SUBFOSSIL LEAVES FROM LANCASTER COUNTY, PENNSYLVANIA REVEAL
A NEW UPLAND FLORAL COMPONENT OF THE PRE-EUROPEAN PIEDMONT

LANDSCAPE

A Thesis in
Geosciences
by
Sara J. Elliott

© 2012 Sara J. Elliott

Submitted in Partial Fulfillment
of the Requirements
for the Degree of
Master of Science

August 2012
The thesis of Sara J. Elliott was reviewed and approved* by the following:

Peter D. Wilf  
Associate Professor of Geosciences,  
Thesis Advisor

Mark E. Patzkowsky  
Associate Professor of Geosciences

Chris J. Marone  
Professor of Geosciences  
Chair of Graduate Program

*Signatures are on file in the Graduate School.
ABSTRACT

Valley bottoms throughout the Piedmont region in the northeastern U.S. consisted of stable, forested, wetland communities with small, interconnected channels and pools during the Holocene. However, as a result of historical European activities, especially milldam construction and the deposition of several meters of fine-grained sediments on the regional landscape, stream geomorphology and riparian vegetation have been significantly modified. The once-broad wetlands were converted into incised, meandering streams with nearly vertical, unstable banks that are currently contributing large quantities of nutrient-rich sediment downstream. Denlingers Mill, in southeastern Pennsylvania, is one of many derelict milldam sites composed of an altered, incised stream with a narrow terrace floodplain. However, this site is unusual compared to other previously studied legacy sediment sites because it has exposed bedrock slopes that support a modern secondary riparian forest adjacent to the stream, presumably growing atop the same substrate that the pre-settlement forest once did. The exceptionally prolific subfossil leaf mats at this site were deposited as the large, overhanging trees of the old-growth forest contributed prodigious quantities of leaves into the stream, similarly to the secondary forest today. Therefore, the leaf macrofossils from this site provide both a strong, novel, non-wetland signal, and an opportunity to directly compare the old-growth pre-settlement forest composition with the altered secondary forest. Very few Holocene paleoecological studies are based on leaves, opting instead for fruits, seeds, wood, or pollen, but due to their fragility and inability to be reworked, macrofossil leaves can supply local information not available from these other sources. The Denlingers Mill subfossil leaf assemblage, removed from a stream cutbank within an organic-rich hydric soil immediately underlying historical sediments, contains representitive species from at least three different pre-colonial plant communities, including a novel non-wetland and upland hardwood forest assemblage supplied by the unusual upland slope areas at Denlingers Mill. Leaves and some fruits and seeds were cleaned of all siliciclastic and organic debris, and mounted on glass slides for identification. A total of eleven species or morphotypes were identified in the subfossil assemblage. Although the majority of the assemblage consists of facultative upland species, particularly American beech (*Fagus grandifolia*), sweet birch (*Betula lenta*), and species of red and white oak (*Quercus* spp.), some facultative wetland species such as willow (*Salix* sp.), red maple (*Acer
rubrum), and black ash (Fraxinus nigra) are also present. Integrating these results with previous studies, the pre-settlement landscape probably consisted of a suite of distinct communities with a continuum of overlapping species, namely a tussock sedge marshland in valley-bottoms, a transitional lowland red maple-black ash forested swamp, and a red oak-beech mixed hardwood forest on slopes and upland areas. When compared to the modern successional forest at Denlingers Mill, dominated by box elder (Acer negundo) and sugar maple (Acer saccharum), it is apparent that post-settlement riparian forests in the region have been significantly modified as a result of European colonization. Furthermore, this illustrates that, in addition to the loss of valley-bottom wetlands due mainly to milldam construction, another important aspect of colonial landscape alteration is the loss of riparian and slope old-growth forests attributable instead to deforestation and agriculture. Riparian vegetation influences fluvial hydrology, geomorphology, and channel bank stability. Therefore, successful restoration including the reestablishment of stream-accessible floodplains, and the creation of self-sustaining riparian buffer flora to reduce erosion and nutrient loading downstream, necessitates an understanding of the pre-European settlement plant communities, which can be greatly improved by incorporating leaf macrofossil studies.
### TABLE OF CONTENTS

