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CONTENTS

Plant Community Classification and the Flora of Native American Shell-middens on the Delmarva Peninsula 1

William A. McAvoy and Jason W. Harrison

Occurrence of *Candidula (Jacosta) intersecta* (Mollusca: Gastropoda: Hygromiidae) in Maryland With a Review of its Biogeography in the United States. 35

Jessica R. Schottruff and Clement L. Counts, III



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PLANT COMMUNITY CLASSIFICATION AND THE FLORA OF
NATIVE AMERICAN SHELL-MIDDENS ON THE
DELMARVA PENINSULA

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ABSTRACT

Fourteen Native American shell-middens were discovered on the Delmarva Peninsula in Kent, Queen Anne's and Dorchester Counties, Maryland. Occupying these shell-middens is a unique and globally rare plant community that supports 202 native species and varieties of vascular plants, including 87 that are rare or uncommon on the Peninsula and 21 that are new additions to the flora of the Delmarva.

INTRODUCTION

In 2001, while the first author (McAvoy) was studying and collecting plants at a site on the Delmarva Peninsula near the Chesapeake Bay in Kent Co., Maryland, he noticed an abundance of what appeared to be oyster shells exposed at the soil surface. Thinking this was unusual, McAvoy decided to explore the area a bit more. The site was a steep, south-facing, sparsely wooded slope above a tidal creek and shells were scattered over the slope and extended to the crest and beyond. It was found that the site was species-rich and contained a number of plants that were rare on the Coastal Plain, as well as several species that he had never seen before on the Delmarva. In addition, McAvoy was finding calciphytes

SUMMER 2012

FLORA OF NATIVE AMERICAN SHELL-MIDDENS

(plants that do not tolerate acidic soil), such as wild columbine (*Aquilegia canadensis*), large-seed forget-me-not (*Myosotis macrosperma*), bottlebrush wild rye (*Elymus hystrix* var. *hystrix*), smooth rockcress (*Boechea laevigata* var. *laevigata*), redbud (*Cercis canadensis* var. *canadensis*), Eastern hop-hornbeam (*Ostrya virginiana*), and yellow chinquapin oak (*Quercus muehlenbergii*). Later, McAvoy studied maps of this region of Kent County in the hope of finding additional sites. Several more sites were found all having a similar suite of plant species and the same physical features (steep slope above a tidal creek and shallow dry soils with oyster shells exposed at the surface). At this point, McAvoy thought it would be wise to inform Jason Harrison (second author), ecologist for the Maryland Wildlife and Heritage Services of what had been found, so that the plant community could be properly classified.

From 2001 to 2009, we searched for new sites on the various Chesapeake Bay tributaries of Kent, Queen Anne's and Talbot Counties, Maryland, and a total of 14 sites were documented and classified, including one site in Dorchester Co., Maryland. We initially thought that this plant community may have developed on late Paleocene [58 to 55 million years before present (MYBP)] marine deposits of the Aquia Formation. The Aquia Formation, developed during sea-level pulses, consists of clays, silts, shells, and glauconitic sands and is randomly exposed, or near the surface, in a continuous arc from the upper Chesapeake Bay to the James River in Virginia (Ward & Powars 2004). However, after reviewing geologic maps it was concluded that only one of our 14 sites correlated with the Aquia Formation, thus refuting our original hypothesis. Shell samples were provided to John Wilson of the Maryland Geological Survey in Baltimore, Maryland, who concluded that the shells are "of modern origin and too young to be from the Paleocene" and they are more likely from Native American shell-middens. Following a recommendation from Charles Hall of the Maryland Historical Trust, Darrin Lowery, a geoarchaeologist with the Smithsonian Institution was consulted. After describing the sites to Lowery and making field visits to several known areas, Lowery confirmed that these sites are indeed Native American shell-middens that could be over 3,000 years old and explained that Native American populations on the Delmarva Peninsula gathered shellfish from the Chesapeake Bay for food. These people cooked and ate their harvests on adjacent high-ground, then discarded the shells which led to the formation of the middens (pers. comm. Lowery 2009). The word "midden" has its roots in the Scandinavian languages, meaning an accumulation of refuse about a dwelling place (Stein

1992). Large shell-middens containing oyster, soft-shell clam, razor clam, hard-shell clam, ribbed mussel, bay scallop, and whelk have been documented around the shorelines of the Delmarva Peninsula (Lowery 2005). Thousands of shell-middens may have once existed, but sea level rise, shoreline erosion, mining, and development have eliminated, destroyed or degraded many of these unique archaeological features (pers. comm. Lowery 2011).

Perhaps the first account of shell-middens on the Delmarva comes from Ducatel and Alexander (1834), who submitted a report to the Maryland House of Delegates, noting that “extensive accumulations of oyster shells, evidently made by the aboriginal inhabitants of the country [were found], and that “extensive accumulations of this kind are said to be met with at Worton Point on the Chesapeake Bay in Kent County.” Jordan (1906) explored shell-middens consisting of the “common oyster” on Still Pond Creek (Queen Anne’s Co.) and estimated them to be “1000 years of age.” In 1938, Moorehead et al. reported finding “shell-heaps” in Kent Co. on Still Pond Creek, Worton Creek, and Farlee Creek [today known as Fairlee Creek (Moorehead et al. 1938)]. Moorehead et al. (1938) also pointed out that, “The situation of Indian shell-heaps on the Chesapeake Bay and its estuaries was probably determined in respective cases by the nearness of oyster bars. It seems likely that the Indians of those parts rarely, if ever, transported their oysters to shores very distant from the bars on which they obtained them.”

This paper examines the ecological and botanical components of Native American shell-middens on the Delmarva Peninsula and describes the plant community and flora that now occurs on these ancient and fascinating features.

THE STUDY AREA

The Delmarva Peninsula (Fig. 1) is an area lying entirely within the Atlantic Coastal Plain physiographic province of the eastern United States. The Peninsula lies south and east of the fall line (a term applied to the boundary between the Appalachian Piedmont province and the Atlantic Coastal Plain) in New Castle County, Delaware, and Cecil County, Maryland, and is bordered on the east by the Delaware River, Delaware Bay and the Atlantic Ocean, and on the west by the Elk River and Chesapeake Bay. It includes the Coastal Plain province of Delaware (New Castle, Kent, and Sussex Counties), the Eastern Shore of Maryland (Cecil, Kent, Queen Anne’s, Caroline, Talbot, Dorchester, Wicomico, Somerset, and Worcester Counties), and the Eastern Shore of Virginia (Accomack

FLORA OF NATIVE AMERICAN SHELL-MIDDENS

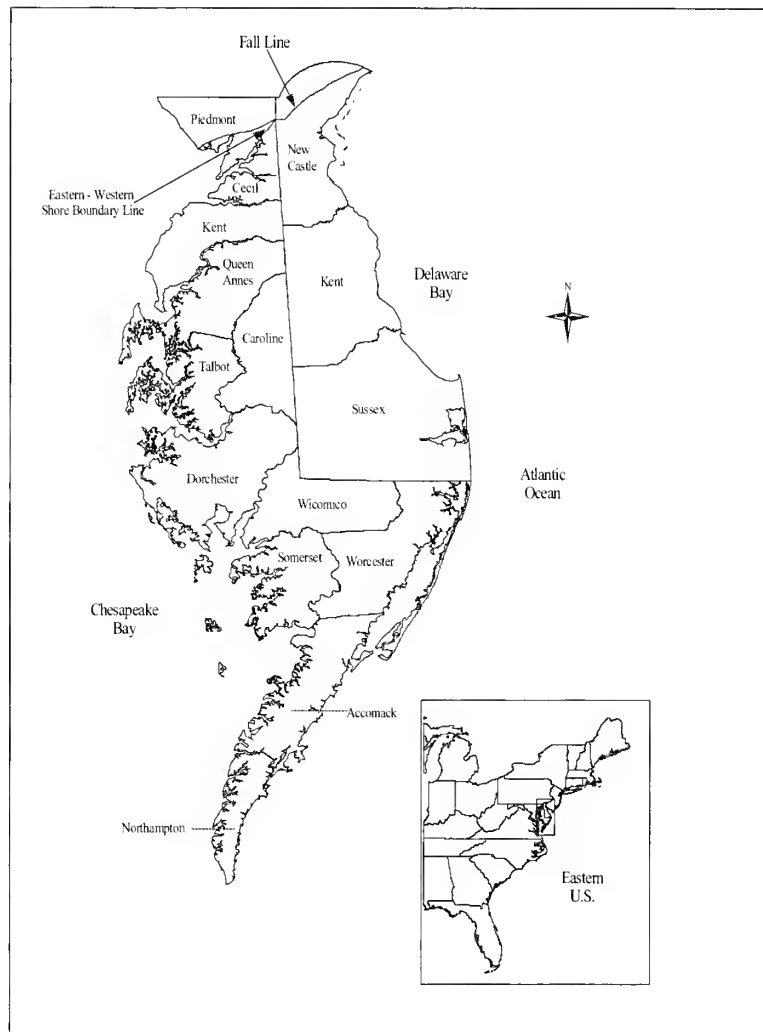


Figure 1. Location map for the Delmarva Peninsula.

and Northampton Counties). Its length north to south is about 200 miles (320 km), its greatest width is about 70 miles (110 km), its narrowest width is about 10 miles (16 km), and the total land area is about 5,800 square miles (15,000 square kilometers). The climate of the Peninsula is moderated by the Delaware Bay, Chesapeake Bay, and the Atlantic Ocean and is characterized by cool winters and warm, humid summers. The landscape of the Delmarva is mostly rural, on flat to

MCAVOY AND HARRISON

gentle sloping sandy plains with slow-flowing rivers and streams that are bordered by extensive swamp forests and tidal marshes. In the coastal areas, barrier islands, salt marshes, tidal flats and inland bays are well developed. The Delmarva's Coastal Plain soils of sands, silts, clays and gravel support forests primarily composed of mixed evergreen [*Pinus taeda* (loblolly pine), *Ilex opaca* var. *opaca* (American holly)] and deciduous tree species [*Quercus* spp. (oaks), *Carya* spp. (hickory's), *Fagus grandifolia* (American beech), *Nyssa sylvatica* (black gum), *Liquidambar styraciflua* (sweet gum), *Acer rubrum* (red maple), and *Liriodendron tulipifera* (tulip poplar)]. The Delmarva Peninsula lies within the Chesapeake Bay Lowlands Ecoregion as defined by The Nature Conservancy (2002), and within the Outer Coastal Plain Mixed Forest Province as mapped by Bailey (1995).

METHODS

The flora was inventoried qualitatively at 14 shell-middens throughout the growing seasons of 2001 to 2009 in an effort to capture the full floristic composition (Appendix I). All taxa (species, subspecies and varieties) were recorded from each shell-midden sampled. In addition, the frequency of occurrence for each taxon, or the number of shell-middens each taxon was recorded from was tallied (Appendix I). Source of botanical nomenclature follows Weakley (2010). In addition, quantitative data were collected from vegetation plots established at three sites using the Relevé method (*sensu* Peet et al. 1998), following guidelines used by the Maryland Natural Heritage Program to classify vegetation to the United States National Vegetation Classification (NVC). Sample sites were chosen subjectively by the authors to represent areas reasonably uniform in physiognomy, floristic composition, and environment.

The physical characteristics, including soil types, soil moisture regime, soil drainage class, surface substrate, aspect, topographic position, and slope shape of each site were measured to gain an understanding of the range of environmental variables that allow these unique communities to persist. Elevation was measured to the nearest 10 ft (~ 3 m) using USGS 7.5 minute topographic quadrangles. Soil surveys (Matthews et al. 1966; White 1982; NRCS 2011) of Kent, Dorchester, and Queen Anne's Counties, Maryland were used to determine which soil series and associations occurred at each site. A total of ten soil samples were collected from four sites and sent to Brookside Laboratories in New Knoxville, Ohio, for nutrient chemical analysis using the Mehlich III method

FLORA OF NATIVE AMERICAN SHELL-MIDDENS

(Mehlich 1984). General soil characteristics such as color and texture were evaluated in the field. Geological information was obtained through GIS software and consultations with geologists of the Maryland Geological Survey.

