Vertigo malleata, a new extreme calcifuge land snail (Gastropoda: Vertiginidae) from the Atlantic and Gulf coastal plains of the USA

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ABSTRACT

Vertigo malleata new species is an extreme calcifuge land snail widely distributed in the Atlantic and Gulf costal plains of the eastern USA. This species appears to have gone undetected because of its small size and restriction to low pH sites—*Sphagnum* bogs, Atlantic white cedar (*Chamaecyparis thyoides* (L.) BSP) swamps, pocosins, and pine woodlands—which, it has been assumed, harbor little or no molluscan diversity. *Vertigo malleata* is distinguished from other members of the genus by the strongly pustulose surface of the body whorl, which gives the shell a malleated appearance at low to moderate magnification. While the major apertural lamellae/folds (parietal, columellar, and palatal) of this species are typical for *Vertigo*, the strongly pustulose shell sculpture, occurrence of an infraparietal lamella, and frequent development of subcolumellar and basal lamellae in the absence of an angular lamella appear unique. Although *V. malleata* is an abundant snail within its range, the common use of short-return fire regimens to manage forests of the eastern USA appears to be artificially limiting its distribution to wet, less frequently burned sites.

Additional key words: Bothriopupa, Nesopupa, biogeography, fire ecology, community ecology, eastern North America

INTRODUCTION

Acidic and lime-poor habitats have long been thought to support depauperate molluscan community abundance and richness (Boycott, 1934; Baker, 1939; Kerney and Cameron, 1979; Burch and Pearce, 1990). Consequently, little molluscan survey work has been attempted in acidic sites even though they can represent a substantial fraction of the landscape. However, such areas should not be ignored for terrestrial gastropod biodiversity because base-poor habitats can be as speciose as base-rich habitats on a per-individual basis (Schilthuizen et al., 2003; Pokryszko and Cameron, 2005), and because some species like the European *Vertigo ronnebyensis* (Westerlund, 1871) and *Zonitoides excavatus* (Alder, 1830) are restricted to or more frequent in base-poor sites (Kerney and Cameron, 1979).

During land snail studies in eastern North America (Nekola, 2002a; Nekola and Coles, 2004; Coles and Nekola, unpublished data) we found that acidic habitats often supported substantial populations of land snail taxa that have been little reported since their original descriptions; e.g., *Vertigo cristata* (Sterki, 1919), *Vertigo nylanderi* Sterki, 1909, *Vertigo alabamensis* Clapp, 1915, and *Vertigo perryi* Sterki, 1905. In fact, *V. alabamensis* and *V. perryi* were each previously known from only two sites worldwide (Pilsbry, 1948; Hubricht, 1985). In the course of these acid-habitat surveys, we examined Saco Heath, an undisturbed domed ombotrophic *Sphagnum* bog in the Atlantic coastal plain of York County, Maine. At this site we located a species of the genus *Vertigo* that was strikingly different from all previously known taxa. This form was subsequently found to represent the most common land snail of highly acid, mesic to wet habitats of the Atlantic and Gulf coastal plains of the eastern USA. Here, we describe this taxon as *Vertigo malleata,* new species, document its biogeography and ecology, and briefly discuss its relevant conservation issues.

MATERIALS AND METHODS

Site Selection: Approximately 130 sites were surveyed along the Atlantic and Gulf coastal plains of the eastern USA from Maine to western Alabama, including peninsular Florida south to Gainesville. These sites encompassed the entire soil base-status and moisture gradient of the region and covered a total geographic extent of 2400 km. Thirty sites represented base-neutral to base-rich habitats (i.e., calcareous wetlands, marl banks, rich forests, and limestone outcrops), while the remaining were base-poor (i.e., pine barrens, pine-wiregrass sa-

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vanna, heaths, Atlantic white cedar swamps, bay forest, *Sphagnum* bogs, and pocosins).

Field Methods: Latitude and longitude of each site was determined using a hand-held GPS. Terrestrial gastropod faunas were documented from a representative 100–1000 m^2 area within each site by hand collection of larger taxa and litter sampling for smaller taxa. Litter sampling was used as the primary method of collection because it provides the most complete assessment of site faunas (Oggier et al., 1998; Cameron and Pokryszko, 2005). As suggested by Emberton et al. (1996), collections were made at places of high micro-mollusk density such as loosely compacted leaf litter lying on top of highly compacted damp soil or humus. This loose litter was removed by hand and aggressively sieved in the field using a shallow sieve of 2 mm mesh nesting loosely inside a sieve of 0.6 mm mesh. The procedure consisted of throwing handfuls of litter onto the coarser mesh accompanied by vigorous shaking, tapping, or other agitation. The process was continued for 15–60 minutes, a time interval that yielded 50–500 ml of fine material (0.6–2.0 mm). In general, sites were sampled in parallel (but independently) by each of the authors, although several sites were sampled by only one worker (see Table 1).

Laboratory Procedures: Samples were slowly and completely dried at room temperature and then passed through an ASTME #30 sieve (0.6 mm mesh) with fractions being hand-picked against a neutral background. All shells, shell fragments, and slug plates were removed, and all identifiable shells from each site were assigned to species using the authors' reference collections and various museum collections (see below). The total numbers of shells per species per site were recorded, as were the number of unidentified immature individuals.

Comparisons: The new species was compared with specimens of all eastern North American and western Eurasian species of *Vertigo*, and to representative taxa in the related genera *Nearctula* of western North America, *Nesopupa* of the Old-World tropics, and *Bothriopupa* of the neotropics. Comparative material consisted of the authors' extensive reference collections, the collections of the Florida Museum of Natural History, Gainsville, FL (UF); the Field Museum of Natural History, Chicago, IL (FMNH), the Carnegie Museum of Natural History, Pittsburgh, PA (CM); the National Museum of Wales–Zoology, Cardiff, UK (NMW.Z); the Natural History Museum, London, UK, and the Queensland Museum, Brisbane, Australia. Additional comparisons were made with material presented by Pilsbry (1920; 1948).

Imaging: Shells were imaged at 40× magnification using a digital camera attached to a stereomicroscope. Approximately 12 separate 1388 × 1040 pixel images were made of each specimen with the image focal lengths positioned at 120μm increments from the front to back of the shell. CombineZ5 freeware (http://www.hadleyweb.pwp.blueyonder.co.uk/CZ5/ combinez5.htm) was used to assemble a final image from the well-focused parts of each separate image. The body whorl surface of the new taxon was also imaged at 150× with 60 images positioned at 5 μm focal length increments and assembled into a single image using CombineZ5. These separate images were imported into Adobe Photoshop, where brightness and contrast were optimized and the background made uniformly black. These images were then compiled into a single plate.

