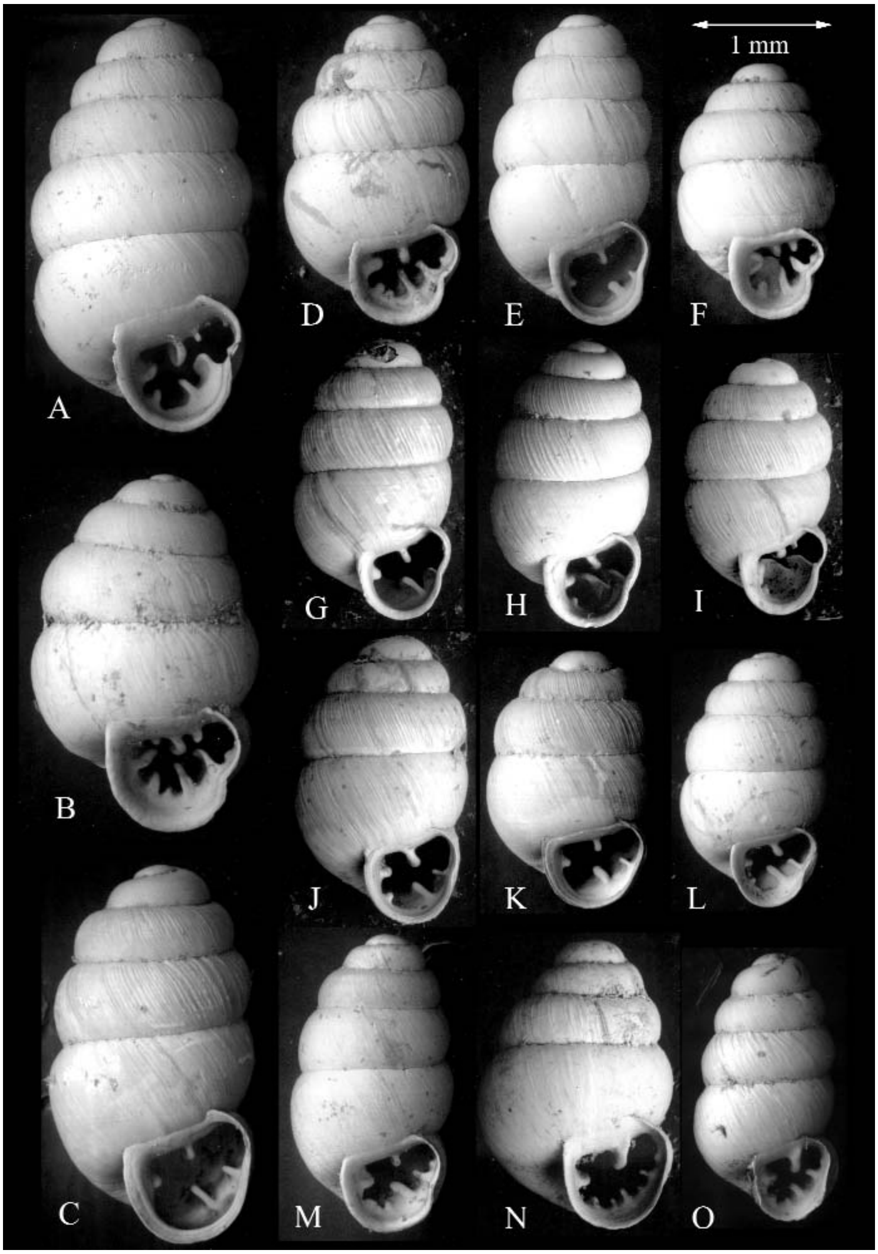

Figure 2. Scanning electron micrographs of selected Vertigo and Gastrocopta species that occur in the study area. A. Vertigo morsei, Summerby Swamp, Mackinac County, Michigan (84º47'43"W, 45º58'15"N), UWGB #3235. B. Vertigo ovata, Kimlark Lake, Marinette County, Wisconsin (87º50'56"W, 45º39'37"N), UWGB 1866. C. Vertigo modesta, Metcalfe Rock, Grey County, Ontario (80º26'31"W, 44º25'3"N), UWGB 2543. D. Vertigo elatior, Allenton Fen, Washington County, Wisconsin (88º18'25"W, 43º22'41"N), UWGB 600. E. Vertigo tridentata, Pictured Rocks County Park, Jones County, Iowa (91º6'18"W, 42º12'28"N), UWGB 919. F. Vertigo milium, Thiry Daems, Kewaunee County, Wisconsin (87º42'14"W, 44º36'8"N), UWGB 1812. G. Vertigo paradoxa, Maple Hill, Chippewa County, Michigan (84º46'55"W, 46º9'34"N), UWGB 2270. H. Vertigo hubrichti, Benderville Wayside, Brown County, Wisconsin (87º50'31"W, 44º36'47"N), UWGB 644. I. Vertigo nylanderi, Garden Corners, Delta County, Michigan (86º32'4"W, 45º53'23"W), UWGB 2967. J. Vertigo gouldi, Toft Point, Door County,Wisconsin (87º5'5"W, 45º4'40"N), UWGB 1062. K. Vertigo cristata, Toft Point, Door County, Wisconsin (87º5'5"W, 45º4'40"N), UWGB 1061. L. Vertigo bollesiana, Ansel's Point, Delta County, Michigan (86º34'26"W, 45º48'12"N), UWGB 538. M. Vertigo pygmaea, Benderville Wayside, Brown County, Wisconsin (87º50'31"W, 44º36'47"N), UWGB 647. N. Gastrocopta tappaniana, Allenton Fen, Washington County, Wisconsin (88º18'25"W, 43º22'41"N), UWGB 590. O. Gastrocopta pentodon, Prairie du Rocher, Randolph County, Illinois (90º11'56"W, 38º6'28"N), UWGB 3895.

throughout the study region. However, populations were most frequently observed south from the Door Peninsula, and occurred most frequently on rock outcrops and lowland grasslands.

Gastrocopta corticaria **(Say, 1816)**

Thirty-one stations for this taxon were encountered south from the Door Peninsula. Populations were limited to rock outcrops. Some of the populations in the south of the study region possessed between 100-250 individuals per sample.

Gastrocopta holzingeri **(Sterki, 1889)**

Fifty-one stations for this taxon were located. Populations were most frequently observed south from Green Bay, and were most often encountered on rock outcrops and upland grasslands. It was not previously reported from the Upper Peninsula of Michigan (Hubricht 1985).

Gastrocopta pentodon **(Say, 1821)** (Fig. 2O)

Ninety-five stations for this taxon were encountered. Populations tended to be less common in the far east of the study region, and were most often observed on rock outcrops.

Gastrocopta similis **(Sterki, 1909)**

Only a single population of this species was located at the region's most southern rock outcrop where it co-occurred with *Gastrocopta armifera*. It differed from that species by possessing narrower adult shells, a plate-like columellar lamella, and a wide lower palatal lamella inserted more deeply into the aperture than the upper palatal.

Gastrocopta tappaniana **(C. B. Adams, 1842)** (Fig. 2N)

Sixty-seven stations for this taxon were encountered. Although found throughout the region, occurrence frequencies were lowest in the northern Door Peninsula. It was most often observed in lowland grasslands and forests. While occasionally sympatric with *Gastrocopta pentodon* (especially in wooded lowlands), intermediates were not noted.

Glyphyalinia indentata **(Say, 1823)**

Sixty-three stations for this taxon were encountered. Populations tended to be more common towards the southwest, and less common on rock outcrops.