**LIST OF TABLES** .......................................................................................................................... vi
**LIST OF FIGURES** .......................................................................................................................... vii
**ACKNOWLEDGMENTS** ....................................................................................................................... x

**I. INTRODUCTION** .............................................................................................................................. 1
   i. Historical Land Use and Ecological Change .............................................................................. 2
   ii. Importance of Riparian Vegetation ....................................................................................... 5
   iii. Northern Piedmont Stream Restoration .............................................................................. 7
   iv. Benefits of Leaf Macrofossils .............................................................................................. 10
   v. Research Objectives ............................................................................................................ 12

**II. MATERIALS AND METHODS** ...................................................................................................... 14
   i. Site Description and Stratigraphy ....................................................................................... 14
   ii. Sample Collection and Processing .................................................................................. 18
   iii. Imaging and Identification ............................................................................................ 20
   iv. Modern Forest Study and Leaf Litter Collection .............................................................. 23

**III. RESULTS: DATING AND CONTEMPORARY FOREST COMPOSITION** ............ 25
   i. Radiocarbon Dating ........................................................................................................... 25
   ii. Contemporary Riparian Forest Composition ................................................................... 26

**IV. RESULTS: DENLINGERS MILL FOSSIL FLORA** ................................................................. 29

**V. DISCUSSION** ................................................................................................................................. 67
   i. Classification of the Contemporary Forest ......................................................................... 68
   ii. Paleocommunity Interpretation and Comparisons .......................................................... 69
   iii. Implications for Restoration ............................................................................................ 74

**VI. CONCLUSIONS** ........................................................................................................................... 76

References Cited .................................................................................................................................. 78

Appendix .............................................................................................................................................. 97
LIST OF TABLES

Table 1. Leaf macrofossils from Denlingers Mill with radiocarbon ages in uncalibrated years BP and calibrated cal AD. See also Fig. 3.................................................................26

Table 2. Denlingers Mill half hectare stand summary. Eighteen identified species are listed in order of abundance. Data was collected from 92 trees total.................................................27

Table 3. Leaf litter summary. A total of 23 species were identified........................................27

Table 4. Spearman’s rank order correlations between stand and leaf litter data.......................28

Table 5. Comparison of the White Clay Creek flora (Miller, 2011) and the Big Spring Run flora (Voli et al., 2009) with the Denlingers Mill subfossil flora.........................................................71
LIST OF FIGURES

Figure 1. Location of the Denlingers Mill subfossil site on the West Branch of the Little Conestoga Creek in Lancaster County, Pennsylvania, USA………………………………...14

Figure 2. Denlingers Mill leaf mat site (arrow). View is to the northeast (A) Schistose bedrock and quartz gravel composing channel bed. (B) Darker hydric soil layer containing plant macrofossils. (C) Approximately 4 m of silty legacy sediment. (D) Exposed bedrock supporting a contemporary riparian forest. Arrow points to exposure from which all subfossils for this study were collected. Each scale bar unit = 1 m. See also Figure 3……………15

Figure 3. Stratigraphic profile of the Denlingers Mill Leaf Mat site (Fig. 2). Green blocks indicate the presence of dense leaf mat layers within the hydric soil unit. Subfossil leaves in this study were taken from all leaf mat layers. Yellow triangles indicate locations of samples taken for 14C dating…………………………………………………………………………..17

Figure 4. Schematic diagram of 50 m x 100 m half hectare plot in the contemporary riparian forest. Diamonds denote the 16 leaf litter collection baskets. The relative locations of all identified trees within the plot are coded by the first letter of the genus and species. There were a total of 92 trees >10 cm dbh. Codes followed by an asterisk (*) were not counted in the stand summary because their stems were <10 cm dbh. Codes followed by a caret (^) denote trees that fell due to flooding from Hurricane Irene in the fall of 2011, and were also not counted. All species are native to North America except Morus alba, which is native to China…………………………………………………………………………………………24

Figure 5. Histogram showing positively correlated rho values for all contemporary forest data. For both abundance and basal area (m), rho is highest for percent leaf weight (i.e. leaf biomass) indicating a strong correlation between these values……………………………………28