Community Ecology: Analysis of co-occurring terrestrial gastropod species and abundance was determined using data for sites sampled by the second author (i.e., all sites with accession numbers prefixed by JCN in Table 1). These analyses were performed for the whole dataset of 49 discrete sites and also by geographic sub-region—New England (Maine, Massachusetts), New Jersey, the North and South Carolina coastal plain, and the Gulf coastal plain—to allow for documentation of compositional gradients across the range of the new species. The physical habitat and plant community from each site was also noted.

Nomenclature: Taxonomic nomenclature follows that of Turgeon et al. (1998) with updates from Nekola (2004). Apertural lamellae and fold nomenclature follows that of Pilsbry (1948: 869, fig. 469), i.e., parietal "teeth" are referred to as "folds" and all other "teeth" are termed "lamellae", whatever their form.

SYSTEMATICS

Class Gastropoda
Subclass Pulmonata
Order Stylommatophora
Family Vertiginidae
Genus *Vertigo* Müller, 1773
Vertigo malleata new species
(Figures 1–15, 20, Tables 1–2)

Diagnosis: Minute; shell ovoid, similar in size and shape to *Vertigo ventricosa* (Morse, 1865) but distinguished by malleated appearance of the body whorl at low to moderate (10–40×) magnification; upper whorls finely rib-striate, minutely decussated by spiral lines; aperture with parietal and columellar lamellae, a small infraparietal lamella (occasionally absent), and two palatal folds; one or more subcolumellar-basal lamellae usually present; angular lamella absent.

Description: Shell 1.8–2.1 mm tall × 1.25–1.4 mm wide (holotype 1.98 × 1.36 mm), ovoid to ovoid-conical, inflated, approximately 4–4.5 whorls, with deep suture; translucent, olive-yellow to brown in color; body whorl approximately 66% of total height. Protoconch and neanic whorls minutely papillose with fine spiral striation; subsequent whorls finely rib-striate; striae most distinct on penultimate whorl where they are minutely decussated by fine spiral lines; on body whorl the sculpture degenerates into an irregularly pustulose surface (Figure

4) which at low to moderate (10–40×) magnification takes on a malleated appearance as it appears hammered with small depressions; behind the aperture the sculpture takes the form of coarse, irregular rib-striae (Figures 2, 11). Aperture rounded, approximately 40% of shell height; lip reflexed but not thickened, peristome usually dark blackish-olive; sinulus moderate-weak; basally the aperture abruptly inflates to form a rounded swelling, but not a distinct crest (Figures 2, 8). Umbilicus closed (Figure 3). Aperture typically with six lamellae and folds (Figures 1, 5, 7, 9, 12–15): a strong, slightly sinuous parietal lamella (Figures 1, 5, 9, 15); a shelf-like columellar lamella that spirals internally around the columella for approximately one whorl; two palatal folds of approximately equal length that extend approximately 0.2 whorls into body whorl, the lower slightly more immersed than the upper (Figures 1, 5–7, 10, 15), both highest at midlength (Figures 1, 5, 6, 15); a nodular infraparietal lamella usually present (Figures 1, 5, 9, 12–15), occasionally vestigial or absent (Figures 6, 10); angular lamella absent; presence of a nodular subcolumellar lamella and nodular subcolumellar-basal lamella variable (Figures 1, 6, 7, 9, 10). Apertural ends of the palatal folds coincide with abrupt inflation of basal aperture (Figures 7–8), in consequence appearing to be raised on a weak crest when viewed within the aperture but not associated with any internal shell thickening; externally shell only slightly impressed over palatal folds. Body of animal grey with several organs of a brown or cream color visible through the upper whorls of shell. All dissected individuals have proven to be aphallic (Beata Pokryszko, personal communication), hence the genitalic anatomy is unknown.

Holotype (Figures 1–4): NMW.Z.2005.011.03830, USA North Carolina, Pender County, Holly Shelter Game Land, Brian Coles, 1 April 2003.

Paratypes (Figures 5–15): NMW.Z.2005.011.03831-03839, figured material, see Figure legends for details; NMW.Z.2005.011.02118-02120, approximately 5100 individuals (split into three approximately equal lots) from type locality; UF 348143, approximately 700 individuals from type locality; CM 73971, 143 individuals from type locality; NMW.Z.2005.011.02597, 90 specimens, Wells Heath, York County, Maine (43°20′2″ N, 70°38′24″ W), Brian Coles; NMW.Z.2005.011.02591, 26 specimens, Skunknett Audubon Preserve, Barnstable County, Massachusetts (41°38′59″ N, 70°22′31″ W); NMW.Z.2005.011.02585, 170 specimens, Peterson Swamp Wildlife Management Area, Plymouth County, Massachusetts (42°0′37″ N, 70°49′4″ W), Brian Coles; NMW.Z.2005.011.02514, 122 specimens, Stafford Forge Wildlife Management Area, Ocean County, New Jersey (39°42′44″ N, 74°22′10″ W), Brian Coles; NMW.Z.2005.011.02197, 250 specimens, Lewis Ocean Bay Preserve, Horry County, South Carolina (33°47′16″ N., 78°50′56″ W.), Brian Coles; NMW.Z.2005.011.03035, 42 specimens, Collins Bay, Ware County, Georgia (31°5′12″ N., 82°36′56″ W.), Brian Coles; NMW.Z.2005.011.03065, 107 specimens, Wilma Station, Liberty County, Florida (30°9′34″ N., 84°57′39″ W.), Brian Coles; NMW.Z.2005.011.03079, 162 specimens, Pond Creek, Conecuh National Forest, Covington County, Alabama (31°6′12″ N., 86°32′3″ W.), Brian Coles.

Type Locality: Holly Shelter Game Land (34°31′57″ N, 77°44′41″ W), Pender County, North Carolina, USA; under dense scrub of mesic bay/pine forest at pocosin margin, individuals sieved from deep bracken fern and pine needle litter, collected by Brian Coles, 1 April 2003.

Other Material (Table 1): Sixty additional lots collected by Brian Coles are deposited in the Coles Collection of the National Museum of Wales. Fifty three lots representing 3133 individuals collected by Jeff Nekola are deposited in the Nekola collection (JCN).

Etymology: The specific name *malleata* refers to the hammered appearance of the body whorl at low to moderate magnification.