PLANT COMMUNITY RESULTS

PHYSICAL CHARACTERISTICS. Surveys conducted throughout the growing seasons of 2001-2009 identified 14 sites on the Delmarva Peninsula that support a unique vegetation consisting of calciphytes (see Botany Discussion below) and several regionally rare and uncommon species (see Botany Discussion below). Sites documented were found on dry, steep slopes and bluffs, contiguous uplands, and spits that were all adjacent to tidal tributaries and the main stems of rivers of the upper Chesapeake Bay. Nine of the 14 sites are located in Kent County, four in Queen Anne's County, and one in Dorchester County (Table 1). The sites identified occupy small irregular patches ranging from 0.16 ha (0.4 ac) to 7.8 ha (mean = 1.8 ha [4.4 ac]) in size. Overall, the 14 sites cover an area totaling 24.9 ha (61.4 ac). Slope aspects are variable among sites with seven oriented to the south, five oriented to the north, and two sites with multiple aspects because of its position on small, narrow spits near the mouths of tidal creeks. The majority of vegetation is best developed on slopes with convex slope curvatures (i.e., vertical) at mid to upper positions ranging in elevation from 2-7 m (~ 6-22 ft) above sea level (USGS 1973-1986). Percent slope among study sites varied widely depending on landform (e.g., spit), topographic position, and proximity to erosive tidal action. Side slopes immediately adjacent to tidal tributaries are very steep ranging from 58-74% and often displayed visible evidence of mechanical erosion. Sites positioned near the proximal end of spit landforms or contiguous landward uplands, are characterized by more gentle, undulating topography. Clinometer measurements of slope in these settings ranged from 8-30%.

We reviewed site locations and digitized versions of the 1968 geologic map of Maryland (Cleaves et al. 1968) in ArcGIS 9.2 (ESRI 2006) to determine surficial geology (Table 1). Due to the spatially coarse nature of these data, other sources were used in conjunction to ascertain geology for each site. County geological surveys (Miller et. al 1926), maps (Owens and Denny 1986; Miller et. al 1915), and personal communication with Maryland Geological Survey geologists, verified the geology for the remaining sites. In addition, a detailed discussion of regional stratigraphy for the Betterton quadrangle, Kent County

MCAVOY AND HARRISON

Table 1. Locality, County, Number of Sites, and Geologic Formation (Cleaves et al. 1968) of shell-midden sites sampled on the Delmarva Peninsula from 2001 to 2009.

Name	County	No. sites	Geologic Formation
Howell Point	Kent	2	Lowland Deposits
Still Pond Creek	Kent	3	Magothy Formation
Churn Creek	Kent	2	Potomac Group
Worton Creek	Kent	2	Lowland Deposits
Fairlee Creek	Kent	1	Lowland Deposits
Chester River	Queen Anne's	1	Lowland Deposits
Southeast Creek	Queen Anne's	2	Lowland Deposits
Transquaking River	Dorchester	1	Lowland Deposits

(Minard 1974) provided us with information for sites at Howell Point and Still Pond Creek. Through these sources we determined that sites at Howell Point, Worton Creek, Fairlee Creek, Southeast Creek, Chester River, and Transquaking River overlie the Lowland Deposits Formation of recent Quaternary [2.6 MYBP to present (Cleaves et al., 1968)]. The Lowland Deposits Formation is a thin layer of chiefly unconsolidated sand and gravel formed during the Pleistocene [2.6 MYBP to 12,000 years before present (YBP)] epoch that cover older formations of Cretaceous (145 MYBP to 65 MYBP) age throughout much of the inner and outer Coastal Plain (Minard 1974; Cleaves et al. 1968). Lower tertiary (65.5 MYBP to 23 MYBP) sediments of the Aquia Formation are mapped along portions of Southeast Creek (Miller et al. 1915; Miller et al. 1926; Cleaves et al. 1968), but are not exposed at the location of our study sites (pers. comm. John Wilson 2009). According to the digitized version of the geologic map of Maryland (Cleaves et al. 1968), the Aquia Formation accounts for 482 ha (1191 ac) in Kent County and only 12 ha (30 ac) in Queen Anne's County. The Aquia Formation is not exposed in Dorchester County. Cretaceous sediments are prevalent at sites adjacent to Still Pond Creek and Churn Creek. The Magothy Formation of quartz sand and discontinuous layers of clay-silt, are exposed along

FLORA OF NATIVE AMERICAN SHELL-MIDDENS

Still Pond Creek northward towards Howell Point, where it reaches basal contact with the Potomac Group (Minard 1974). The Potomac Group consists of continental deposits of gravel, sand, silt, and clay and is locally exposed along portions of Churn Creek, as well as bluffs around Worton and Howell Points.

According to county soil surveys (Matthews et al. 1966; White 1982; NRCS 2011), our 14 study sites are associated with ultisols of deep, well-drained sand and silt loams of the Mattapex, Galestown, Matapeake and Sassafras soil series. These soil series generally range in pH from 3.6 to 5.5 (Matthews et al. 1966; White 1982; NRCS 2011) and overlie older, coarser textured marine sediments (White 1982). According to NRCS (1998) these soil series fall into the “extremely acidic”, “very strongly acidic”, and “strongly acidic” classes of soil pH. Among all sites, approximately 31% (7.5 ha [18.5 ac]) of the total area is mapped as Mattapex silt loam, 18% (4.4 ha [10.9 ac]) is mapped as Galestown loamy sand, 13% (3.2 ha [7.9 ac]) is mapped as Matapeake silt loam, and 10% (2.5 ha [6.25 ac]) is mapped as Sassafras sandy loam. Soil series such as these are widespread on broad uplands, terraces, side slopes, and sandy knolls of the Delmarva Peninsula accounting for more than 30,000 hectares [ca. 75, 000 ac (NRCS 2011)]. The remaining 28% (6.7 ha [16.6 ac]) of sites are mapped as small units of sand and silt loams of the Runclint, Colts Neck, Unicorn-Sassafras, Keyport, and Downer series. All of these series are recognized as moderate to well drained and are strongly acid soils. Field observations at each of the 14 sites indicate that soil drainage class (i.e., well-drained) and soil moisture regime (i.e., dry) are consistent with USDA soil classifications (NRCS 2011).

The surface substrate at each site was variable in the amount of leaf litter and exposed mineral soil present. We determined these characteristics to be correlated with steepness of slope at the majority of sites where active mechanical erosion is a driving factor. A striking and diagnostic feature among all sites was the presence of shells and shell fragments of the Eastern oyster (*Crassostrea virginica*) in the soil and at the soil surface. Our efforts to extract soil samples from augured cores proved difficult because of the density and depth of oyster shells. At most sites, the depth of shells were at least 30 cm (11.8 in), but attempts to determine the maximum depth were not undertaken. Moorehead et al. (1938) reported depths of up to 137 cm (~ 54 in) at Fairlee Creek. The local influence of oyster shells on soil chemistry is evident. Results of nutrient chemical analyses (Table 2) from ten samples at four of our study sites report elevated calcium (Ca) levels ranging from 2,175 ppm (parts per million) to 8,097

MCAVOY AND HARRISON

Table 2. Summary of nutrient and chemical analysis of 10 soil samples from four shell-midden sites using the Mehlich III method (Mehlich 1984).

Soil Parameter	Mean (n=10)	Still Pond Creek 1	Still Pond Creek 2	Still Pond Creek 3	Still Pond Creek 4	Howell Point 1
Cation Exchange Capacity (meq/100g)	23.4	19.8	22.6	12.2	12.4	31.6
pH	7.2	7.1	7.3	7.3	7.2	7.7
Organic Matter (%)	8.5	12.2	8.5	3.9	3.5	11.6
Estimated Nitrogen Release (lb/A)	108	126	117	89	85	126
Soluble Sulfur (ppm)	24	21	20	25	25	27
Phosphorus (ppm)	43.9	21	63	15	11	75
Calcium (ppm)	4406	3711	4236	2227	2232	5967
Magnesium (ppm)	119	120	123	90	106	144
Calcium:Magnesium Ratio	35.7	30.9	34.4	27.4	21.1	41.4
Potassium (ppm)	66.5	57	102	68	56	114
Sodium (ppm)	38.4	30	35	32	37	53
Boron (ppm)	0.96	1.1	0.8	0.7	0.7	1.3
Iron (ppm)	90.3	126	122	60	63	59
Manganese (ppm)	131.7	89	114	67	55	424
Copper (ppm)	2.4	2.0	2.1	1.6	1.5	4.8
Zinc (ppm)	10.4	7.6	11.3	1.7	1.6	21.5
Aluminum (ppm)	359.9	165	128	380	401	535
Total Base Saturation (TBS) (%)	100	100	100	100	100	100
Fertility Index (CEC*TBS/100)	23.4	19.8	22.6	12.2	12.4	31.6

Soil Parameter	Howell Point 1	Howell Point 2	Howell Point 3	Worto Creek	Transqual River
Cation Exchange Capacity (meq/100g)	41.9	11.8	15.9	40.7	24.7
pH	7.1	7.1	6.9	7.1	7.3
Organic Matter (%)	8.8	3.4	3.5	20.7	8.8
Estimated Nitrogen Release (lb/A)	119	84	85	130	119
Soluble Sulfur (ppm)	21	11	14	51	25
Phosphorus (ppm)	41	18	4	29	162
Calcium (ppm)	8097	2175	2969	7785	4665
Magnesium (ppm)	128	88	99	168	124
Calcium:Magnesium Ratio	63.3	24.7	30.0	46.3	37.6
Potassium (ppm)	48	36	34	90	60
Sodium (ppm)	56	23	28	37	53
Boron (ppm)	1.5	0.7	0.6	1.1	1.4
Iron (ppm)	59	118	102	51	143
Manganese (ppm)	166	122	75	90	115
Copper (ppm)	3.0	1.6	2.0	3.4	1.7
Zinc (ppm)	11.7	2.2	2.9	32.9	10.3
Aluminum (ppm)	89	634	594	179	494
Total Base Saturation (TBS) (%)	100	100	100	100	100
Fertility Index (CEC*TBS/100)	41.9	11.8	15.9	40.7	24.7

FLORA OF NATIVE AMERICAN SHELL-MIDDENS

ppm (mean Ca = 4,406 ppm). High calcium levels have resulted in basic soils with pH ranging from 6.9 to 7.7 (mean pH = 7.2) among samples. Other correlates of high pH among soil samples include low organic matter (mean = 8.5%), which when high, facilitates soil acidification, and relatively low levels of iron (mean = 90.3 ppm), and aluminum (mean = 359.9 ppm). Further evidence of soil fertility is supported by high cation exchange capacity (i.e., total exchange capacity), values which ranged from 11.2 meq (milliequivalents)/100 g to 41.9 meq/100 g (mean = 23.4 meq/100 g) and 100% total base saturation among samples.