Glyphyalinia rhoadsi **(Pilsbry, 1899)**

Fourteen stations for this taxon were encountered. Populations tended to be more common towards the northeast, and were limited to upland forests and rock outcrops.

Glyphyalinia wheatleyi **(Bland, 1883)**

Only two stations for this taxon were encountered, both from calcareous mesic woods near the Great Lakes shore. One of these sites had been quite heavily disturbed by human activities.

Guppya sterkii **(Dall, 1888)**

Only four stations for this taxon were encountered from rock outcrops and upland forests in proximity to Green Bay. These populations are the most northern yet reported (Hubricht 1985).

Haplotrema concavum **(Say, 1821)**

Five stations for this taxon were encountered from Drummond Island and the south end of Green Bay. Populations were most often found in lowland forests dominated by black ash. Although absent from rock outcrops in eastern Wisconsin, it is abundant on such habitats in northeastern Iowa and northern Illinois (Nekola in press).

Hawaiia minuscula **(A. Binney, 1840)**

Sixty-nine stations for this taxon were encountered. Populations were most frequently observed to the south of Green Bay in lowland grasslands and rock outcrops.

Helicodiscus parallelus **(Say, 1817)**

Sixty stations for this taxon were encountered across a variety of habitats. Populations were less common in the northern part of the Door Peninsula than elsewhere in the region. Shells of this taxon closely resembled those of *Helicodiscus shimeki*, from which they differed by having wider individual whorls (> 1 mm as measured from the bottom), and relatively deeper and narrower umbilici (Hubricht 1962). Although these two species are usually quite distinct in Wisconsin and the Garden Peninsula, some individuals from the eastern Upper Peninsula appeared intermediate.

Helicodiscus shimeki **Hubricht 1962**

This taxon was observed at 133 stations throughout the study region. Populations demonstrated a preference for rock outcrops and upland forests.

Hendersonia occulta **(Say, 1831)**

Fifty stations for this taxon were encountered along the Lake Michigan shore from Milwaukee to the northern tip of the Door Peninsula and south along the Niagaran Escarpment to Calumet County. Across this extent, populations tended to favor rock outcrops and upland forests. It is also known from the floodplain of the Escanaba River in Delta County (Pearce *et al.* 1992). It is a common Pleistocene fossil over much of the central US (Hubricht 1985).

Mesodon thyroidus **(Say, 1816)**

Four stations for this taxon were encountered. Populations were restricted to rock outcrops in the northern Door Peninsula.

Neohelix albolabris **(Say, 1816)** [*Triodopsis albolabris*]

Eleven stations for this taxon were encountered. Most populations were located in upland forests on the Door Peninsula. This was the largest species observed during this survey.

Nesovitrea binneyana **(Morse, 1864)**

Fifty stations for this taxon were encountered. Populations became more common towards the northeast, and tended to be most common on rock outcrops.

Nesovitrea electrina **(Gould, 1841)**

Seventy-eight stations for this taxon were encountered throughout the region. Populations were most frequently encountered in lowland grasslands and forests. It was only rarely found sympatric with *Nesovitrea binneyana*.

Novisuccinea ovalis **(Say, 1817) [*Succinea ovalis*]**

Fifty-eight stations for this taxon were encountered in the region. Populations were largely limited to eastern Wisconsin, and tended to be most common in upland forests and rock outcrops.

Oxychilus cellarius **(Müller, 1774)**

Only a single population of this introduced Eurasian species was observed from the region, where it occurred on a wooded limestone talus slope at the northern tip of the Door Peninsula. This population was first located by Robert Cameron (pers. comm.) in September 1999.

Oxychilus draparnaudi **(Beck, 1837).**

Only a single population of this Eurasian species was located in the region, where it occurred on a low limestone outcrop and adjacent rocky roadside. Because this population was centered on a summer vacation house, it is possible that introduction occurred via landscape plantings. This population was also located by Robert Cameron (pers. comm.) in September 1999.

Oxyloma retusa **(I. Lea, 1834)**

Twenty-six stations for this taxon were encountered throughout the region. Most populations occurred in lowland grasslands.

Paravitrea multidentata **(A. Binney, 1840)**

Sixty-eight stations for this taxon were encountered. It became less common south of Sturgeon Bay, and was limited to rock outcrops and upland forests.

Planogyra asteriscus **(Morse, 1857)**

Nine stations for this taxon were encountered. Populations were essentially limited to white cedar-dominated upland and lowland forests in the Upper Peninsula. Although Pilsbry (1948) reported it to be limited to alder thickets, dune slacks, and the wooded margins of Sphagnum bogs, I was unable to locate it from such sites.

Pomatiopsis lapidaria **(Say, 1817)**

Four stations for this taxon were encountered. Populations were limited to lowland forests and grasslands. Like Hubricht (1985), I have never encountered this species in an aquatic setting, and feel that it represents a terrestrial species.

Punctum minutissimum **(I. Lea, 1841)**

This taxon was encountered at 133 stations. Populations were largely absent south of Green Bay, and occurred preferentially in rock outcrops and upland forests. Its shells are differentiated those of *Punctum vitreum* H. B. Baker, 1930 by having all ribs of equal size (Pilsbry 1948). Intermediate individuals were infrequently encountered near the southern end of Green Bay.

Punctum vitreum **H. B. Baker, 1930**

Forty-nine stations for this taxon were encountered south from Sturgeon Bay. South of Green Bay it replaces *Punctum minutissimum* as the dominant *Punctum* species of forested habitats. Its shells were distinguished by having every 4^{th} or 5^{th} rib being markedly larger than the intervening ones (Pilsbry 1948). Identification of this species was often made difficult because these larger ribs commonly became worn and almost indistinguishable from the smaller.

Punctum **n. sp. (*sensu* Frest, 1990)**

This undescribed taxon was encountered at nine stations on the Door Peninsula and the eastern sections of the study region, where it was restricted to lowland grasslands and forests. This taxon was first reported by Frest (1990) from Iowa fens. It differs from *Punctum minutissiumum* and *Punctum vitreum* by having large (> 1.2 mm diameter) and tall (> 0.75 mm) shells with inflated whorls, a narrow umbilicus (< $^1/_4$ shell diameter), and a rusty-red color. Additional morphometric and genetic work will be necessary to validate its status.

Pupilla muscorum **(Linné, 1758)**

Two stations for this taxon were encountered in anthropogenically altered calcareous woodlands from the far east of the study region. This species is more common in southern Ontario, where it occurs in a variety of calcareous upland habitats (Oughton 1948, McMillan *et al.* in press). It is also well represented in the central US as a Pleistocene fossil (Hubricht 1985).

***Pupoides albilabris* C. B. Adams, 1841**

Only a single population for this taxon was encountered at a calcareous meadow near the south end of Green Bay. This population is disjunct from the southern and central parts of Wisconsin, and represents one of the most northern reported stations. However, as all recovered shells were opaque-white (and long dead), it is possible that this population is no longer extant.

***Stenotrema barbatum* (Clapp, 1904)**

Three stations for this species were observed in the far south of the study region from lowland grasslands and forests.

***Striatura exigua* (Stimpson, 1847)**

Seventy stations for this taxon were encountered. Populations became more common towards the northeast of the study region. It was most often located in lowland forests dominated by tamarack, white cedar, or black ash.

***Striatura ferrea* Morse, 1864**

Forty-one stations for this taxon were encountered. Populations became more frequent towards the northeast of the study region, and were essentially limited to forests. South of Sturgeon Bay, it was limited to rich, lowland forests.