Variation: *Vertigo malleata* was rather constant in general appearance along its 2400 km range, although some variation in shape, size, color, sculpture, and development of the apertural lamellae was observed. Variation in size and shape has been noted above. In addition, the most southern populations (Georgia, Alabama, and Florida) tended to be darker in color and showed the most strongly developed shell sculpture (Figures 9–12). While the parietal lamella, columellar lamella, and the palatal folds varied little, the infraparietal lamella varied from strong (Figures 1, 5, 19) to weak (Figure 9) to occasionally absent (Figures 6,10). The subcolumellar and nodular basal lamella although usually distinct (Figures 1, 5, 7, 13) were also occasionally absent (Figure 5). Multiple subcolumellar-basal lamellae of variable placement were also noted most frequently in Gulf Coast populations (Figures 9, 10). However, such trends were not distinct enough to support the designation of geographical races, with most of this observed morphological variation occurring within local regions or populations.

Comparison with Other Species of *Vertigo* and of Related Genera: *Vertigo malleata* differs from all other *Vertigo* species by its strongly pustulose body whorl sculpture and possession of an infraparietal and subcolumellar-basal lamellae while lacking an angular lamella. Because of these unusual characteristics, we do not feel assignment of this taxon to a particular subgenus to be prudent at this time. Additional data, possibly based on DNA sequence information, will be required to accurately determine its closest relatives.

On casual inspection, *Vertigo malleata* could be taken for a member of the *V. gouldii* group (e.g. *Vertigo cristata*; see Pilsbry, 1948: 958, figs. 4, 5, 8; 967, figs. 1–16) because of its shell color, striated upper whorls, and silky luster. Like *V. malleata, V. cristata* has four prominent lamellae and strong striation on the penultimate whorl (Pilsbry, 1948: 967, figs. 4–5, 973, fig. 520; Nekola, 2001).

Table 1. *Vertigo malleata*: sites, brief habitat descriptions, collection dates, accession numbers, and total number of specimens taken.

State/County	Site #	Site; Habitat[1]	Coordinates	Date	Accession Number	Specimens
Alabama						
Covington	1	Pond Creek seep (Conecuh NF); *Ilex-Smilax*-bay scrub on seep margin	31°06′12″ N, 86°32′03″ W	May 5 2005	NMW.Z.2005.011.03079 JCN 12365	162 117
	2	Moccasin Branch (Conecuh NF); old pine-bay-heath forest	31°06′42″ N, 86°35′53″ W	May 5 2005	JCN 12371	3
	3	Bear Bay (Conecuh NF); heath-dominated scrub on wetland margin	31°6′29″ N, 86°38′54″ W	May 5 2005	NMW.Z.2005.011.03068	1
Mobile	4	Grand Bay Forever Wild Preserve; wet bay and mixed forest	30°25′07″ N, 88°19′35″ W	May 1 2005	NMW.Z.2005.011.03019	3
Florida						
Columbia	5	Impassable bay (Osceola NF WMA); wet holly-bay scrub	30°23′31″ N, 82°30′05″ W	Jan 8 2005 May 2 2005	NMW.Z.2005.011.02849 JCN 12280	740 71
	6	Osceola National Forest WMA; wet *Pinus-Lyonia-Vaccinium* savanna	30°22′30″ N, 82°32′04″ W	May 2 2005	NMW.Z.2005.011.03026 JCN 12285	213 75
	7	Osceola National Forest WMA; wet *Acer-Taxodium-Lyonia* forest	30°22′39″ N, 82°31′42″ W	Jan 8 2005 May 2 2005 May 2 2005	NMW.Z.2005.011.02845 NMW.Z.2005.011.03024 JCN 12283	38 23 6
Leon	8	Wolf Trap Bay (Apalachicola NF); tall pine-holly-bay forest	30°22′04″ N, 84°34′11″ W	Jan 7 2005 May 4 2005 May 4 2005	NMW.Z.2005.011.02813 NMW.Z.2005.011.03054 JCN 12324	~100 132 137
	9	Wolf Trap Bay (Apalachicola NF); wet-mesic pine-holly-heath forest	30°21′46″ N, 84°34′23″ W	Jan 7 2005 May 4 2005 May 4 2005	NMW.Z.2005.011.02816 NMW.Z.2005.011.03050 JCN 12321	44 7 11
	10	Otter camp (Apalachicola NF); regenerating mesic pine-holly heath	30°20′20″ N, 84°36′41″ W	Jan 7 2005 May 4 2005	NMW.Z.2005.011.02820 NMW.Z.2005.011.03056	~50 4
Liberty	11	Wilma Station; mesic, old pine-magnolia-bay forest	30°09′34″ N, 84°57′39″ W	May 4 2005	NMW.Z.2005.011.03065 JCN 12344	127 30
	12	Juniper Creek Islands (Apalachicola NF); old growth pine-holly-bay forest	30°03′15″ N, 84°45′40″ W	May 4 2005	NMW.Z.2005.011.03062 JCN 12337	65 41
	13	Juniper Creek Islands (Apalachicola NF); white cedar-pine-holly forest	30°04′46″ N, 84°45′41″ W	May 4 2005	NMW.Z.2005.011.03059 JCN 12333	5 75
	14	Juniper Creek Islands (Apalachicola NF); pine-red maple-white cedar forest	30°02′07″ N, 84°49′38″ W	May 4 2005	NMW.Z.2005.011.03064 JCN 12339	~40 48
	15	Carr Bridge (Apalachicola NF); wet-mesic *Ilex* forest	30°07′26″ N, 84°53′31″ W	May 4 2005	JCN 12340	12
Wakulla	16	South of Otter Camp (Apalachicola NF); wet-mesic pine-holly forest	30°16′55″ N, 84°36′54″ W	May 4 2005 May 4 2005	NMW.Z.2005.011.03057 JCN 12327	69 53
	17	W Branch Sopchoppy R. (Apalachicola NF); pine-cypress-bay-holly forest	30°15′05″ N, 84°37′30″ W	May 4 2005	NMW.Z.2005.011.03058 JCN 12328	5 36