Figure 6. Betula lenta (A) Whole subfossil DM16 showing doubly serrated margin. Arrows point to compound agrophic veins. (B) DM12 (left) showing acute apex and DM11 (right) showing acuminate apex. Both subfossils also exhibit a doubly serrated margin. (C) DM11 cuticle and stomata configuration. Epifluorescent image, 100x mag. Inset image is a closeup of subulate trichomes from DM2. Epifluorescent image, 500x mag. (D) Whole subfossil DM16 showing cordate base, doubly serrate margin, and compound agrophic veins (arrows). (E) Axillary trichomes from DM16. Subulate trichomes are also evident on primary and secondary veins (arrows). Epifluorescent image, 100x mag………………………………..33

Figure 7. Ostrya virginiana (A) Whole subfossil DM63 exhibiting straight parallel secondary veins. (B) Closeup of DM63 doubly serrated margin and simple agrophic veins (arrows). (C) Whole subfossil DM40 showing acuminate apex with doubly serrated margin. (D) Pubescent petiole and marginal trichomes of DM63. Epifluorescent image, 100x mag. (E) Arrows point to acicular trichomes on vein and subulate trichome in marginal sinus on DM40. Epifluorescent image, 100x mag. (F) DM7 fruit with enclosed seed. (G) Arrows point
to various trichome types on fruit (DM7). Epifluorescent image, 50x mag……………………………37

Figure 8. *Fagus grandifolia* (A) Whole subfossils from left to right DM1, DM48, and DM25 with regularly spaced, straight, parallel secondary veins, each ending in one rounded tooth. Arrows indicate well-preserved teeth; brackets signify extent of preserved margin exhibiting these features. Specimens also exhibit short petioles and convex (DM1) and cordate (DM48, DM25) base shapes. (B) Image shows dense solitary and filiform axillary trichomes, as well as the puberulent cuticle surface of (DM1). Epifluorescent image, 100x mag. (C) Highly buttressed adaxial epidermal cells (DM1). Epifluorescent image, 100x mag………………………………………………………………………………………...…41

Figure 9. *Castanea dentata* (A) Whole subfossil DM6 showing margin with hooked teeth. (B) *Castanea dentata* reference image from sample Y1-4 of the York County Collection from Wilf (1997). (C) DM6 epifluorescent image, 100x mag. Arrow points to solitary trichomes on veins………………………………………………………………………………………..44

Figure 10. *Quercus* cf. *alba*. (A) Whole white oak subfossil DM15 with arched secondary veins (arrow). (B) Lobe of DM15 with retuse apex and fimbrial vein (arrow), 25x mag. (C) DM26 showing triple crown feature of a true leaf apex. (D) DM27 showing variation in lobe morphology and insect damage……………………………………………….………...…...47

Figure 11. *Quercus* subgenus *Lobatae* morphotypes (A) DM14 (B) DM20 (C) DM28 (D) DM78. Arrows point to preserved acute, bristle-tipped lobes. (E-G) Examples of cuticle variation amongst morphotypes. Epifluorescent images, 100x mag. Inset in middle image shows distinctive t-shaped guard cell junctions; inset scale bar = 30 microns……………...51

Figure 12. *Salix* sp. (A) Characteristic salicoid tooth from left margin (as viewed) of whole subfossil. (B) Complete specimen DM33. (C) Well-defined salicoid tooth from right margin (as viewed) of subfossil also showing well preserved stomata. Epifluorescent image, 100x mag…………………………………………………………………………………………54

Figure 13. *Acer spicatum* (A) Whole subfossil DM9. (B) DM9 axillary tufts of acicular, aduncate, and filiform trichomes. Epifluorescent image, 100x mag. (C) Dense acicular, aduncate, and filiform basal trichomes of sample DM9. Epifluorescent image, 100x mag. (D) and (E) *Acer spicatum* reference image from sample M5-2 of the Allegheny National Forest, Pennsylvania collection from Wilf (1997). Epifluorescent images, 50x mag. (D) Image shows axillary tufts with the same types and configuration of trichomes as (B), while (E) exhibits the same dense basal trichomes seen in (C)……………………………………………………………………………………57

Figure 14. *Acer rubrum* (A) Subfossil DM5 showing coarse, compoundly serrated margin. (B) Subfossil DM13 showing a middle portion of a lobe. (C) Subfossil DM32 showing a lobe apex. (D) *Acer rubrum* reference image from sample M9-1 of the Allegheny National Forest, Pennsylvania collection from Wilf (1997). Letters correspond to the probable areas of a lobe represented by DM5, DM13, and DM32. Arrows in (A-D) point to dichotomizing veins. (E)
Epifluorescent image showing puberulent vein junctions with aduncate trichomes and stomata configuration on DM13, 100x mag.