***Striatura milium* (Morse, 1859)**

This taxon was observed at 125 stations. Populations became more common in occurrence towards the north, and were most often located in lowland forests. In the north it replaced *Punctum minutissimum* as the most common disk-shaped micro-snail. In the south it was less common and limited to rich, wooded wetlands.

***Strobilops aenea* Pilsbry, 1926**

A single colony of this species was located in the study area from a mesic, wooded limestone talus slope along the east shore of Green Bay where it was found crawling on coarse woody debris after a rain. This population was discovered by Brian Coles (pers. comm.) in July 1999. It was previously reported in the region from Peninsula State Park, approximately 20 km north (Levi and Levi 1950). These populations represent this species, known northern range limit, and are likely disjunct from northeastern Iowa (Hubricht 1985).

***Strobilops affinis* Pilsbry, 1893**

Nineteen stations for this taxon were encountered from grasslands and lowland forests. Except for a lone colony in a fen near the Mackinac Straits, populations were limited to the south of Sturgeon Bay.

***Strobilops labyrinthica* (Say, 1817)**

This species was found at 176 stations. Although most frequently encountered in rock outcrops and upland forests to the north of Green Bay, it was found throughout the study region from most surveyed habitat types.

***Vallonia costata* (Müller, 1774)**

Forty-one stations for this taxon were encountered, primarily west from the Garden Peninsula. While found in a wide variety of habitats, it appeared quite tolerant of human disturbance, being characteristic on calcareous roadsides, old fields, and stonepiles.

***Vallonia excentrica* Sterki, 1893**

Only three stations for this taxon were encountered in upland habitats south from Sturgeon Bay. These sites (representing abandoned agricultural fields and stonepiles) have been subjected to high levels of human disturbance. Mature shells of this species are most easily separated from those of *Vallonia pulchella* (Müller, 1774) by their yellowish color, smoother surface, and minor axis diameter of $1^1/_2$ mm or less (Gerber 1996).

***Vallonia gracilicosta* Reinhardt, 1883**

Thirty-two stations for this taxon were encountered throughout the region from rock outcrops. Occurrences of this species follow the Niagaran Escarpment and adjacent carbonate outcrops from southeastern Minnesota to southern Ontario. It is an abundant late Pleistocene fossil throughout central North America (Hubricht 1985).

***Vallonia perspectiva* Sterki, 1892**

Twelve stations for this taxon were encountered south from Lake Winnebago, principally from rock outcrops. These populations often produced over 250 shells per sample.

***Vallonia pulchella* (Müller, 1774)**

Twenty-nine stations for this taxon were encountered. Populations were confined to the west of the Mackinac Straits, and tended to be most common in grasslands. It was often present in sites that had been subjected to intense levels of anthropogenic disturbance. Its shells were differentiated from the similar *Vallonia excentrica* by their white color, distinct growth lines, and minor axis diameter of $1^1/_2$ mm or more (Gerber 1996).

***Vertigo bollesiana* (Morse, 1865)** (Fig. 2L)

Seventy-three stations for this taxon were encountered. Populations were most frequently observed from rock outcrops and upland forests on the Door Peninsula. Shells from populations located from lowland habitats appeared more narrow and striate than those from upland habitats.

***Vertigo cristata* (Sterki, 1919)** (Fig. 2K)

Twenty-five stations for this clearly-marked species (Nekola 2001) were encountered. It was confined to rock outcrops and forests north of 45°N. No intermediates between it and either *Verigo gouldi* (A. Binney, 1843) or *Vertigo paradoxa* Sterki, 1900 were noted, even at sites of co-occurrence.

***Vertigo elatior* Sterki, 1894** (Fig. 2D)

Fifty-eight stations for this taxon were encountered throughout the region. Populations were largely limited to lowland forests and grasslands, where this taxon became the most common *Vertigo* species. It is an abundant late Pleistocene fossil in the central USA (Frest and Dickson 1986).

***Vertigo gouldi* (A. Binney, 1843)** (Fig. 2J)

This taxon was found at 123 stations throughout the region, where it represented the most frequently occurring *Vertigo* species. While most often observed on rock outcrops, it was also occasionally located in upland and lowland forests.

Vertigo hubrichti (Pilsbry, 1934) (Fig. 2H)

Seventy-three stations for this taxon were encountered. Populations were largely limited to rock outcrops, and were most frequently seen on the Door and Garden Peninsulas. This species was first described as a Pleistocene fossil, but was subsequently found alive at approximately 50 sites in the Paleozoic Plateau of northeastern Iowa, southwestern Wisconsin, and southeastern Minnesota (Frest 1991). It is differentiated from *Vertigo paradoxa* Sterki, 1900 by having a strong basal lamella, a more deeply inserted lower palatal lamella, and a deeper depression on the outside of the shell over the lower palatal lamella (Pilsbry 1948, Frest 1991). However, individuals appearing intermediate between it and *V. paradoxa* were also observed throughout the eastern Upper Peninsula and southern Ontario. While morphometric and genetic analysis across the geographic ranges of both taxa will be necessary to determine their status, these preliminary observations suggest that *Vertigo hubrichti* may be best regarded as a subspecies of V. paradoxa that is currently limited to the vicinity of the western Lake Michigan shore and the upper Mississippi River valley.

***Vertigo milium* (Gould, 1840)** (Fig. 2F)

Forty sites for this taxon were encountered. This species was essentially limited to sites south of Sturgeon Bay, where it was found across a wide variety of habitats. It reached its highest population densities (> 300 per sample) on calcareous open meadows and fens.

***Vertigo modesta* (Say, 1824)** (Fig. 2C)

A single population of this species was located in north-eastern Wisconsin, where individuals occurred in leaf litter accumulations under car-sized boulders on a natural, glacially deposited rock pile. This habitat is insulated from summer warmth, with ice persisting until June. The nearest known extant colonies occur approximately 150 km to the north on the northern tip of the Keweenaw Peninsula, 250 km to the northwest on the north shore of Lake Superior in northeastern Minnesota, and 300 km to the east on Manitoulin Island (Nekola *et al.* 1999). All other reported central USA occurrences for this taxon are Pleistocene fossils (Hubricht 1985).

***Vertigo morsei* Sterki, 1894** (Fig. 2A)

Six stations for this taxon were encountered. Although populations were scattered throughout the region, they were all limited to calcareous fens supporting loose accumulations of bryophytes and dead sedge leaves over the ground surface. In Iowa, this species is also very rare and limited to fens (Frest 1990).

***Vertigo nylanderi* Sterki, 1909** (Fig. 2I)

Seventeen stations for this taxon were encountered throughout the region. Populations were essentially limited to rich lowland forests, and were typically dominated by tamarack or black ash. Fewer than 5 mature individuals were secured from all but 2 sites. The only other reports of this species are from Maine, Ontario, Michigan, and northwestern Minnesota (Oughton 1948, Pilsbry 1948, Dawley 1955, Burch and Jung 1988, Pearce *et al.* 1992, Nekola and Massart 2001). It is also known from Pleistocene sediments in central Illinois (Frest 1991, Miller *et al.* 1994), and Holocene sediments from southern Ontario (Rich Meyrick pers. comm.).

***Vertigo ovata* Say, 1822** (Fig. 2B)

Twenty-three stations for this taxon were encountered throughout the region. Populations were limited to lowland grasslands and forests.