Table 1. *Continued*

State/County	Site #	Site; Habitat[1]	Coordinates	Date	Accession Number	Specimens
Georgia						
Ware	18	Collins Bay; wet holly-wax myrtle-bay forest	31°05′12″ N, 82°36′56″ W	May 2 2005	NMW.Z.2005.011.03035	42
					JCN 12300	58
	19	Dixon State Forest; wet *Pinus-Gordonia* forest	31°05′36″ N, 82°16′13″ W	May 3 2005	JCN 12301	4
	20	Dixon State Forest; wet-mesic *Quercus-Ilex-Gordonia* forest	31°06′49″ N, 82°16′16″ W	May 3 2005	NMW.Z.2005.011.03038	1
					JCN 12302	2
Maine						
York	21	Saco Heath 1 (TNC); sedge and heath litter on *Sphagnum* bog	43°32′42″ N, 70°28′33″ W	Oct 14 2002	NMW.Z.2005.011.01550	13
				Aug 8 2004	NMW.Z.2005.011.02567	14
					NMW.Z.2005.011.02577	52
					JCN 12092	10
					JCN 12099	88
					JCN 12101	3
				Oct 01 2004	NMW.Z.2005.011.02614	55
					NMW.Z.2005.011.02616	40
	22	Saco Heath 2 (TNC); low forest with *Carex* groundcover	43°32′50″ N, 70°27′32″ W	Aug 08 2004	NMW.Z.2005.011.02571	45
					JCN 12095	59
	23	Wells Heath (TNC); under heath scrub on *Sphagnum* bog	43°20′02″ N, 70°38′24″ W	Oct 01 2004	NMW.Z.2005.011.02597	90
Massachusetts						
Barnstable	24	Skunknett Audubon Preserve 2; *Myrica-Chamaecyparis* bog margin	41°38′59″ N, 70°22′31″ W	Aug 13 2004	NMW.Z.2005.011.02591	26
					JCN 12180	22
Bristol	25	Noquochoke WMA; *Chamaecyparis-Cryilla* swamp forest	41°39′35″ N, 71°01′07″ W	Aug 12 2004	NMW.Z.2005.011.02592	21
					JCN 12168	17
	26	Noquochoke WMA; leatherleaf island in acid sedge fen	41°39′39″ N, 71°01′12″ W	Aug 12 2004	NMW.Z.2005.011.02590	4
					JCN 12164	12
	27	Pine Swamp Brook; leatherleaf fringe of open acid bog	41°55′57″ N, 71°03′49″ W	Aug 10 2004	NMW.Z.2005.011.02586	9
					JCN 12149	5
Plymouth	28	Peterson Swamp WMA; *Chamaecyparis-Acer rubrum* forest	42°00′37″ N, 70°49′04″ W	Aug 10 2004	NMW.Z.2005.011.02585	~170
					JCN 12145	137
Worcester	29	Tom Bog; *Sphagnum* bog with scrub	42°30′46″ N, 72°12′43″ W	Oct 05 2004	NMW.Z.2005.011.02760	
					NMW.Z.2005.011.02761	~170
New Jersey						
Atlantic	30	Park Road (Wharton SF); moist *Ilex-Gaylussacia-Kalmia* scrub	39°42′58″ N, 74°44′10″ W	May 22 2004	NMW.Z.2005.011.02516	18
					JCN 12050	54
Burlington	31	Swan Bay WMA; low *Nyssa-Ilex-Acer rubrum* forest	39°35′13″ N, 74°30′50″ W	May 20 2004	NMW.Z.2005.011.02479	107
					JCN 11983	103
	32	Lebanon State Forest; open heath-*Smilax* scrub	39°52′28″ N, 74°30′57″ W	May 19 2004	NMW.Z.2005.011.02469	21
				May 21 2004	JCN 12026	14
	33	Roberts Brook; low *Nyssa-Chamaecyparis*-heath forest	39°47′07″ N, 74°39′26″ W	May 19 2004	NMW.Z.2005.011.02466	20
				May 21 2004	JCN 11989	5
	34	Brendan T Byrne State Forest; dry *Chamaecyparis*-bog	39°53′07″ N, 74°30′22″ W	May 22 2004	NMW.Z.2005.011.02499	1
Camden	35	2 miles WSW of Delette; moist bank with pine, oak, wax myrtle	39°46′32″ N, 74°48′21″ W	May 19 2004	NMW.Z.2005.011.02461	6
				May 21 2004	NMW.Z.2005.011.02484	28
					JCN 11995	8

Table 1. *Continued*

State/County	Site #	Site; Habitat[1]	Coordinates	Date	Accession Number	Specimens
Gloucester	36	Winslow WMA; heath scrub in abandoned blueberry field	39°37′08″ N, 74°53′43″ W	May 23 2004	NMW.Z.2005.011.02518 JCN 12054	12 14
Ocean	37	Colliers Mill WMA; acid bog with *Ilex, Chamaedaphne, Aronia*	40°05′35″ N, 74°25′58″ W	May 22 2004	NMW.Z.2005.011.02508 JCN 12036	~150 73
	38	Stafford Forge WMA; moist *Kalmia-Pinus* forest	39°42′44″ N, 74°22′10″ W	May 22 2004	NMW.Z.2005.011.02514 JCN 12045	122 54
			39°53′34″ N, 74°19′58″ W	May 22 2004	NMW.Z.2005.011.02511 JCN 12039	13 15
North Carolina						
Bladen	39	Johnson Mill Bay (Bladen Lakes SF); pocosin with *Chamaecyparis*	34°42′44″ N, 78°31′33″ W	Jun 02 2003	NMW.Z.2005.011.02204 JCN10613	~100 142
Brunswick	40	Green Swamp (TNC); *Chamaecyparis*-bay forest	34°06′14″ N. 78°18′35″ W	Jun 01 2003	NMW.Z.2005.011.02193 JCN 10615	50 94
	41	Green Swamp (TNC); medium pocosin	34°05′42″ N, 78°17′48″ W	Jun 01 2003	NMW.Z.2005.011.02194 JCN 10617	20 19
	42	Prospect Ridge; mature pine-bay forest	34°03′48″ N, 78°20′52″ W	Jun 01 2003	NMW.Z.2005.011.02196 JCN 10622	25 2
Carteret	43	Millis Road (Croatan NF); wet pocosin with leatherleaf	34°46′16″ N, 76°58′39″ W	Feb 24 2003	NMW.Z.2005.011.02128 JCN 10624	82
Craven	44	Sheep Ridge (Croatan NF); medium pocosin	34°56′07″ N, 77°04′14″ W	Feb 24 2003	NMW.Z.2005.011.02132 NMW.Z.2005.011.02130 JCN10693 JCN 10708	~600 30 481 10
	45	Catfish Lake South (Croatan NF); low, wet pocosin	34°55′39″ N, 77°05′05″ W	Feb 24 2003	NMW.Z.2005.011.02126 JCN 10678	~400 257
	46	Catfish Lake South (Croatan NF); roadside ditch in medium pocosin	34°55′10″ N, 77°05′24″ W	Feb 24 2003	JCN 10668	1
	47	Neusiok Trail North (Croatan NF); wet-mesic pine-bay forest	34°54′03″ N, 76°49′06″ W	Jun 01 2003	NMW.Z.2005.011.02190 JCN 10686	20
Jones	48	Catfish Lake Wilderness (Croatan NF); mature bay-pine forest	34°55′07″ N, 77°10′43″ W	Feb 24 2003	NMW.Z.2005.011.02125 JCN 10713	40 64
Moore	49	Pinebluff; bay forest in gulley along US 1	35°06′14″ N, 79°28′28″ W	Jun 03 2003	JCN 10746	18
Pamlico	50	Goose Creek Game Land; pine straw under scrub	35°15′14″ N, 76°35′52″ W	May 31 2003	NMW.Z.2005.011.02188	10
Pender	51	Holly Shelter game land; edge of mature mesic bay/pine forest	34°31′57″ N, 76°44′41″ W	Apr 01 2003	NMW.Z.2005.011.03830 NMW.Z.2005.011.02119 NMW.Z.2005.011.02118 NMW.Z.2005.011.02120 CM73971 UF348143	Holotype ~1700° ~1700° ~1700° 143° ~700°
	52	Holly Shelter game land; dense pocosin scrub	34°32′57″ N, 77°46′54″ W	Apr 01 2003	NMW.Z.2005.011.02428	~600
	53	Holly Shelter game land; dense bay scrub	34°33′06″ N, 77°47′37″ W	Apr 01 2003	NMW.Z.2005.011.02117	115
	54	Lanier Quarry (TNC); Shrubs bordering pine-wiregrass savanna	34°37′49″ N, 77°40′27″ W	Jun 01 2003	NMW.Z.2005.011.02192 JCN 10783	~80 64
Tyrrell	55	Pocosin Lakes NWR; low pocosin	35°42′30″ N, 76′11′11″ W	Apr 03 2003	NMW.Z.2005.011.02122 NMW.Z.2005.011.02123	~900 ~900
				May 31 2003	JCN 10824	92