COMMUNITY COMPOSITION. Sites identified are positioned on steep, linear slopes and adjacent sublevel uplands between tidal waters and agricultural fields. The plant community that develops at these sites is characterized by having open canopies of *Quercus muehlenbergii*, a species more commonly associated with calcareous formations in the Ridge and Valley physiographic province and Piedmont outliers in Maryland. *Quercus muehlenbergii* was reported at 100% constancy and is dominant among all 14 sites. Relevé data collected at three vegetation sample plots indicate *Q. muehlenbergii* has a mean canopy cover of approximately 35%. Local site conditions such as proximity to agricultural fields or past land-use (e.g., logging) were inconsistent in regards to plant community development and canopy structure and vegetation composition was considerably heterogeneous among all sites. This is often the case in small-patch communities that are geographically isolated or require narrow requisite conditions. Species richness varies widely among sites ranging from four to 122 taxa and furthermore affirms the variability among sites. Alpha diversity, or mean species richness, among all sites is reported at 42 taxa. The total number of taxa, or gamma diversity, reported from all sites is 223 (Appendix I). Constant taxa (>75%) associated with *Q. muehlenbergii* in the canopy and subcanopy strata include *Celtis occidentalis* and *Ostrya virginiana*. Of these, *O. virginiana* attained greater canopy coverage at 38% in the relevé data. *Fraxinus americana*, *Carya cordiformis*, and *Juniperus virginiana* var. *virginiana* occur at moderate frequency in the canopy and subcanopy strata at more than 50% of sites surveyed. Occasional individuals of *Tilia americana* var. *americana*, *Quercus rubra*, *Quercus falcata*, *Quercus montana*, *Carya glabra*, *Fagus grandifolia*, *Liriodendron tulipifera*, and *Prunus serotina* var. *serotina* were reported from stands as infrequent low cover associates. The small tree and shrub strata (<6 m

[~19 ft]) is variable in composition and density. Frequent taxa in the small tree and shrub strata include *Viburnum prunifolium*, *Cercis canadensis* var. *canadensis*, *Cornus florida*, *Juniperus virginiana* var. *virginiana*, and *Ulmus rubra*.

The herbaceous stratum includes a diverse, patchily distributed mixture of forbs and graminoids adapted to sub-xeric to xeric soil conditions, and to soils with a high base status. This stratum accounts for 167 taxa, or 75% of all species documented from these sites. Graminoids such as *Elymus villosus*, *Elymus hystrix* var. *hystrix*, and *Bromus pubescens* are characteristic taxa and occur in 50% or more of stands. Infrequent taxa such as *Bromus nottowayanus*, *Tridens chapmanii*, *Elymus virginicus* var. *virginicus*, *Brachyelytrum erectum*, *Tridens flavus*, *Danthonia spicata*, *Avenella flexuosa*, *Poa compressa*, *Schizachyrium scoparium* var. *scoparium*, *Sporobolus clandestinus*, *Dichanthelium boscii*, and *Dichanthelium commutatum* var. *ashei* occur as low-cover associates. The forb component is also diverse and includes species such as *Aquilegia canadensis*, *Boechera laevigata* var. *laevigata*, *Ageratina altissima* var. *altissima*, and *Solidago ulmifolia* var. *ulmifolia*. Other low cover associates that occur at lesser frequencies include *Asplenium platyneuron*, *Carex blanda*, *Menispermum canadense*, *Anemone virginiana* var. *virginiana*, *Bidens bipinnata*, *Carex cephalophora*, *Carex muehlenbergii*, *Solidago caesia*, *Antennaria plantaginifolia*, *Carex rosea*, *Galium circaezans*, *Hackelia virginiana*, *Micranthes virginensis*, and *Myosotis macrosperma*.

PLANT COMMUNITY CLASSIFICATION. In 2007, quantitative vegetation sample plot data collected at Still Pond Creek and Worton Creek were combined in a large 1,250-plot regional dataset analysis for the National Capital Region and Mid-Atlantic National Parks vegetation mapping projects (NatureServe, in prep.). These projects span the Ridge and Valley, Blue Ridge, Piedmont, and Coastal Plain physiographic provinces of Maryland, Virginia, and West Virginia and account for the mapping of over 67,000 hectares (165,000 acres) of National Park Service land. These data and data from 22 plots in Virginia emerged from the analysis as a distinct vegetation group of highly calcareous settings with floristic similarities scattered throughout the Coastal Plain of Maryland and Virginia. Following guidelines for describing associations and alliances of the NVC (ESA 2004), a concept was developed based on these data for the *Quercus muehlenbergii* / *Cercis canadensis* / *Dichanthelium boscii* –

FLORA OF NATIVE AMERICAN SHELL-MIDDENS

Bromus pubescens – *Erigeron pulchellus* var. *pulchellus* – *Aquilegia canadensis* Forest (NVC Identifier Code CEG007748). This association is recognized as a globally rare forest type (NatureServe 2011) because of small patch size, limited distribution (i.e., Coastal Plain of Maryland and Virginia), and the degraded or vulnerable nature of many contemporary stands.

In Virginia, this vegetation is known from a wide area of the inner Coastal Plain, from Stafford and Westmoreland Counties on the north to James City, Surry, and York Counties, and the City of Suffolk in southeastern Virginia. Initially, the Virginia habitats were thought to develop on dry, steep, convex, south-facing slopes of deep ravines and stream-fronting bluffs incised into Pliocene and Miocene shell deposits or limesands, primarily of the calcium-rich Yorktown Formation (pers. comm. Gary Fleming 2004, NatureServe 2011). However, recent discussions regarding this vegetation association between the second author and Gary Fleming of the Virginia Natural Heritage Program, have clarified the environmental context of Virginia stands. According to Fleming's research, it now appears that six of the 18 known Virginia stands have also developed over shell-middens of Native American origin, while the remaining 12 stands occur on natural calcareous deposits of several Tertiary and Quaternary Formations in non-estuarine settings (pers. comm. Gary Fleming 2011). As in Virginia, similar vegetation has also been reported over natural calcareous deposits of Tertiary age (i.e., Aquia Formation) at Fort Washington National Historical Park on the inner Coastal Plain of Maryland. Here, stands occupy dry, steep, convex slopes with southerly aspects much like the Virginia stands. Both Fleming and the second author agree that species composition among Maryland and Virginia stands of this vegetation association over shell-middens and Tertiary or Quaternary Formations are similar enough to be recognized as a single vegetation type despite slightly variable landscape settings. Interestingly, these findings demonstrate a possible ecological relationship among stands of shell-middens and those of natural calcareous deposits. A likely scenario is shell-middens locally serve as surrogate habitats with requisite conditions for plants otherwise restricted to plant communities of natural calcareous deposits. Further research is needed to fully understand this relationship and subsequent development of plant communities over shell-middens of Native American origin.

MCAVOY AND HARRISON

BOTANICAL RESULTS

SUMMATION OF THE FLORA. The results of this study found that Native American shell-middens on the Delmarva Peninsula support 223 species, subspecies and varieties of native (202) and non-native (21) vascular plants [192 species and 31 subspecies and varieties (Appendix I)], represented by 74 families and 149 genera. The largest families (Table 3) are: Asteraceae (28 taxa), Poaceae (28 taxa), Cyperaceae (18 taxa), and Fagaceae (11 taxa). The largest genera (Table 3) are: *Carex* (15 taxa), *Quercus* (10 taxa), and *Solidago* (6 taxa). Eighty-seven (87) taxa documented are thought to be rare or uncommon on the Delmarva Peninsula (Appendix I). Of this figure, 21 taxa are new additions to the native flora of the Delmarva Peninsula [based on the literature (Tatnall 1946, Brown & Brown 1972, Brown & Brown 1984), and herbaria searches], and are reported here for the first time (Appendix I, highlighted in bold). Four taxa documented from shell-middens on the Delmarva are Maryland state listed species (Appendix I), and one species was a new addition to the native flora of the state of Maryland [*Tridens chapmani* (Appendix I)]. All rare and uncommon species have been vouchered, with specimens deposited at the Claude Phillips Herbarium [DOV (herbarium acronyms follow Index Herbariorum 2010)], Delaware State University, Dover, Delaware.

Table 3. Largest families and genera of the flora of Native American shell-middens on the Delmarva Peninsula.

Family	No. of Taxa	Genera	No. of Taxa
Asteraceae	28	<i>Carex</i>	15
Poaceae	28	<i>Quercus</i>	10
Cyperaceae	18	<i>Solidago</i>	6
Fagaceae	11		
Fabaceae	9		
Rosaceae	9		
Lamiaceae	7		
Apocynaceae	6		
Brassicaceae	6		
Apiaceae	5		
Caprifoliaceae	5		

FLORA OF NATIVE AMERICAN SHELL-MIDDENS

DISCUSSION

The results of this study found that Native American shell-middens on the Delmarva Peninsula support a high diversity of plants, with 202 native taxa documented (Appendix I). Of this figure, 21 taxa are new additions to the flora of the Delmarva and 87 are thought to be rare or uncommon on the Peninsula [43% of the flora (Appendix I)].

As suggested by soil chemistry analyses, the presence of abundant calcium in the soil from oyster shells is likely the principal environmental factor determining the floristic composition of the Native American shell-middens on the Delmarva Peninsula. Over time, as the shells decompose, they slowly release calcium carbonate into the surrounding soil creating a highly fertile and circumneutral soil (McMillan 2003). As discussed above, 10 soil samples were taken from 4 of the 14 sites documented, and analysis found that the average soil pH for Delmarva shell-middens was 7.2 (Table 2). The most productive soils have intermediate pH values, being not too acidic and not too alkaline, a pH range of perhaps 6.0 to 7.2 is most suitable for plant growth (Brady 1990), and favors the activity of a number of soil organisms, particularly the nitrifying bacteria (Riefner & Hill 1984). The fertility of calcium rich soils and associated high plant species diversity has been shown in Hill (1992), where he listed 161 species of plants that primarily occur on calcareous habitats in South Carolina. Additionally, Boone (1984) and Riefner & Hill (1984) collectively, listed 86 species of rare plants that are found on limestone formations in Maryland.

There is scarce information available in the literature on the physiology of most plants to prove calcium dependency, but of the 202 native taxa documented from shell-middens on the Delmarva Peninsula (Appendix I), 58 (Appendix I) have been reported by various sources as typically occurring in calcareous habitats in parts of their ranges (Fernald, 1950; Boone, 1984; Riefner & Hill, 1984; Gleason & Cronquist, 1991; Hill, 1992; Simmons et al., 1995; Simmons, 1999; Stalter et al., 1999; Steury, 2001; Stalter & Kincaid, 2004; Weakley, 2010). In these sources, habitat descriptions such as: "limestone formations," "calcium-rich soils," "calcareous woods," "soils over basic rocks," "circumneutral soils," "calcareous soils," "basic soils," "calcareous deposits," "soils over mafic rocks" and "over limestone" have been used. Though these species may not be obligate calciphytes in some geographic areas, in this paper they will be referred to as calciphytes.

Calcareous soils on the Chesapeake Bay Coastal Plain of the Delmarva Peninsula, the inner Coastal Plain of the Western Shore of Maryland, and the northern and southeastern Coastal Plain of Virginia are rare, but do exist in areas containing fossiliferous, calcareous shell deposits. These deposits are found in geologic formations created during the Tertiary Era, about 65 to 2 MYBP (Cleaves et al. 1968; VDMR 1993). Formations such as the Aquia, Brightseat, Hornerstown, Piney Point, Yorktown, Calvert, St. Mary's, and Choptank all contain prominent shell beds in addition to other geologic material (Cleaves et al. 1968, VDMR 1993), and when these formations are close to the surface, or when streams or rivers have down-cut into them, nutrient rich, circumneutral soils develop that favor plant growth and the development of unique calcareous plant communities. An example of a calcareous habitat on the Western Shore of Maryland is the Shell-Marl Ravine Forest [rich forests in deep ravines on highly fertile soil, pH = 6.5 (Simmons 1999; Steury 2001)]. Several examples of calcareous habitat in northern and southeastern Virginia include: Coastal Plain Calcareous Ravine Forest [rich mesophytic to submesophytic forests of calcareous ravines (Fleming & Patterson 2010)]; Coastal Plain Dry Calcareous Forest [fertile, sub-xeric to xeric forests on slopes of deep ravines or stream-fronting bluffs; soils are slightly acidic to circumneutral, with high calcium levels, average pH value = 6.5 (Fleming and Patterson 2010)]; and Coastal Plain Basic Mesic Hardwood Forest [mesophytic forests of sheltered ravines and slopes with base-rich soils in the northern portions of the Coastal Plain (Fleming and Patterson 2010)]. Calcareous habitats on the Delmarva Peninsula are locally known as Coastal Plain Rich-Woods. Though biotic and abiotic differences exist, the second author has included this community in the Coastal Plain Basic Mesic Hardwood Forest (Harrison 2011), as described in Virginia (Fleming & Patterson 2010). Though the soil pH values of Coastal Plain Rich-Woods of the Delmarva tend to be lower than neutral (7.0), pH values have been measured up to 6.8.