***Vertigo paradoxa* Sterki, 1900** (Fig. 2G)

Eighteen stations for this taxon were encountered. Populations became more common towards the east and tended to occur most often in soil pockets on mesic, wooded cliffs. It largely replaced *Vertigo hubrichti* east of Schoolcraft County. *Vertigo paradoxa* was previously reported in the eastern USA only from northern Maine, the northern Lower Peninsula of Michigan, and the Black Hills of South Dakota (Frest and Johannes 1993). It is a wide-ranging fossil from Pleistocene sediments in the central USA (Frest and Johannes 1993).

***Vertigo pygmaea* (Draparnaud, 1801)** (Fig. 2M)

Thirty-five stations for this taxon were encountered across a wide variety of habitats. Populations were more frequently encountered south of Sturgeon Bay and were often observed in areas subjected to high levels of anthropogenic disturbance.

***Vertigo tridentata* Wolf, 1870** (Fig. 2E)

Five stations for this taxon were located on rock outcrops south of Green Bay. These populations are the most northern yet reported (Hubricht 1985).

***Vitrina limpida* Gould, 1850**

Seventeen stations for this taxon were encountered. Populations were found in a wide variety of habitats, and became more common towards the east. In the west of the study region, it appeared limited to sites near to the Lake Michigan shore. It also appeared able to tolerate fairly high levels of anthropogenic disturbance.

Webbhelix multilineata* (Say, 1821)** [Triodopsis miltilineata***]

Six stations for this taxon were observed from Sturgeon Bay to Lake Winnebago in a variety of habitats.

***Zonitoides arboreus* (Say, 1816)**

One hundred and seventy-three stations for this taxon were encountered throughout the region. Although found in almost every habitat type, it was most frequently located on rock outcrops and lowland forests. Only rarely were more than a dozen mature shells secured from a single site.

***Zonitoides nitidus* (Müller, 1774)**

Twenty-nine stations for this taxon were encountered from a wide variety of habitats. Populations were largely limited to sites south from the Door Peninsula, where they appeared tolerant of anthropogenic disturbance.

***Zoogenetes harpa* (Say, 1824)**

Eleven stations for this taxon were encountered. Populations occurred more frequently to the northeast, and were limited to rock outcrops and upland forests.

Excluded Species

Two taxa previously reported from the region were considered to be erroneously reported by earlier workers. *Mesodon pennsylvanicus* (Green, 1827) was listed from Marinette County by Jass (1986). This report (and all others in that paper) is based upon specimen identifications made by Leslie Hubricht during the mid-1980's. I have found specimens identified during this time in the Hubricht Collection at FMNH to be commonly misidentified. As neither this species, nor other extralimital taxa (*Triodopsis tridentata* [Say, 1816], *Triodopsis vulgata* Pilsbry, 1940) reported by Jass (1986) from just beyond the study region were located during this more exhaustive survey, I have chosen to consider these reports as unreliable.

Additionally, Hubricht (1985) reports *Vertigo ventricosa* (Morse, 1865) from Mackinac County. My observations of material at FMNH have shown this species to be commonly misidentified by Hubricht and others. Shells of *V. ventricosa* differ from those of *Vertigo pygmaea* and *Vertigo elatior* by having an aperture that is approximately 1/3 of the shell height, a weak sinulus, a very weak (or absent) callus between the palatal lamellae, a weak crest, very weak to absent striae, and an almost transparent shell of light brown color (Pilsbry 1948). I have not yet observed this suite of characteristics from any individual collected west of central New York State. Vertigo ventricosa appears to possess a narrow range extending from Newfoundland to West Virginia along the crest of the Appalachians, therefore I have chosen to consider all reports of this species from the western Great Lakes to be based on misidentifications.

Species richness patterns

The number of species encountered per county was found to differ substantially (Table 2). Door County had the maximum number of observed taxa at 70, followed by Brown (63), Delta (57), Chippewa (55), Manitowoc (53), Calumet (51), and Mackinac (50). The lowest richness levels were (not surprisingly) limited to counties with only single collection sites, including Washington (19), Green Lake (17), and Langlade (12).

The number of encountered species was also found to differ among habitat types (Table 3). Carbonate cliffs and rocky woodlands harbored the greatest number of species (63 and 61, respectively), accounting for approximately 75% of the regional fauna. Lakeshore carbonate ledges, lakeshore woodlands, tamarack wetlands, white cedar wetlands, fens, and calcareous meadows were found to harbor between 49-40 taxa (58%-48% of the regional total). The most depauperate fauna was that of sand dunes, where only 4 taxa were observed (5% of total).

Occurrence Frequency *vs.* Geography

Thirty-one of the encountered taxa were found to vary significantly in their occurrence frequencies across the study region (Table 4). Fourteen (*Allogona profunda*, *Catinella* cf. *gelida*, *Cochlicopa lubrica*, *Deroceras* spp., *Gastrocopta corticaria*, *Gastrocopta holzingeri*, *Hawaiia minuscula*, *Hendersonia occulta*, *Novisuccinea ovalis*, *Punctum vitreum*, *Vallonia costata*, *Vallonia perspectiva*, *Vertigo milium*, *Vertigo pygmaea*) increased in occurrence frequency toward the southwest. Another 13 (*Columella simplex*, *Nesovitrea binneyana*, *Paravitrea multidentata*, *Planogyra asteriscus*, *Punctum minutissimum*, *Striatura exigua*, *Striatura ferrea*, *Striatura milium*,

Table 4. Occurrence frequency for each taxa within five geographic subregions. Area 1 (51 sites) ranges from Lake Winnebago and south. Area 2 (64 sites) ranges from Sturgeon Bay and southern Oconto County to the north side of Lake Winnebago. Area 3 (74 sites) ranges from from Rock Island and Marinette County to Sturgeon Bay and central Oconto County. Area 4 (23 sites) ranges across Delta and Schoolcraft counties, including all of the Garden Peninsula. Area 5 (30 sites) ranges from Drummond Island west to central Mackinac counties. P-values are based on log-likelihood ratio contengency table analyses, with bold-faced entries representing those taxa demonstrating significant deviation from equal frequencies across all geographic areas. The significance threshold was modified, using a Bonferroni correction, to p = 0.000610.