Table 1. *Continued*

State/County	Site #	Site; Habitat[1]	Coordinates	Date	Accession Number	Specimens
	56	Pocosin Lakes NWR; maple-oak-pine woodland	35°40′19″ N, 76°12′16″ W	Apr 03 2003	NMW.Z.2005.011.02121	50
	57	Frying Pan Landing (Pocosin Lake NWR); pine pocosin	35°48′03″ N, 76°06′00″ W	Apr 03 2003 May 31 2003	NMW.Z.2005.011.02174 JCN 10823	1 1
South Carolina						
Horry	58	Lewis Ocean Bay Preserve; medium pocosin on roadside	33°47′14″ N, 78°50′36″ W	Jun 02 2003	NMW.Z.2005.011.02201 JCN 10955	~200 300
	59	Lewis Ocean Bay Preserve; mesic pine-bay forest	33°47′16″ N, 78°50′56″ W	Jun 02 2003	NMW.Z.2005.011.02197 JCN 10960	~250 123
	60	Lewis Ocean Bay Preserve; mesic longleaf pine forest	33°47′33″ N, 78°51′02″ W	Jun 02 2003	NMW.Z.2005.011.02200 JCN 10964	25 26

[1] Abbreviations used are: NF National Forest, NWR National Wildlife Refuge, SF State Forest, TNC The Nature Conservancy, WMA wildlife management area.

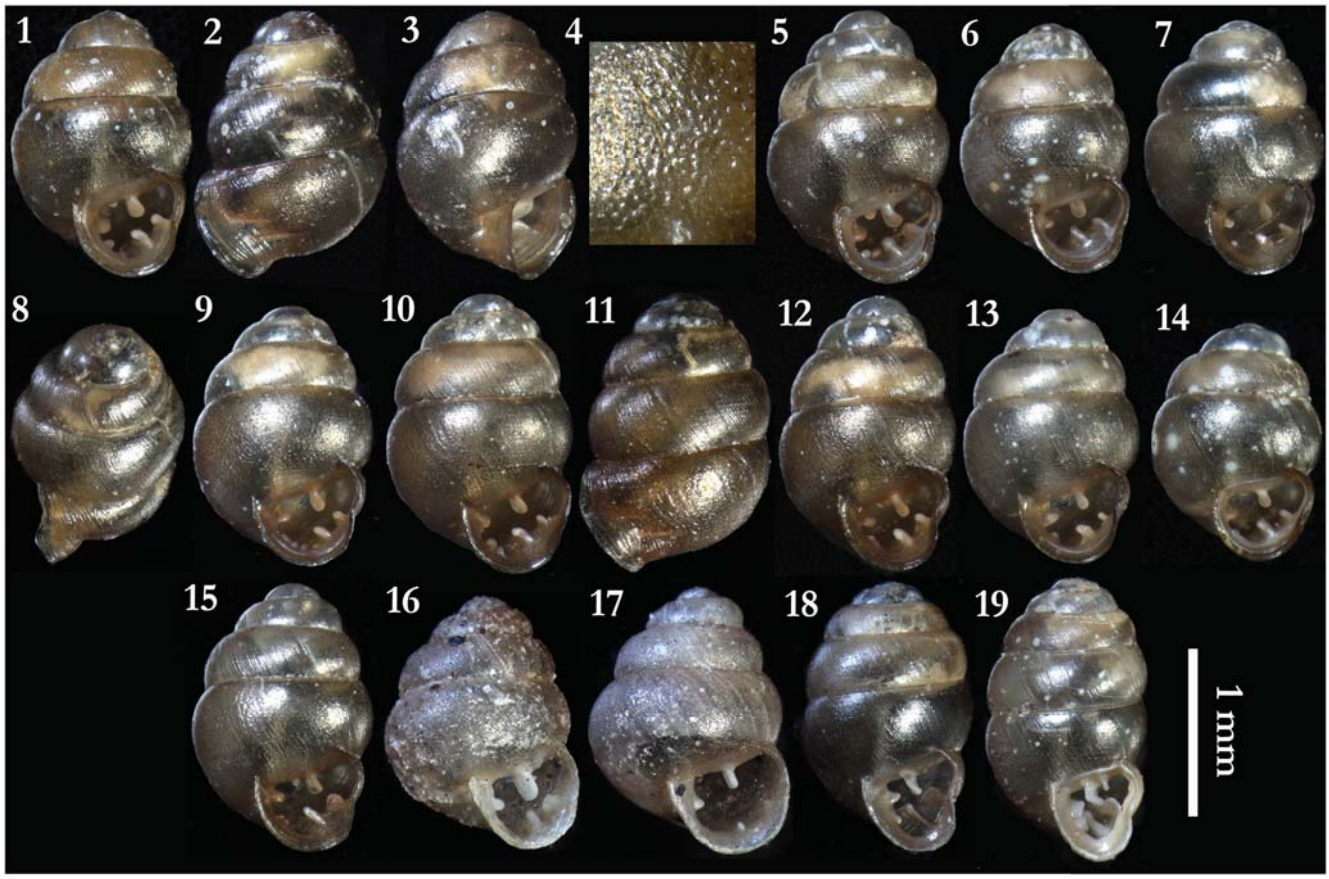
However, *V. cristata* has striate (not pustulose) sculpture on the body whorl, has a weak crest (rather than a basal inflation), lacks an infraparietal lamellae, and has a nodular (not shelf-like) columellar lamella. These two species were found co-occurring in several New England locations (Table 1, sites 21, 22, 23, and 29), where they could readily be distinguished under low magnification.