In researching the distribution of the calciphytic plants of the Delmarva shell-middens (Appendix I), the various sources consulted (Fernald 1950; Brown & Brown 1984; Gleason & Cronquist 1991; VBA 2006; Weakley 2010; Kartesz 2011) show that these species are all rare or uncommon on the Atlantic Coastal Plain and more commonly occur in habitats of the Piedmont or Mountain provinces of the eastern United States. So the question arises, why are these plants

FLORA OF NATIVE AMERICAN SHELL-MIDDENS

growing on the Coastal Plain of the Delmarva Peninsula in such rare and isolated habitats and how did they get here?

Modern-day distributions of organisms have direct links to the past, both recent and ancient, and plant migrations, especially local migrations are due to changes in the environment (Sauer 1988). The discarding of oyster shells by Native Americans over thousands of years in local upland areas was clearly a major disturbance. Existing vegetation was likely trampled, or possibly cleared intentionally during shellfish harvesting and processing (cooking and eating). These perturbations likely created an open, sunny area that was sparsely vegetated, and in conjunction with oyster shells influencing soil chemistry, an environment was created that was attractive to calcium-loving plants and gave these species an opportunity to colonize a new habitat. Thus, events of the past, condition where plants grow today.

Reznicek (1994) analyzed the disjunct Coastal Plain flora of the glaciated Great Lakes region and proposed that these species migrated into the region through “dispersal jumps” of varying distances between areas of suitable habitat. The authors here accept this same proposal as to how calcareous plants with Mountain and Piedmont affinities may have migrated to the Delmarva Coastal Plain shell-middens. Suitable habitat for dispersal jumps within the Chesapeake Bay region would include habitats previously described: Shell-Marl Ravine Forests of the Western Shore of Maryland, Coastal Plain Calcareous Ravine Forest, Coastal Plain Dry Calcareous Forest, and the Coastal Plain Basic Mesic Hardwood Forest of northern and southeastern Virginia, and the Coastal Plain Rich-Woods of the Delmarva Peninsula. In fact, when comparing the calcareous shell-midden plants of the Delmarva with species found in these calcareous habitats, it was found that they have much in common in regards to plant species composition. For example, there are 138 native species of the Coastal Plain Dry Calcareous Forests of northern and southeast Virginia that are also common to Delmarva shell-middens (unpublished plot data, Virginia Natural Heritage Program 2010). Similarly, there are 27 species of plants from the Shell-Marl Ravine Forests of the Western Shore of Maryland (Simmons 1999; Steury 2001) that also occur on Delmarva shell-middens. Furthermore, there are 40 species that are found in Coastal Plain Rich-Woods of the Delmarva that were also found on shell-middens (20 years of unpublished field data collected by the first author). These commonalities in plant species composition between Delmarva shell-middens and other calcareous habitats of the Chesapeake Bay region, further

suggests these habitats were used for dispersal jumps to Delmarva shell-middens. In addition, the thousands of shell-middens that may have once existed around the shorelines of the Delmarva Peninsula, but have been lost or degraded due to sea level rise, shoreline erosion, mining, and development, could have provided ample opportunities for these plants to colonize and continue to migrate to other middens. Winds, currents, tides, floods, mammals, and birds are likely some of the environmental elements responsible for the migration and establishment of calcareous plants on the Delmarva shell-middens, but Native Americans may also have had a hand in introducing some of these species. For example, perhaps some of these species were used medicinally or for cooking by the natives, and propagules were either intentionally or unintentionally transported to sites where shell-middens were created.

Based on terrestrial archaeological research done by Lowery (2005 and 2010), we can estimate the time period when the flora and plant community of Delmarva shell-middens likely began to develop. Current data indicates that Native American populations on the Delmarva Peninsula were using estuarine and marine shellfish resources as early as the terminal Late Archaic Period [3,800 – 3,200 YBP], and the use of these resources continued until the Contact Period [400 - 300 YBP (Lowery 2005 and 2010)]. However, exploitation of shellfish by Native American populations intensified during the Middle Woodland Period (2,000 – 1,000 YBP) to the Late Woodland Period [1,000 - 400 YBP (Lowery 2005)]. Therefore, the flora of shell-middens on the Delmarva could have begun to develop as late as 3,800 years ago, or more likely 2000 to 400 years ago, during the Middle to Late Woodland Periods when the greatest amounts of shellfish were being harvested. Occupation of areas where shell-middens were created were usually intermittent and may have been inactive for years while oyster beds replenished themselves after continual harvesting (pers. comm. Darrin Lowery 2011), subsequently, plants may have been able to establish and spread during periods when an area was not occupied. Comparable ages of shell-middens have been found in other parts of the country: Karalius and Alpert (2009) found shell-middens along the California coast to be at least 2000 years old; McMillan (2003) reported that shell-middens in South Carolina are approximately 2000 to 4000 years old; and Stalter et al. (1999) made note that shell-middens in South Carolina and Georgia have been carbon-dated at about 3,100 to 3,900 years.

FLORA OF NATIVE AMERICAN SHELL-MIDDENS

According to Jacobson et al. (1987), with the last remaining ice in northeastern Canada completely melted around 6000 years ago, broad patterns of vegetation (e.g., southeastern evergreen forests) in eastern North America began to approach modern-day conditions. When the flora of the Delmarva shell-middens first began to develop when speculated, during the Late Archaic Period (3,800 – 3,200 YBP), research suggests there were a series of climatic changes (Lowery 2005). During the Early Woodland Period (3,200 - 2000 YBP) the climate was wet and cold (Lowery 2005). The Middle Woodland Period (2,000 – 1,000 YBP) initially had a climate that was warm with wet conditions, and then changed to warm and dry conditions (Lowery 2005). The climate of the Late Woodland Period to the Contact Period (1,000 - 400 YBP), transitioned from warm and dry conditions, to a period of colder winter temperatures, along with periods of prolonged droughts (Lowery 2005).

From a geologic perspective, the Chesapeake Bay is a relatively recent phenomenon. The Bay itself began to form about 10,000 years ago when rising sea levels at the end of the last ice age flooded the area known as the Susquehanna River Valley (Reshetiloff 2004). The Chesapeake Bay assumed its present shape about 3,000 years ago (Reshetiloff 2004). When Native Americans were harvesting oysters from the Bay about 3,800 years ago, the Bay was significantly narrower than it is today. Water levels were about 25 feet lower than the present (pers. comm. Darrin Lowery 2011) and were between 3 and 8 feet lower 1,000 to 2,000 years ago (pers. comm. Darrin Lowery 2011) when the Delmarva middens may have been near their peak of construction. Today, the average depth of the Bay is 21 feet (Reshetiloff 2004) Therefore, plant propagules may not have had to migrate over a vast area to reach the Eastern Shore of the Bay from the Western Shore. However, plants did not necessarily need to migrate across the Bay west-to-east to reach calcareous habitats and shell-middens on the Delmarva, but could migrate to the north of the Bay through upland areas in Cecil Co., Maryland, and then move south finding Coastal Plain Rich-Woods and already established shell-middens.

Solbrig (1972) discusses the use of the term “disjunct” and points out that range disjunctions usually refer to large discontinuities in the distribution of a species, but there is no standard as to what scale of discontinuity qualifies as a range disjunction. As a result, we see the term applied equally to small discontinuities in the order of perhaps 100 miles, and to large ones involving thousands of miles. As mentioned previously, the calciphytic plants of the

Delmarva shell-middens are all rare on the Atlantic Coastal Plain and have closer affinities with habitats of the Mountain and Piedmont provinces, so in the broad sense, it may be that the calciphytes of the Delmarva shell-middens are all disjunct to some degree, but in the narrow sense, perhaps the only true disjunct found on Delmarva shell-middens would be *Zizia trifoliata*, where it was discovered from a shell-midden on the outer-Coastal Plain in Dorchester Co., Maryland. Prior to this discovery, the species was only found in Maryland at higher elevations in the western part of the state in Garrett County (Brown and Brown 1984, Kartesz 2011, pers. comm. W. Knapp 2011). *Zizia trifoliata* is a southern species, here on the Delmarva Peninsula near its northern extreme and is primarily a Mountain and Piedmont plant, where it ranges from West Virginia and south to Georgia (Weakley 2010). On the Coastal Plain it is rare, where it is found from Virginia [inner Coastal Plain, one county, Henrico (pers. comm. J. Townsend 2011, Weakley 2010)], and south to Florida (Weakley 2010). So the Dorchester Co. occurrence is considerably removed from its closest populations in Maryland [about 322 kilometers (200 miles) southeast from the center of Garrett Co., Maryland (Google Earth 2007)], and Virginia [about 161 kilometers (100 miles) northeast from the center of Henrico Co., Virginia (Google Earth 2007)]. Solbrig (1972) also adds that the interruption in the range of a species can have two origins: (1) the range was once continuous and the intermediate populations have become extinct, and (2) the range was never continuous and the disjunct populations have become established with the aid of some event that carried the propagules over the landscape. Due to the infrequent occurrence of calcareous habitats within the Chesapeake Bay Coastal Plain, the range of calciphytes within the region was likely never continuous, so the second type of origin would likely apply to the Delmarva shell-midden flora.

As discussed above, the soils of all 14 shell-midden sites documented are mapped as moderate, to well drained loams of sand and silt that range in acidity from strongly, to extremely acidic. Additionally, several of the sites (e.g., Still Pond Creek, Transquaking River) have warm aspects (south or west facing slopes). Due to the soil conditions just described, as well as the warm aspects of some sites, a number of shell-midden species occur more widely in sub-xeric to xeric habitat conditions on the Delmarva and are not considered to be calciphytes (Appendix I). When Native Americans were harvesting oysters from the Chesapeake Bay, the soils of the adjacent upland sites they selected for processing

FLORA OF NATIVE AMERICAN SHELL-MIDDENS

the oysters, prior to oyster shell decomposition, were either very similar or identical to what was just previously described. At that time, these soils likely supported the drought-tolerant species that are found today, such as *Commelina erecta*, *Opuntia humifusa*, *Vaccinium stamineum* and *Carya pallida*. With the creation of shell-middens and the subsequent decomposition of oyster shells, soil conditions were changed locally within a site (i.e., circumneutral pH), but the well-drained sand and silt loams remained and the sub-xeric to xeric plant species persisted.

Several studies on the flora and ecology of Native American shell-middens have been conducted in the past (Brown 1936; Laessle 1942; Dorroh 1971; Norman 1976; Eleuterius & Otvos 1979; Stein 1992; Stalter et al. 1999; Stalter & Kincaid 2004; Karalius & Alpert 2009). Stein (1992) points out that shell-middens are found in nearly every coastal area of the world, and that all shell-middens have certain properties in common: the shells primarily come from freshwater or marine animals, and sites are usually located adjacent to aquatic environments. In Mississippi, Eleuterius (1979) noted an array of plant species previously unreported from the state that were growing on shell-middens and that most were calcium-loving species. Stalter and Kincaid (2004) examined five shell-middens in Florida, and found that they all occupy high ground immediately adjacent to tidal creeks and salt marshes, are composed almost exclusively of oysters and collectively, support 190 species of plants.

In searching herbaria (BALT, DOV, MARY and PH) for early collections of rare shell-midden plants on the Delmarva, the only collections uncovered that gave any indication of shell-midden habitat were two specimens of *Quercus muehlenbergii*, both from Talbot County, Maryland (E. Earle 3776, 1942, PH; E. Earle 3863, 1943, PH). The labels from both collections point out that the plants were collected on "shell-bearing soil," that was "dry" and were on "banks" along tidal rivers. A series of collections made by P. Gladu in 1965 from Kent Co., Maryland [*Cercis canadensis*, *Cornus racemosa*, *Ostrya virginiana*, *Quercus muehlenbergii*, *Solidago ulmifolia*, *Ulmus rubra*, *Viburnum prunifolium* (MARY, no numbers assigned)], are species typical of shell-midden habitat on the Delmarva and were collected from an area where the authors had also identified shell-midden habitat. When cross-checking the rare shell-midden plants that were discovered during this study in Robert Tatnall's *Flora of Delaware and the Eastern Shore* (1946), no citations were found that indicated the existence of shell-midden habitat.