Taxa	Occurrence Frequency					
	Area 1	Area 2	Area 3	Area 4	Area 5	p
Allogona profunda	**27.45**	**6.25**	**10.81**	**4.35**	**0.00**	**0.000397**
Anguispira alternata	49.02	46.88	59.46	56.52	53.33	0.618003
Carychium exiguum	23.53	45.31	24.32	21.74	30.00	0.046232
Carychium exile	49.02	57.81	35.14	52.17	23.33	0.007238
Catinella avara	9.80	12.50	2.70	13.04	3.33	0.123466
Catinella exile	5.88	0.00	2.70	4.35	6.67	0.187976
Catinella* cf. *gelida	**27.45**	**7.81**	**0.00**	**0.00**	**0.00**	**0.000000**
Catinella cf. *vermeta*	0.00	0.00	0.00	0.00	3.33	0.378966
Cochlicopa lubrica	**47.06**	**37.50**	**14.86**	**17.39**	**23.33**	**0.000534**
Cochlicopa lubricella	15.69	28.13	9.46	13.04	6.67	0.024425
Cochlicopa morseana	1.96	6.25	8.11	17.39	23.33	0.016082
Columella simplex	**23.53**	**42.19**	**71.62**	**69.57**	**73.33**	**0.000000**
***Deroceras* spp.**	**47.06**	**34.38**	**16.22**	**26.09**	**10.00**	**0.000297**
Discus catskillensis	37.25	43.75	68.92	65.22	66.67	0.001033
Discus whitneyi	19.61	21.88	4.05	13.04	13.33	0.015699
Euchemotrema fraternum	29.41	12.50	25.68	17.39	30.00	0.126935
Euchemotrema leai	15.69	17.19	8.11	8.70	3.33	0.174227
Euconulus alderi	19.61	20.31	13.51	17.39	20.00	0.831441
Euconulus fulvus	33.33	34.38	56.76	47.83	50.00	0.035898
Euconulus polygyratus	11.76	21.88	25.68	26.09	33.33	0.176595
Gastrocopta armifera	11.76	12.50	1.35	0.00	0.00	0.002200
Gastrocopta contracta	49.02	54.69	36.49	26.09	20.00	0.004581
Gastrocopta corticaria	**33.33**	**14.06**	**6.76**	**0.00**	**0.00**	**0.000002**
Gastrocopta holzingeri	**39.22**	**35.94**	**8.11**	**8.70**	**0.00**	**0.000000**
Gastrocopta pentodon	33.33	48.44	44.59	43.48	13.33	0.007738
Gastrocopta similis	1.96	0.00	0.00	0.00	0.00	0.536340
Gastrocopta tappaniana	**29.41**	**45.31**	**12.16**	**21.74**	**30.00**	**0.000483**
Glyphyalinia indentata	9.80	28.13	29.73	30.43	36.67	0.026584
Glyphyalinia rhoadsi	0.00	4.69	5.41	8.70	16.67	0.026496
Glyphyalinia wheatleyi	0.00	0.00	1.35	0.00	3.33	0.433273
Guppya sterkii	0.00	3.13	1.35	4.35	0.00	0.388246
Haplotrema concavum	0.00	6.25	0.00	0.00	3.33	0.040479
Hawaiia minuscula	**49.02**	**48.44**	**6.76**	**21.74**	**10.00**	**0.000000**
Helicodiscus parallelus	**27.45**	**35.94**	**5.41**	**21.74**	**43.33**	**0.000008**
Helicodiscus shimeki	43.14	54.69	64.86	56.52	40.00	0.077097
Hendersonia occulta	**19.61**	**43.75**	**16.22**	**0.00**	**0.00**	**0.000000**
Mesodon thyroidus	0.00	0.00	5.41	0.00	0.00	0.047091
Neohelix albolabris	1.96	0.00	12.16	0.00	3.33	0.002886
Nesovitrea binneyana	**7.84**	**10.94**	**20.27**	**26.09**	**60.00**	**0.000001**
Nesovitrea electrina	25.49	40.63	29.73	30.43	20.00	0.260305
Novisuccinea ovalis	**33.33**	**35.94**	**22.97**	**4.35**	**0.00**	**0.000005**
Oxychilus cellarius	0.00	0.00	1.35	0.00	0.00	0.666393
Oxychilus draparnaudi	0.00	0.00	1.35	0.00	0.00	0.666393
Oxyloma retusa	13.73	15.63	5.41	13.04	6.67	0.266881
Paravitrea multidentata	**3.92**	**23.44**	**41.89**	**34.78**	**40.00**	**0.000005**
Planogyra asteriscus	**0.00**	**0.00**	**1.35**	**13.04**	**16.67**	**0.000255**
Pomatiopsis lapidaria	3.92	1.56	1.35	0.00	0.00	0.560707
Punctum minutissimum	**1.96**	**42.19**	**81.08**	**86.96**	**83.33**	**0.000000**
Punctum n. sp.	9.80	1.56	4.05	0.00	0.00	0.066742
Punctum vitreum	**56.86**	**31.25**	**0.00**	**0.00**	**0.00**	**0.000000**
Pupilla muscorum	0.00	0.00	0.00	0.00	6.67	0.075778

Table 4. (continued)

Taxa	Occurrence Frequency					
	Area 1	Area 2	Area 3	Area 4	Area 5	p
Pupoides albilabris	0.00	1.56	0.00	0.00	0.00	0.614180
Stenotrema barbatum	5.88	0.00	0.00	0.00	0.00	0.050049
Striatura exigua	**1.96**	**25.00**	**35.14**	**26.09**	**70.00**	**0.000000**
Striatura ferrea	**1.96**	**10.94**	**20.27**	**21.74**	**43.33**	**0.000026**
Striatura milium	**17.65**	**48.44**	**62.16**	**73.91**	**73.33**	**0.000000**
Strobilops aenea	0.00	0.00	1.35	0.00	0.00	0.666393
Strobilops affinis	9.80	17.19	2.70	0.00	3.33	0.005728
Strobilops labyrinthica	**47.06**	**76.56**	**82.43**	**78.26**	**80.00**	**0.000401**
Vallonia costata	**23.53**	**28.13**	**9.46**	**17.39**	**0.00**	**0.000328**
Vallonia excentrica	3.92	1.56	0.00	0.00	0.00	0.274481
Vallonia gracilicosta	9.80	10.94	16.22	13.04	16.67	0.789687
Vallonia perspectiva	**23.53**	**0.00**	**0.00**	**0.00**	**0.00**	**0.000000**
Vallonia pulchella	15.69	21.88	6.76	8.70	0.00	0.003467
Vertigo bollesiana	**7.84**	**32.81**	**54.05**	**21.74**	**10.00**	**0.000000**
Vertigo cristata	**0.00**	**0.00**	**20.27**	**13.04**	**23.33**	**0.000000**
Vertigo elatior	21.57	28.13	17.57	30.43	30.00	0.462544
Vertigo gouldi	45.10	45.31	59.46	52.17	50.00	0.448656
Vertigo hubrichti	**11.76**	**20.31**	**50.00**	**47.83**	**16.67**	**0.000002**
Vertigo milium	**27.45**	**39.06**	**1.35**	**0.00**	**0.00**	**0.000000**
Vertigo modesta	0.00	0.00	1.35	0.00	0.00	0.666393
Vertigo morsei	1.96	0.00	4.05	0.00	6.67	0.160618
Vertigo nylanderi	5.88	12.50	1.35	8.70	10.00	0.080021
Vertigo ovata	11.76	6.25	13.51	8.70	3.33	0.385160
Vertigo paradoxa	**0.00**	**0.00**	**8.11**	**17.39**	**26.67**	**0.000004**
Vertigo pygmaea	**19.61**	**32.81**	**4.05**	**0.00**	**3.33**	**0.000001**
Vertigo tridentata	7.84	1.56	0.00	0.00	0.00	0.034972
Vitrina limpida	**3.92**	**3.13**	**1.35**	**17.39**	**26.67**	**0.000224**
Webbhelix multilineata	7.84	3.13	0.00	0.00	0.00	0.034572
Zonitoides arboreus	58.82	71.88	81.08	56.52	80.00	0.028374
Zonitoides nitidus	23.53	15.63	6.76	4.35	3.33	0.012781
Zoogenetes harpa	**0.00**	**0.00**	**1.35**	**17.39**	**20.00**	**0.000015**

Strobilops labyrinthica, *Vertigo cristata*, *Vertigo paradoxa*, *Vitrina limpida*, *Zoogenetes harpa*) increased in frequency towards the northeast. *Vertigo bollesiana* and *Vertigo hubrichti* had their highest occurrence frequencies along the Door and Garden Peninsulas, while *Gastrocopta tappaniana* and *Helicodiscus parallelus* had their minimum occurrence frequencies in this same region.