Vertigo malleata also resembles *Vertigo ventricosa* (Morse, 1865) and *Vertigo perryi* Sterki, 1905 with respect to the ovoid shape, large aperture vs. shell height ratio, reflected lip (Pilsbry, 1948: 958, figs. 1–3, 7), and basal apertural inflation (Coles and Nekola, *unpublished data*); *V. perryi* also has a dark colored peristome (Pilsbry, 1948: 968). However, these species cannot easily be confused because *V. ventricosa* and *V. perryi* have glossy shells with only weakly developed striae, lack an infraparietal lamella, and have a peg-like columellar lamella.

Although not previously reported in the genus *Vertigo*, the pustulose sculpture of the body whorl in *Vertigo malleata* is not unique to this species; *Vertigo alabamensis* and *Vertigo conecuhensis* (Pilsbry, 1948: 949, fig. 510, 9, 12–14; 950, fig. 511) of southeastern North America also weakly exhibit this trait (Figures 18, 19). At low magnification, the sculpture of *V. malleata* also somewhat resembles the pitted or granular surface of members of the Nesopupinae. However, members of the Nesopupinae commonly have an angular lamella (i.e., *Nesopupa, Sterkia*), while none are known to have an infraparietal lamella. Superficially, *V. malleata* also appears similar to the neotropical genus *Bothriopupa* (Pilsbry, 1948: 1011, fig. 539). However, with respect to shape, color, nature of the surface sculpture and configuration of the major apertural lamellae and folds, *V. malleata* much more closely resembles other members of the genus *Vertigo* (Figures 16, 17).

Geographic Distribution: *Vertigo malleata* occurs from southern Maine to southeastern Georgia along the Atlantic coastal plain to the west side of Mobile Bay along the Gulf coastal plain, apparently excluding peninsular Florida (Table 1, Figure 20). This distribution includes a number of regions of particular ecological interest and conservation concern, e.g., the Pine Barrens of New Jersey (sites 30, 32–35, 37–38), the sandhills and pocosins of the North Carolina and South Carolina coastal plain (sites 39–48, 51–60), the Okefenokee Swamp of southeastern Georgia (sites 19, 20), and the Appalachicola sand plain of western Florida (sites 8–17). It seems likely that its distribution extends into the Gulf coastal plain of Mississippi and eastern Louisiana. Although it is not yet known whether the species range extends beyond the eastern USA, given the known ranges of Atlantic coastal plain plant species (Sorrie and Weakley, 2001) the sand plains of southern Nova Scotia would appear to be an appropriate location for future surveys.

Preferred Habitats: *Vertigo malleata* occurred in approximately two-thirds of all surveyed acid habitats. In southern Maine and Massachusetts it was found in damp and lightly compacted leaf litter on *Sphagnum* bogs under a dense cover of ericaceous and other acidophile shrubs (e.g., *Gaylussacia, Vaccinium, Kalmia,* and *Myrica*). In this region it was also present in Atlantic white cedar bogs, where it occurred in leaf litter accumulations on mossy hummocks. In the New Jersey Pine Barrens *V. malleata* was found in dense leaf litter under tall heath (*Vaccinium, Gaylussacia, Kalmia*), *Myrica,* and *Ilex* scrub at the edges of bogs, Atlantic white cedar swamp forest, and mesic microsites in upland pine-oak forest. Populations in North and South Carolina were primarily located under dense heath, bay, holly, and wax myrtle scrub in pocosins, bay forest, wet-mesic pine woodland, and pine-wiregrass savanna. At Pocosin Lakes National Wildlife Refuge, for example, *V. malleata* was abundant in leaf litter on scrub vegetation islands within flooded pond pine woodland (Table 1, site 55), absent in adjacent broadleaf woodland, and present only in relatively low numbers at the transition zone (site 56). Popu-



Figures 1–19. *Vertigo malleata* and related taxa. **1–4.** *Vertigo malleata*. Holotype, NMW.Z.2005.011.03830, Holly Shelter Game Lands, Pender County, North Carolina, 34°31′57″ N, 77°44′41″ W; **1.** Apertural view. **2.** Abapertural view. **3.** View showing parietal and upper palatal lamellae. **4.** Sculpture on body whorl surface, width of detail is 0.25 mm. **5.** *Vertigo malleata*, second specimen from the type locality, NMW.Z.2005.011.03831, showing more conical shell shape. **6.** *Vertigo malleata*, NMW.Z.2005.011.03832, Stafford Forge WMA, Ocean County, New Jersey, 39°42′44″ N., 74°22′10″ W, showing small size and lack of infraparietal and subcolumellar-basal lamellae. **7–8.** *Vertigo malleata*, NMW.Z.2005.011.03833, Wells Heath, York County, Maine, 43°20′2″ N, 70°38′24″ W. **7.** Apertural view. **8.** View from apex showing apical whorls and the basal apertural dilation. **9.** *Vertigo malleata*, NMW.Z.2005.011.03834, Wilma Station, Liberty County, Florida, 30°9′34″ N, 84°57′39″ W, showing strong shell sculpture, a series of subcolumellar-basal lamellae, and a weak infraparietal lamella. **10, 11.** *Vertigo malleata*, NMW.Z.2005.011.03835, Pond Creek seep, Covington County, Alabama, 31°6′12″ N, 86°32′3″ W. **10.** Apertural view showing subcolumellar and basal lamellae, an indistinct nodule below the columellar lamella, and lack of an infraparietal lamella. **11.** Abapertural view. **12.** *Vertigo malleata*, NMW.Z.2005.011.03836, Collins Bay, Ware County, Georgia, 31°05′12″ N, 82°36′56″ W, showing elongate shape, fused subcolumellar and basal lamellae, and distinct sinulus. **13.** *Vertigo malleata*, NMW.Z.2005.011.03837, Skunknett Audubon Preserve 2, Barnstable County, Massachusetts, 41°38′59″ N, 70°22′31″ W, showing light shell color and basal lamella only. **14.** *Vertigo malleata*, NMW.Z.2005.011.03838, Peterson Swamp WMA, Plymouth County, Massachusetts, 42°00′37″ N, 70°49′4″ W, showing small size, vestigal infraparietal, and reduced basal lamellae. **15.** *Vertigo malleata*, NMW.Z.2005.011.03839, Lewis Ocean Bay Preserve, Horry County, South Carolina, 33°47′16″ N, 78°50′56″ W, showing bi-lobed basal lamella. **16.** *Bothriopupa tenuidens* (C.B. Adams, 1845), FMNH 106420, Louis Brand Collection, Columbia University. **17.** *Bothriopupa conoidea* (Pfeiffer, 1853), FMNH 119055, Kyk-Over-All Island, Kartabo, British Guiana. **18.** *Vertigo conecuhensis*, JCN 12364, Pond Creek seep, Covington County, Alabama, 31°6′12″ N, 86°32′3″ W. **19.** *Vertigo alabamensis*, JCN 10781, Lanier Quarry, Pender County, North Carolina, 34°37′49″ N, 77°40′27″ W.