MCAVOY AND HARRISON

Native American shell-middens on the Delmarva Peninsula are rare natural and cultural resources that should receive high priority for conservation and protection. As noted earlier in the text, 21 species of non-native plants were documented from the shell-middens on the Delmarva (Appendix I), many of which are invasive, such as: *Ailanthus altissima*, *Alliaria petiolata* and *Microstegium vimineum*. The adjacency to agricultural lands of several of the shell-midden sites provides a greater opportunity for non-native plants to find their way to shell-middens and become established. Plans to control non-native invasive species should be developed in order to maintain the unique and rare native flora of these habitats. Extant shell-middens that have developed a characteristic calcareous plant community on the Delmarva are very rare, and if a population of a rare calciphite were to die-out due to displacement by non-native invasive species, there may not be a seed source close enough for re-establishment to take place.

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MCAVOY AND HARRISON

APPENDIX

Systematic List of Plants Associated with Native American Shell Middens on the
Delmarva Peninsula,
Their frequency of occurrence, status, and soil preferences.

	Frequency of Occurrence	Delmarva Status	Calciphyte Xeric Soils	Sub-xeric to Xeric Soils
Ferns				
ASPLENIACEAE				
<i>Asplenium platyneuron</i> (L.) B.S.P.	6	common	--	--
DENNSTAEDTIACEAE				
<i>Pteridium aquilinum</i> (L.) Kuhn var. <i>latiusculum</i> (Desv.) Underwood ex Heller	1	common	--	x
DRYOPTERIDACEAE				
<i>Woodsia obtusa</i> (Spreng.) Torr. subsp. <i>obtusa</i>	1	rare	x	--
EQUISETACEAE				
<i>Equisetum hyemale</i> L. subsp. <i>affine</i> (Engelm.) Calder & Taylor	1	rare	--	--
Gymnosperms				
CUPRESSACEAE				
<i>Juniperus virginiana</i> L. var. <i>virginiana</i>	6	common	--	x
PINACEAE				
<i>Pinus taeda</i> L.	1	common	--	--
<i>Pinus virginiana</i> P. Mill.	3	common	--	x
Monocotyledons				
ALLIACEAE				
<i>Allium canadense</i> L. var. <i>canadense</i>	1	uncommon	-	--
ARACEAE				
<i>Arisaema dracontium</i> (L.) Schott	1	rare	x	--
COLCHICACEAE				
<i>Uvularia perfoliata</i> L.	2	uncommon	--	--
<i>Uvularia sessilifolia</i> L.	1	common	--	--
COMMELINACEAE				
<i>Commelina erecta</i> L.	1	rare	--	x
CYPERACEAE				
<i>Carex albicans</i> Willd. ex Spreng. var. <i>albicans</i>	2	common	--	--
<i>Carex blanda</i> Dewey	8	common	--	--
<i>Carex cephalophora</i> Muhl. ex Willd.	5	common	--	--
<i>Carex digitalis</i> Willd. var. <i>digitalis</i>	2	common	--	--
<i>Carex granularis</i> Muhl. ex Willd.	2	rare	x	--
<i>Carex jamesii</i> Schwein.	3	rare	--	--

FLORA OF NATIVE AMERICAN SHELL-MIDDENS

	Frequency of Occurrence	Delmarva Status	Calciphyte Xeric Soils	Sub-xeric to Xeric Soils
<i>Carex muehlenbergii</i> Schkuhr ex Willd. var. <i>enervis</i> Boott	3	rare	x	--
<i>Carex muehlenbergii</i> Schkuhr ex Willd. var. <i>muehlenbergii</i>	5	common	--	x
<i>Carex nigromarginata</i> Schwein.	1	common	--	x
<i>Carex planispicata</i> Naczi	1	rare	--	--
<i>Carex rosea</i> Schkuhr ex Willd.	4	common	--	--
<i>Carex sparganioides</i> Muhl.	1	rare	--	--
<i>Carex striatula</i> Michx.	1	uncommon	--	--
<i>Carex tosa</i> (Fern.) Bickn. var. <i>tonsa</i>	2	common	--	x
<i>Carex umbellata</i> Schkuhr ex Willd.	1	common	--	x
<i>Cyperus lupulinus</i> (Spreng.) Marcks	1	common	--	x
<i>Cyperus refractus</i> Engelm. ex Boeckeler	1	rare	--	x
<i>Cyperus retrofractus</i> (L.) Torr.	1	rare	--	x
IRIDACEAE				
<i>Sisyrinchium angustifolium</i> Miller	4	common	--	--
<i>Sisyrinchium mucronatum</i> Michx.	1	rare	x	--
POACEAE				
<i>Avenella flexuosa</i> (L.) Drejer	4	common	--	x
<i>Brachyelytrium erectum</i> (Schreb.) P. Beauv.	1	rare	x	--
<i>Bromus japonicus</i> Thunb. ex Murr.	1	non-native	--	--
<i>Bromus nottowayanus</i> Fern.	1	rare	--	--
<i>Bromus pubescens</i> Muhl. ex Willd.	6	rare	x	--
<i>Danthonia spicata</i> (L.) Beauv. ex Roemer & J.A. Schultes	3	common	--	x
<i>Dichanthelium boscii</i> (Poiret) Gould & Clark	2	common	--	--
<i>Dichanthelium commutatum</i> (Schult.) Gould var. <i>ashei</i> (Pearson ex Ashe) Mohlenbrock	2	common	--	x
<i>Dichanthelium dichotomum</i> (L.) Gould var. <i>dichotomum</i>	1	common	--	--
<i>Dichanthelium oligosanthes</i> (Schult.) Gould var. <i>oligosanthes</i>	1	common	--	x
<i>Elymus hystrix</i> L. var. <i>hystrix</i>	6	rare	x	--
<i>Elymus villosus</i> Muhl.	12	uncommon	x	--
<i>Elymus virginicus</i> L. var. <i>virginicus</i>	5	common	--	--
<i>Eragrostis spectabilis</i> (Pursh) Steud.	1	common	--	x
<i>Festuca rubra</i> L.	1	common	--	--
<i>Festuca subverticillata</i> (Pers.) Alexeev	4	common	--	--
<i>Microstegium vimineum</i> (Trin.) A. Camus	2	non-native	--	--
<i>Muhlenbergia sobolifera</i> (Muhl. ex Willd.) Trin.	1	rare	x	--
<i>Piptochaetium avenaceum</i> (L.) Parodi	1	common	--	x
<i>Poa compressa</i> L.	4	non-native	--	--

McAVOY AND HARRISON

	Frequency of Occurrence	Delmarva Status	Calciphyte Xeric Soils	Sub-xeric to Xeric Soils
<i>Poa cuspidata</i> Nutt.	1	rare	x	--
<i>Poa sylvestris</i> A. Gray	1	rare	x	--
<i>Schizachyrium scoparium</i> (Michx.) Nash var. <i>scoparium</i>	4	common	--	x
<i>Sphenopholis vitida</i> (Biehler) Scribn.	2	common	--	--
<i>Sporobolus clandestinus</i> (Biehler) A.S. Hitchc.	1	rare	--	x
<i>Tridens chapmanii</i> (Small) Chase	2	rare	--	--
<i>Tridens flavus</i> (L.) A. Hitchc.	4	common	--	--
<i>Vulpia octoflora</i> (Walt.) Rydb.	1	common	--	x
RUSCACEAE				
<i>Polygonatum biflorum</i> (Walt.) Ell. var. <i>biflorum</i>	3	common	--	--
SMILACACEAE				
<i>Smilax glauca</i> Walt.	3	common	--	--
<i>Smilax hispida</i> Muhl. ex Torr.	1	rare	x	x
<i>Smilax rotundifolia</i> L.	2	common	--	--
Dicotyledons				
ACANTHACEAE				
<i>Ruellia caroliniensis</i> (J.F. Gmel.) Steud.	2	rare	x	--
ALTINGIACEAE				
<i>Liquidambar styraciflua</i> L.	2	common	--	--
ANACARDIACEAE				
<i>Toxicodendron radicans</i> (L.) Kuntze var. <i>radicans</i>	2	common	--	--
ANNONACEAE				
<i>Asimina triloba</i> (L.) Dunal	5	common	--	--
APIACEAE				
<i>Sanicula canadensis</i> L.	2	common	--	--
<i>Sanicula marilandica</i> L.	1	rare	x	--
<i>Taenidia integerrima</i> (L.) Drude	2	rare	x	--
<i>Zizia aptera</i> (Gray) Fern.	1	rare	--	--
<i>Zizia trifoliata</i> (Michx.) Fern.	1	rare	--	--
APOCYNACEAE				
<i>Apocynum cannabinum</i> L.	3	common	--	--
<i>Asclepias tuberosa</i> L. subsp. <i>tuberosa</i>	1	common	--	--
<i>Asclepias variegata</i> L.	2	rare	--	X
<i>Asclepias verticillata</i> L.	2	rare	x	--
<i>Asclepias viridiflora</i> Raf.	1	uncommon	x	--
<i>Matelea carolineensis</i> (Jacq.) Woods	3	uncommon	x	--
AQUIFOLIACEAE				
<i>Ilex opaca</i> Ait. var. <i>opaca</i>	1	common	--	--
ARALIACEAE				
<i>Hedera helix</i> L.	3	non-native	--	--
ARISTOLOCHIACEAE				

FLORA OF NATIVE AMERICAN SHELL-MIDDENS

	Frequency of Occurrence	Delmarva Status	Calciphyte Xeric Soils	Sub-xeric to Xeric Soils
<i>Endodeca serpentaria</i> (L.) Raf.	2	uncommon	x	--
ASTERACEAE				
<i>Achillea millefolium</i> L.	3	non-native	--	--
<i>Ageratina altissima</i> (L.) King & H.E. Robins. var. altissima	8	common	--	--
<i>Antennaria howellii</i> Greene subsp. Neodioica (Greene) Bayer	1	common	--	--
<i>Antennaria plantaginifolia</i> (L.) Richards.	4	common	--	--
<i>Bidens bipinnata</i> L.	5	common	--	x
<i>Erigeron pulchellus</i> Michx. var. <i>pulchellus</i>	2	common	--	x
<i>Erigeron strigosus</i> Muhl. ex Willd. (Fisch. & C.A. Mey) Torr. & Gray ex Gray var. <i>strigosus</i>	2		--	
<i>Eupatorium album</i> L. var. <i>vaseyi</i> (Porter) Cronq.	2	uncommon	--	--
<i>Eupatorium hyssopifolium</i> L.	1	common	--	--
<i>Eutrochium purpureum</i> (L.) E.E. Lamont	1	rare	x	--
<i>Helianthus decapetalus</i> L.	2	rare	--	x
<i>Helianthus divaricatus</i> L.	1	rare	x	--
<i>Heliopsis helianthoides</i> (L.) Sweet var. <i>helianthoides</i>	2	rare	x	--
<i>Hieracium venosum</i> L.	3	common	--	--
<i>Prenanthes altissima</i> L.	2	common	--	--
<i>Smallanthus uvedalia</i> (L.) Mackenzie ex Small	1	uncommon	x	x
<i>Solidago arguta</i> Ait. var. <i>arguta</i>	1	rare	--	--
<i>Solidago bicolor</i> L.	3	common	--	--
<i>Solidago caesia</i> L.	5	common	--	--
<i>Solidago rugosa</i> P. Mill. var. <i>aspera</i> (Ait.) Cronq.	1	common	--	x
<i>Solidago speciosa</i> Nutt. var. <i>speciosa</i>	1	rare	--	--
<i>Solidago ulmifolia</i> Muhl. ex Willd. var. <i>ulmifolia</i>	6	rare	x	x
<i>Symphotrichum laeve</i> (L.) Nesom var. <i>concinnum</i> (Willd.) Nesom	2	rare	x	--
<i>Symphotrichum laeve</i> (L.) Nesom var. <i>laeve</i>	4	rare	x	--
<i>Symphotrichum patens</i> (Ait.) Nesom var. <i>patens</i>	3	uncommon	--	--
<i>Verbesina alternifolia</i> (L.) Britton	4	rare	--	--
<i>Verbesina occidentalis</i> (L.) Walt.	2	common	--	--
<i>Vernonia glauca</i> (L.) Willd.	1	rare	x	--
BERBERIDACEAE				
<i>Berberis thunbergii</i> DC.	1	non-native	--	--
BETULACEAE				
<i>Ostrya virginiana</i> (Miller) K. Koch	9	rare	x	--
BIGNONIACEAE				
<i>Campsis radicans</i> (L.) Seem. ex Bureau	1	common	--	--
BORAGINACEAE				
<i>Hackelia virginiana</i> (L.) I.M. Johnston	4	uncommon	--	--