A number of other taxa also demonstrated non-significant, but possibly important, trends in occurrence frequency. Many of these taxa did not attain statistically significant trends in their distributions due to their reduced occurrences. Species that tended towards greater occurrence frequency in the south and west included *Gastrocopta armifera*, *Gastrocopta contracta*, *Gastrocopta pentodon*, *Gastrocopta similis*, *Stenotrema barbatum*, *Strobilops affinis*, *Vallonia excentrica*, *Vertigo tridentata*, and *Webbhelix multilineata*. Species that tended towards greater occurrence frequency in the north and east included *Discus catskillensis*, *Glyphyalinia indentata*, *Glyphyalinia rhoadsi*, and *Pupilla muscorum*. Species that tended towards highest occurrence frequencies in the Door and Garden Peninsulas included *Guppya sterkii*, *Mesodon thyroidus*, *Neohelix albolabris*, *Oxychilus cellarius*, *Oxychilus draparnaudi*, and *Strobilops aenea*.

Occurrence Frequency *vs.* Habitat

Forty-one species demonstrated significant variation in their occurrence frequencies among the five habitat groups (Table 5). These patterns were less easy to categorize, with species tending to possess more individualistic relationships. However, three main response types were noted. Fifteen taxa (*Carychium exiguum*, *Catinella exile*, *Euchemotrema leai*, *Euconulus alderi*, *Gastrocopta tappaniana*, *Nesovitrea electrina*, *Oxyloma retusa*, *Punctum* n. sp., *Striatura exigua*, *Striatura milium*, *Strobilops affinis*, *Vertigo elatior*, *Vertigo morsei*, *Vertigo nylanderi*, *Vertigo ovata*) possessed highest occurrence frequencies in lowland grasslands and/or forests. Thirteen taxa (*Anguispira alternata*, *Catinella* cf. *gelida*, *Discus catskillensis*, *Euchemotrema fraternum*, *Gastrocopta corticaria*, *Gastrocopta holzingeri*, *Gastrocopta pentodon*, *Strobilops labyrinthica*,

Table 5. Occurrence frequency for each taxon within five general habitat groupings. Group 1 consists of Rock Outcrops (RO; 107 sites). Group 2 consists of Upland Forests (UF; 44 sites). Group 3 consists of Lowland Forests (LF; 48 sites). Group 4 consists of Upland Grasslands (UG; 10 sites). Group 5 consists of Lowland Grasslands (LG; 33 sites). P-values are based on log-likelihood ratio contengency table analyses, with bold-faced entries representing those taxa demonstrating significant deviation from equal frequencies across all habitat groupings. The significance threshold was modified, using a Bonferroni correction, to p = 0.000610.

Taxa	**Occurrence Frequency**					
	RO	UF	LF	UG	LG	p
Allogona profunda	**20.56**	**11.36**	**0.00**	**0.00**	**0.00**	**0.000006**
Anguispira alternata	**92.52**	**56.82**	**6.25**	**0.00**	**3.03**	**0.000000**
Carychium exiguum	**3.74**	**6.82**	**83.33**	**10.00**	**75.76**	**0.000000**
Carychium exile	**59.81**	**43.18**	**29.17**	**50.00**	**15.15**	**0.000013**
Catinella avara	0.93	0.00	12.50	40.00	24.24	0.000000
Catinella exile	0.00	0.00	0.00	0.00	24.24	0.000001
Catinella* cf. *gelida	**17.76**	**0.00**	**0.00**	**0.00**	**0.00**	**0.000001**
Catinella cf. *vermeta*	0.00	0.00	0.00	10.00	0.00	0.166558
Cochlicopa lubrica	**26.17**	**59.09**	**12.50**	**40.00**	**18.18**	**0.000015**
Cochlicopa lubricella	17.76	22.73	4.17	10.00	18.18	0.068383
Cochlicopa morseana	10.28	18.18	4.17	0.00	3.03	0.055085
Columella simplex	**70.09**	**61.36**	**29.17**	**20.00**	**36.36**	**0.000001**
Deroceras spp.	33.64	11.36	25.00	0.00	42.42	0.000883
Discus catskillensis	**89.72**	**50.00**	**20.83**	**10.00**	**12.12**	**0.000000**
Discus whitneyi	9.35	15.91	18.75	10.00	21.21	0.341968
Euchemotrema fraternum	**45.79**	**11.36**	**2.08**	**0.00**	**0.00**	**0.000000**
Euchemotrema leai	**0.93**	**2.27**	**20.83**	**10.00**	**45.45**	**0.000000**
Euconulus alderi	**0.00**	**2.27**	**50.00**	**0.00**	**54.55**	**0.000000**
Euconulus fulvus	**62.62**	**45.45**	**20.83**	**20.00**	**24.24**	**0.000001**
Euconulus polygyratus	**30.84**	**36.36**	**6.25**	**10.00**	**6.06**	**0.000040**
Gastrocopta armifera	12.15	2.27	0.00	10.00	0.00	0.001711
Gastrocopta contracta	**60.75**	**18.18**	**25.00**	**10.00**	**39.39**	**0.000000**
Gastrocopta corticaria	**28.97**	**0.00**	**0.00**	**0.00**	**0.00**	**0.000000**
Gastrocopta holzingeri	**41.12**	**6.82**	**4.17**	**20.00**	**0.00**	**0.000000**
Gastrocopta pentodon	**64.49**	**18.18**	**27.08**	**30.00**	**6.06**	**0.000000**
Gastrocopta similis	0.93	0.00	0.00	0.00	0.00	0.802044
Gastrocopta tappaniana	**2.80**	**11.36**	**60.42**	**50.00**	**75.76**	**0.000000**
Glyphyalinia indentata	38.32	22.73	10.42	30.00	12.12	0.000701
Glyphyalinia rhoadsi	8.41	11.36	0.00	0.00	0.00	0.007192
Glyphyalinia wheatleyi	0.93	2.27	0.00	0.00	0.00	0.683532
Guppya sterkii	2.80	2.27	0.00	0.00	0.00	0.426856
Haplotrema concavum	0.93	2.27	6.25	0.00	0.00	0.251832
Hawaiia minuscula	36.45	15.91	18.75	10.00	39.39	0.009955
Helicodiscus parallelus	23.36	25.00	35.42	20.00	18.18	0.442604
Helicodiscus shimeki	**79.44**	**54.55**	**27.08**	**20.00**	**15.15**	**0.000000**
Hendersonia occulta	**28.97**	**29.55**	**10.42**	**0.00**	**3.03**	**0.000110**
Mesodon thyroidus	3.74	0.00	0.00	0.00	0.00	0.157759
Neohelix albolabris	5.61	11.36	0.00	0.00	0.00	0.016560
Nesovitrea binneyana	31.78	13.64	10.42	20.00	9.09	0.003708
Nesovitrea electrina	**7.48**	**6.82**	**79.17**	**40.00**	**63.64**	**0.000000**
Novisuccinea ovalis	28.97	36.36	10.42	10.00	15.15	0.009486
Oxychylus cellarius	0.00	2.27	0.00	0.00	0.00	0.488870
Oxychilus draparnaudi	0.93	0.00	0.00	0.00	0.00	0.802044
Oxyloma retusa	**0.93**	**0.00**	**12.50**	**10.00**	**54.55**	**0.000000**
Paravitrea multidentata	**52.34**	**27.27**	**0.00**	**0.00**	**0.00**	**0.000000**

Table 5. (continued)