lations in Georgia, Florida, and Alabama were found primarily in bay scrub along swamp margins, small water courses, and seepage zones within pinelands. Populations were also rarely encountered in mesic pine forest fragments that had escaped frequent fire management (see below); again, individuals were restricted to humid litter accumulations. Throughout its range, *Vertigo malleata* appeared to avoid even moderately less acidic habitats such as sedge meadows (Maine, Massachusetts), cattail swamps and marshes (Maine, Massachusetts, New Jersey), and bottomland bald cypress/water tupelo/sweetgum forests (North and South Carolina, Georgia, Florida, and Alabama).

Associated Land Snails and Community Composition: Across all 49 analyzed sites (Table 2), *Vertigo malleata* constituted 35% of total individuals. This fraction appeared to be inversely correlated with latitude,

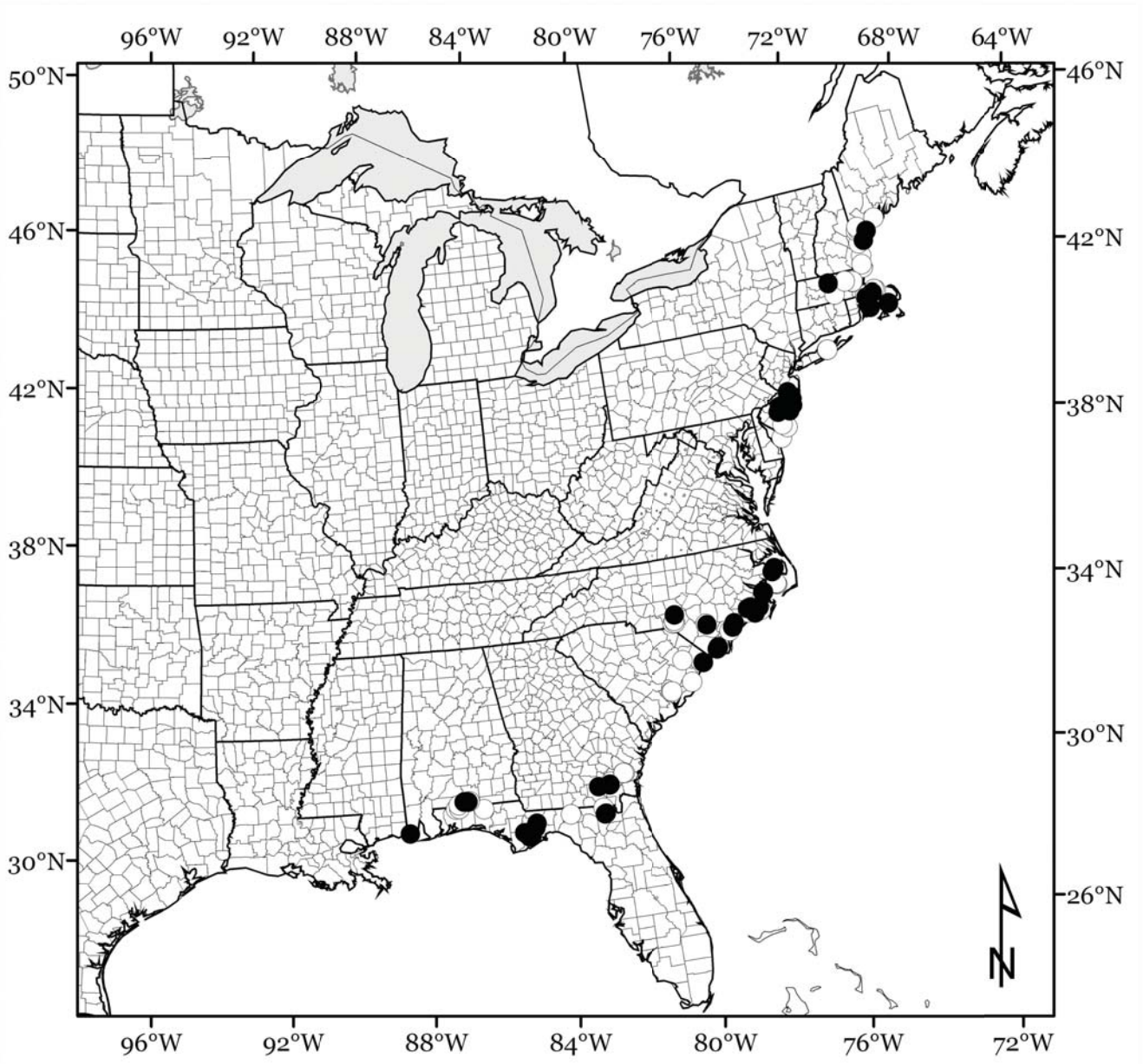


Figure 20. Distribution of *Vertigo malleata* in eastern North America. Black circles represent sites supporting populations and open circles represent inventoried sites that do not harbor this species.

ranging from 17% in the New Jersey Pine Barrens to 32% in New England, 35% in the Carolina coastal plains, and 76% in the Gulf coastal plain. Population densities of *V. malleata* were frequently observed to exceed 500 per m^2, with an estimated density of the order of 2000 per m^2 at the type locality (Table 1, site 51). These densities range among the highest reported for any land snail species (Frest and Johannes 1995, Cameron 2003).