McAVOY AND HARRISON

	Frequency of Occurrence	Delmarva Status	Calciphyte Xeric Soils	Sub-xeric to Xeric Soils
<i>Myosotis macrosperma</i> Engelm.	4	rare	x	--
BRASSICACEAE				
<i>Alliaria petiolata</i> (Bieb.) Cavara & Grande	6	non-native	--	--
<i>Arabidopsis lyrata</i> (L.) O'Kane & Al-Shehbaz subsp. <i>lyrata</i>	2	rare	x	--
<i>Barbarea vulgaris</i> Ait. f.	1	non-native	--	--
<i>Boechera canadensis</i> (L.) Al-Shehbaz	1	rare	x	--
<i>Boechera laevigata</i> (Muhl. ex Willd.) Al-Shehbaz var. <i>laevigata</i>	6	rare	x	--
<i>Cardamine concatenata</i> (Michx.) Sw.	3	uncommon	x	--
CACTACEAE				
<i>Opuntia humifusa</i> (Raf.) Raf.	2	common	--	x
CAESALPINIACEAE				
<i>Cercis canadensis</i> L. var. <i>canadensis</i>	8	rare	x	--
CAMPANULACEAE				
<i>Campanulastrum americanum</i> (L.) Small	2	rare	x	--
CAPRIFOLIACEAE				
<i>Lonicera japonica</i> Thunb.	2	non-native	--	--
<i>Lonicera morrowii</i> Gray	2	non-native	--	--
<i>Triosteum angustifolium</i> L. var. <i>eamesii</i> Wiegand	1	rare	x	--
<i>Triosteum perfoliatum</i> L.	2	rare	x	--
<i>Viburnum prunifolium</i> L.	10	common	--	--
CARYOPHYLLACEAE				
<i>Dianthus armeria</i> L.	2	non-native	--	--
<i>Silene antirrhina</i> L.	1	common	--	--
CELASTRACEAE				
<i>Celastrus orbiculatus</i> Thunb.	2	non-native	--	--
<i>Euonymus americanus</i> L.	1	common	--	--
CISTACEAE				
<i>Crocanthemum canadense</i> (L.) Britt.	1	common	--	x
CONVOLVULACEAE				
<i>Ipomoea pandurata</i> (L.) G.F.W. Mey.	1	common	--	x
CORNACEAE				
<i>Cornus florida</i> L.	7	common	--	--
<i>Cornus racemosa</i> Lam.	2	rare	--	x
EBENACEAE				
<i>Diospyros virginiana</i> L.	1	common	--	--
ELAEAGNACEAE				
<i>Elaeagnus umbellata</i> Thunb.	1	non-native	--	--
ERICACEAE				
<i>Chimaphila maculata</i> (L.) Pursh	3	common	--	--
<i>Vaccinium pallidum</i> Ait.	2	common	--	x

FLORA OF NATIVE AMERICAN SHELL-MIDDENS

	Frequency of Occurrence	Delmarva Status	Calciphyte Xeric Soils	Sub-xeric to Xeric Soils
<i>Vaccinium stamineum</i> L.	2	common	--	x
EUPHORBIACEAE				
<i>Acalypha virginica</i> L.	1	common	--	--
<i>Euphorbia corollata</i> L.	1	common	--	x
<i>Euphorbia ipecacuanliae</i> L.	2	common	--	x
FABACEAE				
<i>Amorpha fruticosa</i> L.	4	common	--	--
<i>Chamaecrista fasciculata</i> (Michx.) Greene var. <i>fasciculata</i>	1	common	--	--
<i>Desmodium canescens</i> (L.) DC.	1	common	--	x
<i>Desmodium laevigatum</i> (Nutt.) DC.	1	common	--	x
<i>Desmodium paniculatum</i> (L.) DC. var. <i>paniculatum</i>	2	common	--	x
<i>Galactia volubilis</i> (L.) Britt. var. <i>volubilis</i>	1	common	--	x
<i>Lespedeza procumbens</i> Michx.	2	common	--	x
<i>Lespedeza violaceae</i> (L.) Pers.	1	common	--	x
<i>Robinia pseudoacacia</i> L.	1	non-native	--	--
FAGACEAE				
<i>Fagus grandifolia</i> Ehrh.	1	common	--	--
<i>Quercus alba</i> L.	1	common	--	x
<i>Quercus coccinea</i> Muenchh.	2	common	--	--
<i>Quercus falcata</i> Michx.	3	common	--	x
<i>Quercus montana</i> Willd.	4	common	--	x
<i>Quercus muhlenbergii</i> Engelm.	14	rare	x	--
<i>Quercus nigra</i> L.	1	common	--	--
<i>Quercus phellos</i> L.	1	common	--	--
<i>Quercus rubra</i> L.	5	common	--	--
<i>Quercus stellata</i> Wangenh.	2	common	--	x
<i>Quercus velutina</i> Lam.	2	common	--	--
FUMARIACEAE				
<i>Dicentra cucullaria</i> (L.) Bernh.	3	rare	x	--
HYDROPHYLLACEAE				
<i>Hydrophyllum virginianum</i> L.	1	rare	x	--
HYPERICACEAE				
<i>Hypericum punctatum</i> Lam.	1	common	--	x
<i>Hypericum stragulum</i> P. Adams & Robson	1	common	--	--
JUGLANDACEAE				
<i>Carya alba</i> (L.) Nutt. ex Ell.	1	common	--	--
<i>Carya cordiformis</i> (Wangenh.) K. Koch	6	common	--	x
<i>Carya pallida</i> (Ashe) Engl. & Graebn.	1	common	--	--
<i>Juglans nigra</i> L.	1	common	--	--
LAMIACEAE				
<i>Agastache nepetoides</i> (L.) Kuntze	1	uncommon	x	--

MCAVOY AND HARRISON

	Frequency of Occurrence	Delmarva Status	Calciphyte Xeric Soils	Sub-xeric to Xeric Soils
<i>Clinopodium vulgare</i> L.	2	non-native	--	--
<i>Perilla frutescens</i> (L.) Britt.	1	non-native	--	--
<i>Pycnanthemum incanum</i> (L.) Michx. var. <i>incanum</i>	1	rare	--	--
<i>Salvia lyrata</i> L.	4	common	--	--
<i>Scutellaria elliptica</i> Muhl. ex Spreng. var. <i>elliptica</i>	2	common	--	x
<i>Trichostema setaceum</i> Houtt.	1	rare	--	--
MAGNOLIACEAE				
<i>Liriodendron tulipifera</i> L.	2	common	--	--
MALVACEAE				
<i>Tilia americana</i> L. var. <i>americana</i>	4	rare	x	--
MENISPERMACEAE				
<i>Menispermum canadense</i> L.	7	common	--	--
MYRICACEAE				x
<i>Morella pensylvanica</i> (Mirbel) Kartesz	1	common	--	--
OLEACEAE				
<i>Fraxinus americana</i> L.	7	rare	x	--
ONAGRACEAE				
<i>Circaea canadensis</i> (L.) Hill	3	common	--	--
PAPAVERACEAE				
<i>Sanguinaria canadensis</i> L.	2	common	--	--
PASSIFLORACEAE				
<i>Passiflora lutea</i> L.	4	common	--	--
PAULOWNIACEAE				
<i>Paulownia tomentosa</i> (Thunb.) Sieb. & Zucc. ex Steud.	1	non-native	--	--
PLANTAGINACEAE				
<i>Penstemon hirsutus</i> (L.) Willd.	1	rare	--	--
POLYGONACEAE				
<i>Persicaria virginiana</i> (L.) Gaertner	2	common	--	--
RANUNCULACEAE				
<i>Anemone americana</i> (DC.) Hara	2	rare	x	--
<i>Anemone virginiana</i> L. var. <i>virginiana</i>	6	rare	x	--
<i>Aquilegia canadensis</i> L.	8	rare	x	--
<i>Thalictrum thalictroides</i> (L.) Eames & Boivin	1	uncommon	x	--
ROSACEAE				
<i>Agrimonia gryposepala</i> Wallr.	1	uncommon	x	--
<i>Agrimonia pubescens</i> Walbr.	3	uncommon	--	--
<i>Amelanchier arborea</i> (Michx. f.) Fern.	3	common	--	--
<i>Crataegus uniflora</i> Muenchh.	1	uncommon	--	x
<i>Geum canadense</i> Jacq.	1	common	--	--
<i>Prunus serotina</i> Ehrh. var. <i>serotina</i>	2	common	--	--

FLORA OF NATIVE AMERICAN SHELL-MIDDENS

	Frequency of Occurrence	Delmarva Status	Calciphyte Xeric Soils	Sub-xeric to Xeric Soils
<i>Rosa carolina</i> L. subsp. <i>carolina</i>	1	uncommon	--	x
<i>Rosa multiflora</i> Thunb. ex Murr.	5	non-native	--	--
<i>Rubus phoenicolasius</i> Maxim.	4	non-native	--	--
RUBIACEAE				
<i>Galium circaezans</i> Michx. var. <i>circaezans</i>	4	common	--	--
<i>Galium pilosum</i> Aiton var. <i>pilosum</i>	3	common	--	x
SAXIFRAGACEAE				
<i>Heuchera americana</i> L.	2	uncommon	x	--
<i>Micranthes virginensis</i> (Michx.) Small	4	rare	x	--
SCROPHULARIACEAE				
<i>Scrophularia marilandica</i> L.	4	uncommon	x	--
<i>Verbascum thapsus</i> L.	4	non-native	--	--
SIMAROUBACEAE				
<i>Ailanthus altissima</i> (P. Mill.) Swingle	4	non-native	--	--
STAPHYLEACEAE				
<i>Staphylea trifolia</i> L.	2	uncommon	x	--
ULMACEAE				
<i>Celtis occidentalis</i> L.	11	common	--	--
<i>Ulmus americana</i> L.	2	common	--	--
<i>Ulmus rubra</i> Muhl.	6	common	x	--
URTICACEAE				
<i>Parietaria pensylvanica</i> Muhl.	3	rare	x	--
VALERIANACEAE				
<i>Valerianella radiata</i> (L.) Dufur.	1	common	--	--
VERBENACEAE				
<i>Phryma leptostachya</i> L.	2	uncommon	x	--
<i>Verbena urticifolia</i> L.	2	common	--	--
VIOLACEAE				
<i>Hybanthus concolor</i> (T.F. Forst.) Spreng.	1	rare	x	--
<i>Viola pubescens</i> Aiton	1	rare	--	--
VITACEAE				
<i>Parthenocissus quinquefolia</i> (L.) Planch.	3	common	--	--
<i>Vitis rotundifolia</i> Michx.	2	common	--	--

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OCCURRENCE OF *CANDIDULA (JACOSTA)*
INTERSECTA (MOLLUSCA: GASTROPODA:
HYGROMIIDAE) IN MARYLAND
WITH A REVIEW OF ITS BIOGEOGRAPHY IN THE
UNITED STATES

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ABSTRACT

The land snail *Candidula intersecta* (Poiret) [= *Helicella caperata* (Montagu)] is reported for the first time in the state of Maryland. A review of the taxonomic changes associated with the species is presented along with remarks on the distribution of this European species in the United States is presented with a digest of documented specimens from the states of Hawaii, Maryland, North Carolina, South Carolina, and Virginia and notation of its occurrence in the Pacific northwest.