Taxa	Occurrence Frequency					
	RO	UF	LF	UG	LG	p
Planogyra asteriscus	2.80	4.55	6.25	0.00	3.03	0.759055
Pomatiopsis lapidaria	0.00	0.00	4.17	0.00	6.06	0.060175
Punctum minutissimum	**69.16**	**59.09**	**35.42**	**40.00**	**36.36**	**0.000180**
***Punctum* n. sp.**	**0.00**	**0.00**	**6.25**	**0.00**	**18.18**	**0.000117**
Punctum vitreum	27.10	20.45	20.83	0.00	3.03	0.002837
Pupilla muscorum	0.00	2.27	2.08	0.00	0.00	0.419751
Pupoides albilabris	0.00	0.00	0.00	0.00	3.03	0.404473
Stenotrema barbatum	0.00	0.00	2.08	0.00	6.06	0.111997
Striatura exigua	**20.56**	**29.55**	**58.33**	**0.00**	**21.21**	**0.000006**
Striatura ferrea	16.82	22.73	25.00	0.00	3.03	0.010618
Striatura milium	**48.60**	**50.00**	**81.25**	**10.00**	**33.33**	**0.000003**
Strobilops aenea	0.93	0.00	0.00	0.00	0.00	0.802044
Strobilops affinis	**0.00**	**0.00**	**18.75**	**10.00**	**27.27**	**0.000000**
Strobilops labyrinthica	**93.46**	**52.27**	**66.67**	**50.00**	**48.48**	**0.000000**
Vallonia costata	18.69	11.36	8.33	40.00	24.24	0.077704
Vallonia excentrica	0.00	2.27	0.00	20.00	0.00	0.012558
Vallonia gracilicosta	**29.91**	**0.00**	**0.00**	**0.00**	**0.00**	**0.000000**
Vallonia perspectiva	10.28	2.27	0.00	0.00	0.00	0.004560
Vallonia pulchella	7.48	9.09	6.25	30.00	33.33	0.001871
Vertigo bollesiana	**56.07**	**18.18**	**10.42**	**0.00**	**0.00**	**0.000000**
Vertigo cristata	**19.63**	**4.55**	**4.17**	**0.00**	**0.00**	**0.000204**
Vertigo elatior	**0.00**	**6.82**	**60.42**	**20.00**	**72.73**	**0.000000**
Vertigo gouldi	**96.26**	**31.82**	**12.50**	**0.00**	**0.00**	**0.000000**
Vertigo hubrichti	**64.49**	**6.82**	**0.00**	**10.00**	**0.00**	**0.000000**
Vertigo milium	17.76	4.55	22.92	10.00	21.21	0.079342
Vertigo modesta	0.00	2.27	0.00	0.00	0.00	0.488870
Vertigo morsei	**0.00**	**0.00**	**0.00**	**0.00**	**18.18**	**0.000052**
Vertigo nylanderi	**0.00**	**4.55**	**31.25**	**0.00**	**0.00**	**0.000000**
Vertigo ovata	**0.00**	**0.00**	**12.50**	**0.00**	**51.52**	**0.000000**
Vertigo paradoxa	14.02	4.55	2.08	0.00	0.00	0.003858
Vertigo pygmaea	14.02	13.64	2.08	30.00	30.30	0.003276
Vertigo tridentata	4.67	0.00	0.00	0.00	0.00	0.081368
Vitrina limpida	3.74	15.91	2.08	40.00	3.03	0.001113
Webbhelix multilineata	2.80	2.27	2.08	0.00	3.03	0.960081
Zonitoides arboreus	**89.72**	**56.82**	**83.33**	**20.00**	**30.30**	**0.000000**
Zonitoides nitidus	5.61	15.91	16.67	10.00	21.21	0.066758
Zoogenetes harpa	7.48	6.82	0.00	0.00	0.00	0.030018

Vallonia gracilicosta, *Vertigo bollesiana*, *Vertigo cristata*, *Vertigo gouldi*, *Vertigo hubrichti*) were most commonly encountered on rock outcrops. Nine others (*Allogona profunda*, *Columella simplex*, *Euconulus fulvus*, *Euconulus polygyratus*, *Helicodiscus shimeki*, *Hendersonia occulta*, *Paravitrea multidentata*, *Punctum minutissimum*) were found most frequently in both rock outcrops and upland forests.

DISCUSSION

The 82 taxa encountered from the 242 sample sites represent over 50% of the taxa previously reported from Illinois, Indiana, Iowa, Michigan, Minnesota, southern Ontario, and Wisconsin, and 15% of the taxa reported from eastern North America (Oughton 1948, Pilsbry 1948, Burch 1962, Hubricht 1985).

Some of these have rather limited ranges in the eastern USA (Pilsbry 1948, Hubricht 1985, Frest 1991, Nekola 2001, Nekola and Massart 2001). *Catinella exile* is otherwise known only from Iowa fens. *Catinella* cf. *gelida* is otherwise limited to limestone cliff and talus slopes in northeastern Iowa and the Black Hills. *Hendersonia occulta* is otherwise limited to the Ridge and Valley province in the central and southern Appalachians, and to the Paleozoic Plateau in the Upper

Midwest. *Planogyra asteriscus* is otherwise known only from northern New England and the upper Great Lakes. *Strobilops affinis* is otherwise found from eastern Minnesota to Missouri, the southern Great Lakes shore, and eastern Massachusetts. *Vallonia gracilicosta* is otherwise known in eastern North America from isolated populations confined to carbonate outcrops from the Paleozoic Plateau eastward along the Niagaran Escarpment to central New York State, eastern Maine, and Massachusetts. *Vertigo bollesiana* is otherwise limited to the New England states south along the Appalachians and Allegheny Plateau to western North Carolina and west along the Great Lakes to southeastern Michigan. *Vertigo cristata* is otherwise known from northern Wisconsin, northern Minnesota, and the western Upper Peninsula of Michigan. *Vertigo hubrichti* was previously known only from algific talus slopes in the Paleozoic Plateau. *Vertigo modesta* was previously reported from the eastern US only as a Pleistocene fossil, although extant colonies have recently been documented from northern Minnesota and Michigan. *Vertigo morsei* was known from scattered fens extending from Iowa and Minnesota through the southern Great Lakes to central New York State. *Vertigo nylanderi* was otherwise known only from northern Maine, northeastern Ontario, the northern Lower Peninsula of Michigan, and northwestern Minnesota. *Vertigo paradoxa* was otherwise known only from northern Maine, the northern Lower Peninsula of Michigan, and the Black Hills. *Zoogenetes harpa* was otherwise known only from the northern Great Lakes and northern New England.

Species Richness Patterns

A substantial amount of the observed diversity in land snails in the region is maintained at relatively small geographic scales, with up to 80% of the regional fauna being recorded from a single county (Door). Individual 1000 m≤ areas within the region are capable of supporting up to 34 taxa, or 40% of the regional fauna (Nekola 1999), while some 400 cm≤ areas within these sites may harbor up to 21 co-occurring taxa, or 25% of the regional fauna (Nekola and Smith 1999). The mechanisms that allow for these levels of mycrosympatry are not yet fully elucidated.

The bulk of species richness also occured within a relatively small subset of habitats that included carbonate cliffs, lakeshore carbonate ledges, rocky woodlands, forested wetlands (black ash, tamarack, or black spruce), and fens. These habitats individually harbored from 50-75% of the entire regional fauna. Only 2 of the encountered taxa (*Catinella* cf. *vermeta*, *Pupoides albilabris*) were not located within at least one of these habitats. These same habitat types are also among the most important for land snail diversity in northwestern Europe (Kerney and Cameron 1979).

Biogeographic Patterns and Affinities

A clear trend in faunistic composition was found across the region, with 14 taxa being more common to the southwest and 13 more common to the northeast. This result is not unexpected, as this region straddles the Northern and Eastern Provinces of the Eastern North American Molluscan Division. However, these data demonstrate that this transition is not abrupt, with faunistic turnover occurring over the region's entire 250 km extent.