A total of 34 terrestrial mollusk taxa and 5886 individuals were observed from these sites (Table 2). The average number of co-occurring taxa was 3.69 ± 0.37, and ranged from 0–9. Throughout its range, the ten most frequently co-occurring taxa were: *Striatura milium* (17% of all other individuals), *Strobilops texasiana* (15%), *Vertigo milium* (13%), *Punctum minutissimum* (11%), *Vertigo alabamensis* (9%), *Striatura meridionalis* (8%), *Gastrocopta pentodon* (8%), *Euconulus trochulus* (4%), *Euconulus chersinus* (2%), and *Gastrocopta contracta* (2%). The most frequent co-occurring taxa varied by region: *Striatura milium* and *Punctum minutissiumum* in New England; *Striatura meridionalis*, *Striatura milium*, *Punctum minutissimum*, and *Gastrocopta pentodon* in the New Jersey Pine Barrens; *Strobilops texasiana*, *Vertigo milium*, and *Vertigo alabamensis* along the Carolina coastal plain; and *Vertigo alabamensis*, *Striatura meridionalis*, and *Gastrocopta pentodon* along the Gulf coastal plain. Co-occurring *Vertigo* taxa also varied by region: *Vertigo cristata*, *Vertigo perryi*, and *Vertigo*

Table 2. Frequency of co-occurring species across the range of *Vertigo malleata*[1]

Taxon	Number of co-occurring individuals (%)				
	New England	New Jersey	Carolina coastal plain	Gulf coastal plain	Total
Vertigo malleata sp. nov.	308	340	1807	779	3234
Striatura milium (Morse, 1859)	480	407	119		1006
Strobilops texasiana Pilsbry & Ferris, 1906		61	835	11	907
Vertigo milium (Gould, 1840)			768		768
Punctum minutissumum (I. Lea, 1841)	113	398	164		675
Vertigo alabamensis Clapp, 1915			494	64	558
Striatura meridionalis (Pilsbry & Ferris, 1906)		413	25	46	484
Gastrocopta pentodon (Say, 1821)	6	258	156	45	465
Euconulus trochulus (Reinhardt, 1883)			216		216
Euconulus chersinus (Say, 1821)			120	3	123
Gastrocopta contracta (Say, 1822)			109		109
Glyphyalinia solida (H. B. Baker, 1930)		15	64	19	98
Glyphyalinia sp.[2]		28	63		91
Vertigo oralis Sterki, 1898			61	6	67
Hawaiia miniscula (A. Binney, 1840)			53		53
Glyphyalinia luticola Hubricht, 1966		28	12	3	43
Vertigo conecuhensis Clapp, 1915				39	39
Gastrocopta tappaniana (C. B. Adams, 1842)	4		28		32
Zonitoides arboreus (Say, 1816)	12	5		14	31
Euconulus fulvus (Müller, 1774)	20				20
Vertigo ovata Say, 1822					20
Vertigo ovata Say, 1822			20		20
Neohelix solemi Emberton, 1988	1		18		19
Ventridens cerinoideus (Anthony, 1865)			19		19
Vertigo cristata (Sterki, 1919)	13				13
Nesovitrea electrina (Gould, 1841)	6				6
Vertigo perryi Sterki, 1905	5				5
Gastrocopta riparia Hubricht, 1978			3		3
Helicodiscus parallelus (Say, 1817)			3		3
Troidopsis soelneri (J. B. Henderson, 1907)			3		3
Deroceras sp.			2		2
Glyphyalinia indentata (Say, 1823)	1		1		2
Vertigo rugosula Sterki, 1890			2		2
Vertigo ventricosa (Morse, 1865)	2				2
Striatura ferrea Morse, 1864	1				1
Triodopsis hopetonensis (Shuttleworth, 1852)			1		1
Total co-occurring individuals	664	1613	3359	250	5886
Co-occurring species richness	13	9	26	10	34

[1] Data taken from 49 discrete sites of the junior author collection (lots prefixed by JCN in Table 1).
[2] Juveniles and young adults of unclear identity.

ventricosa were sympatric in New England, while *Vertigo milium*, *Vertigo alabamensis*, *Vertigo oralis*, *Vertigo conecuhensis*, and *Vertigo rugosula* were sympatric in the Carolina and Gulf coastal plains.

CONSERVATION IMPLICATIONS

The data presented here show that *Vertigo malleata* is a characteristic component of the base-poor biota of the Atlantic and Gulf coastal plains, having been found in 66% of surveyed acid sites, and accounting for up to 75% of all mollusks in these sites. The abundance and widespread occurrence of *V. malleata* would seemingly suggest that it is not of immediate conservation concern. However, it appears that the species is in fact under threat because of the widespread use of fire as a management tool. Many coastal plain habitats, including those of *V. malleata* (i.e., pine woods, pine-wiregrass savanna, and pine barrens), have come to be viewed by many plant ecologists as pyrogenic (Myers, 1985; Christensen, 1988) and are being typically managed by anthropogenic fire return intervals of <5 years, with many areas being burned annually. However, such high-frequency fire management policies have been shown to exact a strong negative impact on total biodiversity, including Lepidoptera, Homoptera, Hymenoptera, Araneae, Collembola (Swengel, 1996, 1998; Harper et al., 2000), and terrestrial Mollusca (Nekola, 2002b).

The impact of fire on *Vertigo malleata* is illustrated by its distribution in the Appalachicola uplands of Florida.

We were unable to find *V. malleata* in forest that had been burned within three years, however, the presence of substantial populations in a tiny unburned inholding of mesic pine forest (Table 1 site 11), unburned mesic pine-red maple-Atlantic white cedar forest (Table 1 site 14), and unburned mesic margins of wetlands (Sites 8, 9, 12–13, 15–17) suggest that while it is not physiologically restricted to wetlands, it has become largely limited to these sites simply because they remain unburned. While these observations require further investigation, we estimate that at least 95% of the *V. malleata* population of the Apalachicola National Forest has been eliminated by management practices. Conversely, the presence of *V. malleata* in mesic bay-pine forest that had regenerated after burn (Table 1 site 10) shows that, apart from its intrinsic interest as an extreme calcifuge, this snail can potentially be used to monitor recovery from over-burning.

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