REPORT

On 17 June 2012, one of us (JRS) discovered shells of *Candidula (Jacosta) intersecta* (Poiret, 1801) on grass and shrubs adjacent to the Maryland Department of Natural Resources shellfish laboratory and entrance to Law Cove, Deal Island, Somerset County, Maryland, at 38°10'03"N, 75°56'52"W which represents the first occurrence of the species in the state. Voucher specimens have been placed in the collection of the Delaware Museum of Natural History (DMNH 238381). The species has been found nearby at Chincoteague Island, Accomack County, Virginia, by the second author (CLC) in 1991 (see Appendix

SUMMER 2012

CANDIDULA INTERSECTA IN MARYLAND

l) and this population still persists. That locality is on the Atlantic coast, while Deal Island is a site on Chesapeake Bay, the opposite side of the Delmarva Peninsula. Collections made along the coast of North Carolina in 1991 indicate that the species was commonly found at sites where vehicular traffic was heavy (e.g., NCSR 12 running the length of the Outer Banks) and the electronic report of Hitchcox (2007) demonstrates the ability of these gastropods to hitchhike on man-made structures such as shipping containers. This ability to hitchhike may have been the mechanism of dispersal of this exotic snail along the mid-Atlantic coast.

DISCUSSION

The taxonomy of the land snail *Candidula (Jacosta) intersecta* (Poiret, 1801) (Fig. 1) has undergone several iterations. Poiret (1801) described the species as *Helix intersecta*. Montague (1803) redescribed the species as *Helix caperata* from specimens collected in England. Montague also noted that the species had been seen by Solander and Gmelin. The first formal report of the species in the United States (Wood 1951) reported the species as *Helicella caperata* (Montague 1803) and Horace Burrington Baker, in a footnote to this report, noted that *Jacosta (Candidula) caperata* (Montague 1803) may be a synonym of *Jacosta intersecta* (Poiret). In the paper immediately following Wood's account, Saunders (1951) used the name *Jacosta (Candidula) intersecta* (Poiret 1801). Generally, the species appears in the literature as *Helicella caperata* but more recently has come to be classified as *Candidula intersecta* (Poiret 1801).

Henry A. Pilsbry reported *Helicella terrestris* (Pennant 1777) from Charleston, South Carolina (Pilsbry 1897) and later reported that William G. Mazyck had deposited specimens of *H. terrestris* in the Academy of Natural Sciences of Philadelphia in 1909 collected at Charleston (Pilsbry 1910) and specimens from Mazyck's backyard, identified as *Helicella ventricosa* (Draparnaud 1801) were deposited there in 1931 (ANSP 157204). Also at Philadelphia, a single lot of *Helicella (Candidula) subrutilla* (Mighels 1845) is found in the collections of the Academy (ANSP 323429) whose locality is given as Hawaii, Sandwich Islands. No date is provided with this lot although the use of "Sandwich Islands" was more or less abandoned by the 1870s.

Wood (1951) reported the presence of *Helicella caperata* at Yorktown, Virginia, where it was reported to be well-established on a beach on the York River where it was associated with several species of native land snails. Wood

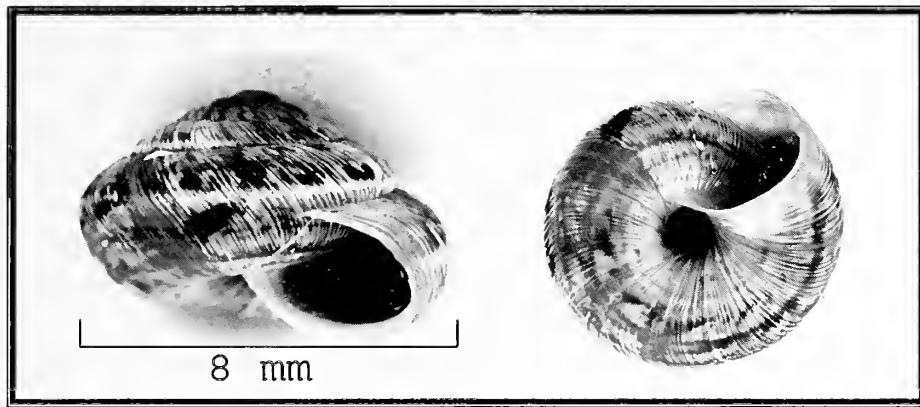


Figure 1. *Candidula intersecta* from Oregon. Photographs: Mark Hitchcox, U.S. Animal and Plant Health Inspection Service – Plant Protection and Quarantine, 2010.

noted that although he could not state with certainty the time period in which these snails were introduced, York had been a port as early as 1691 and was intensively used from 1700 to 1770 and ceased to be a point of transshipment to Europe by 1800. Saunders (1951) report noted the occurrence of the species in the Beaufort, North Carolina, area at two localities, but made no statement on probable dates of introduction. Despite Wood's speculations on how early *Candidula intersecta* was introduced, no mention of the species in made in Pilsbry's monograph of the land Mollusca of North America (1939-1948) with regard to its presence on the continent. Townes (1957) reported *Helicella elegans* (Gmelin 1791) to have been introduced at Charleston, South Carolina, at St. Peter's Church yard on Logan Street, in 1875 and noted the species was still surviving in large number by 1931.

Dundee (1974), in her review of introduced species of molluscs in eastern North America, reported three species in genus *Helicella*: *Helicella caperata*, originally from western Europe; *Helicella elegans* from the Mediterranean coasts of France and Spain, Tunisia, the Baleari Islands, Morocco, and Tunis; and *Helicella striata* (Müller 1774) from middle Europe. These three were believed to have established themselves in the United States. She further noted the

CANDIDULA INTERSECTA IN MARYLAND

interception of 49 species in genus *Helicella* at United States ports (Table 1). More recently, Hitchcox (2007) has reported *Candidula intersecta* from active port sites on the southern Oregon coast. He further noted its presence in Benton, Clackamas, Clatsop, Columbia, Coos, Curry, Douglas, Jackson, Klamath, Lane, Lincoln, Marion, Multnomah, Polk, Washington and Yamhill counties in the state and noted that the species is frequently intercepted at Portland on cargo containers from Italy, Columbia, and Chile (Hitchcox 2007). Hitchcox also noted the ability of these snails to hitch-hike on shipping containers. This comports with evidence of hitch-hiking by those specimens found along the North Carolina coast (Appendix 1) where it is noted that most collection localities for the snail were parking lots, campgrounds, or roadside rest areas.

It has been reported that this species can become a serious agricultural pest in orchards or on field crops. Dundee (1971) reported the species to have been intercepted on a wide variety of agricultural products and Hitchcox (2007) noted that *C. intersecta* is a potential threat to crops in Oregon. Godan (1983) reported the species to infest tree fruits such as pears, prunes, and apples, damaging so as to allow fungal attacks. These problems have not been reported in South Carolina, North Carolina, or Virginia, so the possibility of such future impacts on Maryland agriculture cannot be predicted with certainty.

ACKNOWLEDGEMENTS

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CANDIDULA INTERSECTA IN MARYLAND

Table 1. Species in the genus *Helicella* intercepted at United States ports and states in which the interceptions occurred (after Dundee, 1974)

Species	Port of Interception	Species	Port of Interception
<i>Helicella amanda</i> (Rossmessler)	SC, TX	<i>Helicella larnacensis</i> (Kobelt)	VA
<i>Helicella apicina</i> (Lamarck)	DE, GA, NY, NC	<i>Helicella littoralis</i> (Mousson)	NY
<i>Helicella arigonis</i> (Rossmessler)	DE	<i>Helicella maritima</i> (Draparnaud)	AL, DE, FL, IL, LA, MD, MA, MI, MN, NY, OH, PA, SC, VA, WA, WI
<i>Helicella armillata</i> (Lowe)	MA	<i>Helicella mada</i> (Porro)	LA, NY, PA
<i>Helicella barcinensis</i> (Bourguinait)	DE	<i>Helicella neglecta</i> (Draparnaud)	DE, LA
<i>Helicella calcarata</i> (Benson)	NY	<i>Helicella neritella</i> (Lamarck)	FL
<i>Helicella candidula</i> (Studer)	LA, MD, NJ, NY, PA	<i>Helicella obvia</i> (Menke)	NY, SC
<i>Helicella cincta</i> (Müller)	FL, MI, NY	<i>Helicella oweniana</i> (Pfeiffer)	LA, TX,
<i>Helicella conspurcata</i> (Draparnaud)	DE, FL, IL, LA, MD, MA, NJ, NY, NC, PA, SC, TX, VA, WA	<i>Helicella peritella</i> (Lamarck)	FL
<i>Helicella cinvexa</i> (Pfeiffer)	FL, NY, SC	<i>Helicella profuga</i> (Schmidt)	LA
<i>Helicella corrugata</i> (Gmelin)	MA	<i>Helicella protea</i> (Zeigler)	DE, FL, LA, MI, NJ, NY, VA, DC
<i>Helicella cretica</i> (Férussac)	AL, DE, GA, IL, LA, MD, MA, MI, NY, NC, PA, SC, TX, VA, DC	<i>Helicella pyramidata</i> (Draparnaud)	DE, LA, MA, MI, NY, NC, SC, VA
<i>Helicella derbentina</i> (Andrezejowski)	AL, DE, LA, NJ, NY, OH, SC, TN, VA	<i>Helicella seetzeni</i> (Koch.)	NY
<i>Helicella elegans</i> (Gmelin)	PA	<i>Helicella striolata</i> (Pfeiffer)	AL, DE, LA, NJ, NY, OH, TX
<i>Helicella explanata</i> (Müller)	NC	<i>Helicella substriata</i> (Gray)	FL
<i>Helicella figulina</i> (Parreys)	DE, IL, NY	<i>Helicella terrestris</i> (Pennant)	NY
<i>Helicella gigas</i> (Charpentier)	NJ	<i>Helicella trochooides</i> (Poiret)	DE, LA, NY, NY, NC, PA, TX, VA
<i>Helicella itala</i> (Linné)	AL, LA, PA, NJ, NY	<i>Helicella tuberculosa serrulata</i> (Beck)	MA
<i>Helicella holotricia</i> (Boettger)	TX	<i>Helicella variabilis</i> (Draparnaud)	DE, FL, GA, IL, LA, MD, MA, NJ, NY, NC, PA, SC, TX, VA
<i>Helicella languinosa</i> Boissy	LA	<i>Helicella vestalia</i> (Pfeiffer)	LA
<i>Helicella joppensis</i> (Toth)	AL, DE, LA, MA, NY, PA	<i>Helicella virgata</i> DaCosta	DE, LA, MA, NY, PA, OH, SC, TX, VA
<i>Helicella krynickii</i> (Andrezejowski)	DE, LA, MD, NJ, NY, SC, TX		

SCHOTTROFF AND COUNTS

APPENDIX 1

Documented Materials in the Genus *Candidula* and *Helicella* in Institutional Collections (ANSP = Academy of Natural Sciences of Philadelphia; DMNH – Delaware Museum of Natural History; NMC – National Museum of Nature of Canada. Species are identified as [a] = *Helicella caperata*, [b] = *Helicella striata*, [c] = *Candidula intersecta*, [d] = *Helicella terrestris*, [e] = *Helicella ventricosa*, [f] = *Helicella intersecta*, [g] = *Helicella subrutilla*). NCSR = North Carolina State Route, VASR = Virginia State Route, US = United States highway).

HAWAII. *Island of Hawaii.* Unnamed locality and undated (ANSP 323429 [g]).