The biogeographic affinities of species sharing a given occurrence pattern within the region are also not uniform. While many Interior Province taxa were more common in the southwest (*e.g.*, *Allogona profunda*, *Gastrocopta armifera*, *Gastrocopta contracta*, *Gastrocopta corticaria*, *Gastrocopta holzingeri*, *Gastrocopta pentodon*, *Gastrocopta similis*, *Hawaiia minuscula*, *Stenotrema barbatum*, *Strobilops affinis*, *Vallonia perspectiva*, *Vertigo milium*, *Vertigo tridentata*, *Webbhelix multilineata*), and many of the Northern Province forms were more common to the northeast (*e.g.*, *Discus catskillensis*, *Nesovitrea binneyana*, *Planogyra asteriscus*, *Pupilla muscorum*, *Striatura exigua*, *Striatura milium*, *Vertigo cristata*, *Vertigo paradoxa*, *Vitrina limpida*, *Zoogenetes harpa*), not all within-region distributions reflected such larger-scale patterns. For instance, *Cochlicopa lubrica*, *Novisuccinea ovalis*, *Vallonia costata*, *Vallonia pulchella*, *Vallonia excentrica*, *Vertigo pygmaea* are all species characteristic of the northeastern US (Hubricht 1985), yet reached their greatest occurrence frequency in the southwest of the study region. Additionally, *Glyphyalinia rhoadsi*, *Paravitrea multidentata*, and *Striatura ferrea* reached their greatest occurrence frequencies in the northeast of the region, even though their ranges are primarily centered on the Appalachians (Hubricht 1985). *Columella simplex*, *Punctum minutissimum*, and *Strobilops labyrinthica* are all wide ranging species of the eastern US (Hubricht, 1985), yet reached their peak occurrence frequencies in the northeast of the region.

Those species reaching their peak abundances along the Door and Garden Peninsulas also proved to have diverse affinities. *Mesodon thyroidus* is found throughout the eastern US, while *Neohelix albolabris* and *Vertigo bollesiana* are limited to the northeastern US. *Guppya sterkii* and *Strobilops aenea*, however, are characteristic of the southeastern US. *Vertigo hubrichti* represents an upper Midwestern endemic. Such patterns help demonstrate that the transition from Interior to Northern Province faunas in the region is not only diffuse, but also complex.

Conservation Recommendations

Only 3 species with more than 20 occurrences (*Glyphyalinia indentata*, *Cochlicopa lubricella*, and *Discus whitneyi*) possessed statistically similar frequencies across all habitat groups and geographic subregions. All remaining taxa demonstrated either significant partitioning across space and/or environment, or were too scarce (< 20 occurrences) to provide reliable results due to low statistical power.

These data suggest that conservation of land snail richness and compositional diversity within the region will require the protection of multiple habitat types across the entire landscape. Given the high number of species that they harbor, carbonate cliffs, rocky upland woods, wooded wetlands (black ash, tamarack, white cedar), and fens should be given particular consideration. By protecting representative examples of these habitats within each of the geographic subregions, roughly 97% of the regional land snail diversity could be conserved.

However, some of these habitats are experiencing severe losses within parts of the region. For instance, most of the carbonate cliffs in eastern Wisconsin have already been altered or are currently under threat from development, road construction, and/or grazing. Unless conservation groups and agencies take immediate action to protect such sites across the region, irrevocable losses in land snail diversity may occur.

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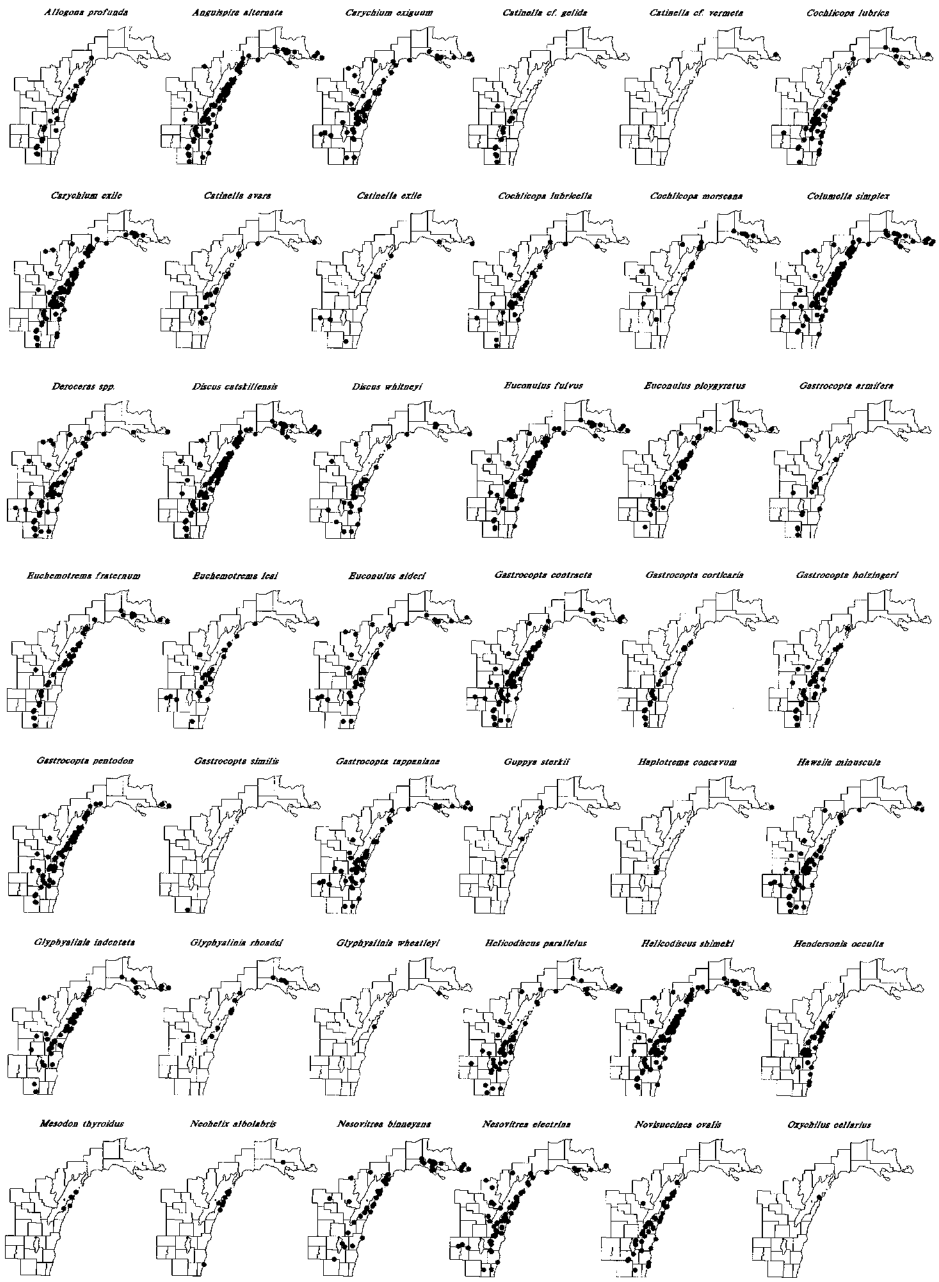
APPENDIX 1

Distribution maps for all species encountered within all 242 sites sampled within the study region. Species maps are alphabetically arranged.



APPENDIX 1 (continued)