MARYLAND. *Somerset County.* Grass and shrubs adjacent to Maryland Department of Natural Resources shellfish laboratory and entrance to Law Cove, Deal Island, 38°10'03"N, 75°56'52"W, 17 June 2012 (DMNH 238381 [c]);

NORTH CAROLINA. *Brunswick County:* County Road 104, 9.0 km east of Lockwood Folly Inlet, west end of Oak Island, Long beach, 33°55'14"N, 78°08'03"W, 20 July 1991 (DMNH 238364 [c]). *Carteret County.* Atlantic Beach water tower, NCSR 58, 7.6 km west of Fort Macon State Park, Bogue Banks, sandy substratum, 34°42'02"N, 75°45'33"W, 13 April 1991 (DMNH 238361 [c]); 28th Street and Homes Drive, Morehead City, in grass, 34°43'27"N, 76°44'28"W, 13 April 1991 (DMNH 238358 [c]); NCSR 58 at Intracoastal Waterway bridge, south side, west end of bank, Bogue Banks, sandy substratum, 34°39'39"N, 75°03'38"W, 13 April 1991 (DMNH 238357 [c]); Fort Macon State Park terminal parking lot, sandy substratum at woods edge, Bogue Banks, 34°41'55"N, 75°40'44"W, 13 April 1991 (DMNH 238356 [c]); Bogue Banks, Cedar Tree Road at NCSR 58, 57.4 km west of Fort Macon State park, Sandy substratum at woods edge, 34°40'21"N, 76°59'11"W, 13 April 1991 (DMNH 238386 [c]); Waterfront at Orange Street, Beaufort, residential yard, 34°43'07"N, 76°40'06"W, 14 April 1991 (DMNH 238359 [c]); Indian Beach, about 20.0 km west of Fort Macon State Park, just north of NCSR 58, Bogue Banks, sandy substratum, 34°42'12"N, 75°53'43"W, 14 April 1991 (DMNH 238360 [c]); Davis at Cape Lookout (South Core Banks) ferry landing, 35°47'42"N, 76°27'29"W, 22 July 1991 (DMNH 238370 [c]); At Cape Lookout lighthouse, 34°37'22"N, 76°31'29"W, 22 July 1991 (DMNH 238372 [c]); Cedar Island, Ocracoke Ferry landing, 35°01'03"N,

CANDIDULA INTERSECTA IN MARYLAND

76°18'54"W, 22 July 1991 (DMNH 238366 [c]); South Core Banks, National Park Service dock at Les and Sally's, Cape Lookout, 34°37'29"N, 76°31'24"W, 22 July 1991 (DMNH 238373 [c]). **Dare County.** Frisco, Pea Island, 4.9 km north of Hatteras, near Pamlico Sound in *Zostera marina* washed ashore, 35°42'00"N, 75°29'37"W, 17 February 1991 (DMNH 238333 [c]); Fulcher's Family Cemetery on south side of NCSR 12, Hatteras Island, sand substratum, 35°13'47"N, 75°37'57"W, 16 March 1991 (DMNH 238248 [c]); Whalebone Junction near junction of NCSR 12 and US 64, sand substratum, 35°54'22"N, 75°35'55"W, 16 March 1991 (DMNH 238352 [c]); Turn-out parking lot 36.1 km south of Old Oregon Inlet Coast Guard Station, Hatteras Island, sand substratum, 35°37'28"N, 75°28'10"W, 16 March 1991 (DMNH 238338 [c]); Entrance to Oregon Inlet Campground, just north of Oregon Inlet, Bodie Island, sand substratum, 35°48'01"N, 75°32'45"W, 16 March 1991 (DMNH 238345 [c]); Vegetation in parking lot between Harbor Drive and Tuna Terrace Lane, Avon, Hatteras Island, sand substratum, 35°21'07"N, 75°30'12"W, 16 March 1991 (DMNH 238344 [c]); Hatteras Island, National Seashore parking lot about 1.6 km north of Buxton, Dead on *Zostera marina*, 35°17'20"N, 73°30'31"W, 16 March 1991 (DMNH 238378 [c]); Buxton, NCSR 12 North at Connor Road, Hatteras Island, sand substratum, 35°16'06"N, 75°31'58"W, 16 March 1991 (DMNH 238341 [c]); Hatteras Island, Hatteras, National Seashore Beach Access near Coast Guard Station and Hatteras-Ocracoke ferry terminal, 35°12'20"N, 75°42'16"W, 16 March 1991 (DMNH 238340 [c]); Frisco, Hatteras Island, entrance to Frisco Campground, Cape Hatteras National Seashore, sand substratum, 35°14'00"N, 75°36'05"W, 16 March 1991 (DMNH 238346 [c]); Old Coast Guard Station, Oregon Inlet, Hatteras Island, sand/leaf litter substratum, 35°45'54"N, 75°31'12"W, 16 March 1991 (DMNH 238347 [c]); Roanoke Island, corner of The Lane and Thicket Lump, Wancheese, sand substratum, 35°50'15"N, 75°37'14"W, 17 March 1991 (DMNH 238353 [c]); North Carolina Aquarium grounds, Manteo, sand substratum, 35°55'06"N, 75°47'18"W, 17 March 1991 (DMNH 238354 [c]); Roanoke Island, Wancheese, corner of the Lane and Mill Landing Road, Assembly of God Church, 35°50'34"N, 75°37'36"W, 17 March 1991 (DMNH 238353 [c]); NCSR 12, north edge of Buxton, Hatteras Island, sand substratum, 35°16'14"N, 75°31'08"W, 17 March 1991 (DMNH 238355 [c]); Brach grass, landward side of dunes just east of Ocracoke-Hatteras Ferry landing, Hatteras Island, sand substratum, 35°12'25"N, 75°42'01"W, 17 March 1991 (DMNH 238349 [c]); Cape Lookout National Seashore Visitors Center, Harkers

SCHOTTROFF AND COUNTS

Island, sandy substratum, 34°41'06"N, 76°31'38"W, 13 April 1991 (DMNH 238368 [c]); Bogue Banks, end of Inlet Road, westernmost end of bogue Banks, sandy substratum, 34°38'13"N, 77°05'50"W, 13 April 1991 (DMNH 238385 [c]); NCSR 12, in parking lot of "Marylin's Deli, Rodanthe, sand substratum, 35°35'35"N, 75°28'04"W, 7 December 1991 (DMNH 238374 [c]); Hatteras Inlet Ferry landing, Hatteras, Hatteras Island, sand substratum, 35°12'25"N, 75°42'02"W, 7 December 1991 (DMNH 238376 [c]); North Carolina Aquarium grounds, Manteo, sand substratum, 35°54'22"N, 75°35'55"W, 7 December 1991 (DMNH 238377 [c]); Parking lot west of Hatteras Inlet Ferry landing and Coast Guard Station, Cape Hatteras National Seashore, Hatteras, sandy substratum, 35°12'25"N, 75°42'07"W, 7 December 1991 (DMNH 238375 [c]); Dunes just north of lighthouse (old location), Cape Hatteras, 35°15'12"N, 75°31'20"W, 7 December 1991 (DMNH 238379 [c]); Commercial marina north of Oregon Inlet, southeast parking lot in grass, sand substratum, 35°47'42"N, 75°32'51"W, 7 December 1991 (DMNH 238380 [c]); Buxton Woods Nature Trail about 100 m from parking lot, Buxton, 35°14'47"N, 75°34'56"W, 8 December 1991 (DMNH 238384 [c]); Turn-out parking lot, north side of NCSR 12, about 1.6 km east of Hatteras water tower, sand substratum, 35°13'16"N, 75°38'24"W, 16 December 1991 (DMNH 238339 [c]). **Hyde County.** Shrubs and woods along marsh bordering Pamlico Sound, Ocracoke Island, sandy substratum, 35°07'11"N, 75°58'40"W, 16 February 1991 (DMNH 238332 [c]); Ocracoke Village, shrubs along the shore of Silver Lake, Ocracoke Island, sand substratum, 35°06'47"N, 75°58'55"W, 16 February 1991 (DMNH 238331 [c]); Hatteras-Ocracoke Ferry terminal, Ocracoke Island, sand flats and marsh near parking lot, 35°12'20"N, 75°42'21"W, 17 March 1991 (DMNH 238343 [c]); Pony Pen parking lot, 9.8 km east of Ocracoke Village, Ocracoke Island, sand substratum, 35°08'53"N, 75°52'17"W, 17 May 1991 (DMNH 238350 [c]); National Park Service Ocracoke Campground parking lot meadow, Ocracoke Island, sand substratum, 35°06'30"N, 75°57'14"W, 17 May 1991 (DMNH 238342 [c]). **Onslow County.** NCSR 1568, 2.5 km south of New River Inlet, 4.0 km north of intersection with NCSR 210, southwest of Chadwick Acres, 34°30'59"N, 77°22'02"W, 21 July 1991 (DMNH 238371 [c]). **Pender County.** About 16.0 km north of Topsail Inlet, Lot 1708 on road closest to Atlantic Ocean, Surf City, 34°24'57"N, 77°33'28"W, 21 July 1991 (DMNH 238369 [c]); NCSR 50 just northwest of the Intracoastal Waterway, fringes of woods, Surf City, 34°26'01"N, 77°33'07"W, 21 July 1991

CANDIDULA INTERSECTA IN MARYLAND

(DMNH 238268 [c]); NCSR 50 just north of New Topsail Inlet, end of paved road, Topsail Beach, 34°20'54"N, 77°39'03"W, 21 July 1991 (DMNH 238365 [c]); "Ocean Ridge at North Shore," NCSR 50, Surf City, 34°25'33"N, 77°32'47"W, 21 July 1991 (DMNH 238363 [c]); NCSR 50 (2708 South Shore Drive), 8.3 km north of Topsail Inlet, Surf City, 34°34'51"N, 77°33'49"W, 21 July 1991 (DMNH 238367 [c]);

SOUTH CAROLINA. Charleston County. Charleston, undated [but part of the W. G. Binney Collection received in 1910) (MCZ 12577 [d]); Charleston, undated [Binney collection] (MCZ 368333 [d]); St. Peter's churchyard, undated (ANSP 10689 [d]); Charleston, undated (ANSP 98547 [d], 10690 [d]); 56 Montague Street, Charleston, back yard of W. G. Mazyck's house, 1931 (ANSP 157204 [e]).

VIRGINIA. Accomack County. Campground at Bunting Street, Chincoteague, Chincoteague Island, 37°55'17"N, 75°22'48"W, 28 February 1991 (DMNH 238337 [c]); Tom's Cove Campground, Chincoteague, Chincoteague Island, sandy substratum, 37°54'42"N, 75°23'16"W, 28 February 1991 (DMNH 238335 [c]); Vegetated bank across the street from Chincoteague High School, Chincoteague, Chincoteague Island, 37°56'35"N, 75°21'56"W, 28 February 1991 (DMNH 238336 [c]); Cemetery at Bunting Street, Chincoteague, Chincoteague Island, sand substratum, 37°55'11"N, 75°22'52"W, 28 February 1991 (DMNH 238334 [c]); VASR 175 causeway at Queen Sound bridge, about 3.3 km east of NASA runway, Wallops Island Flight facility, 37°56'06"N, 75°25'12"W, 2 April 1991 (DMNH 238362 [c]). **Norfolk County** (now *Chesapeake*). Herron Avenue and West Olney Road, undated (DMNH 157663 [a], 160954 [a]); May Avenue and Olney Road, Norfolk, 1945 (ANSP 181357 [a]), 1975 (DMNH 75945 [a]); Ghent Section of Norfolk, 1954 (ANSP 219106[f]); Vacant lots in Ghent section of Norfolk, before 1956 (MCZ 203760 [a]); Southampton and Herron avenues, Atlantic City District, Norfolk, before 1959 (NMC 60194 [a]); West Olney Road, 1960 (DMNH 128751 [a]); Vacant lot, Little Bay Avenue, Norfolk, 7 May 1962 (NMC 90650 [b]). **York County.** Yorktown, undated (DMNH 160953 [a]), 1953 (ANSP 189802 [b]); 7 May 1962 (NMC 60195 [a]).

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