**Figure 15.** *Fraxinus nigra* (A) Whole subfossil DM8 showing flat, elliptical seed body with extended wing containing midvein (arrow) and retuse apex. (B) Close up of midvein and retuse apex with small projection (arrow), 25x mag.

**Figure 16.** *Platanus occidentalis* (A) Whole subfossil DM42 showing a bristle-tipped tooth, slightly offset, decurrent basal veins (black arrows), and compound agrophic veins (white arrows). (B) Arrows point to characteristic multiradiate (tall and branched) trichomes in vein junctions. Epifluorescent image, 100x mag.

**Figure 17.** Diagram of palustrine and upland vegetation in proximity to stream base level, illustrating a potential model of the pre-settlement landscape interpreted using plant macrofossils from 3 sites around SE Pennsylvania. (A) Palustrine persistent emergent wetlands with tussock sedge vegetation as described in Voli et al., (2009). (B) Red maple-Black ash deciduous swamp forest described in Miller (2011) and here. (C) Slope and upland communities interpreted from the Denlingers Mill subfossil assemblage representing a potential red oak-beech mixed hardwood forest dominated by *Quercus* spp., *F. grandifolia*, and *A. rubrum*. The highlighted box represents an area in which all species found in the subfossil assemblage at Denlingers Mill could potentially occur. Modified from Cowardin (1979), not to scale.
ACKNOWLEDGEMENTS

I am very grateful for all of the support I have received here at Penn State; this project would not have been possible without the help and encouragement of many individuals. My appreciation to Dr. Bob Walter and Dr. Dorothy Merritts of Franklin and Marshall College for taking the time to help me identify a fantastic field site with beautifully preserved fossils, and for lending their continued interest and invaluable expertise. Thanks to my thesis committee members, Dr. Mark Patzkowsky and Dr. Russ Graham, for their support and assorted and diverse knowledge. I would like to thank Eriks Perkons and Christopher Landry for their invaluable assistance in the field, as well as Christy Miller and Yumiko Watanabe for their help in developing and testing various methods for cleaning samples. I would especially like to thank my advisor, Dr. Peter Wilf, for helping to substantially improve this thesis, as well as for his never-ending enthusiasm, expertise, support, and compassion. Thanks also to the Groff family, landowners of the field site, for allowing this study to be conducted on their property. This project was funded in part by a Geological Society of America Student Research Grant, the P.D. Krynine Memorial Fund, and the David and Lucile Packard Foundation.
I. INTRODUCTION

Stream hydrology and riparian forests have changed significantly as a result of European settlement in eastern North America (Gottschalk, 1945; Foster et al., 1998; Cogbill, 2000; Walter and Merritts, 2008). Centuries of land clearing, agriculture, and milldam construction as settlements expanded led to rapid and severe landscape alterations (Walter and Merritts, 2008). Ultimately, the secondary forests dominating the riparian landscape today do not provide the same functionality provided by old-growth pre-settlement forests (Keeton et al., 1997). Evidence of these upstream modifications is corroborated by ecological damage in vital downstream watersheds such as the Chesapeake Bay, which is the largest estuary in the United States (Phillips, 2002), as well as one of the most commercially important water bodies. Plant macrofossils contribute a critical piece of knowledge, namely the pre-settlement flora composition, to our understanding of historical anthropogenic landscape modifications. Because plant assemblages directly affect fluvial hydrology and geomorphology (Richardson et al., 2007), a precise representation of the pre-settlement flora, encompassing wetland and non-wetland trees, as well as herbaceous species, can directly affect the success of future stream restoration and conservation.

Recent studies have used both sedimentological and paleontological data to quantify the impacts of European colonization on wetland and riparian vegetation in the Northeastern U.S. Fossil fruits and seeds from stream cutbanks in southeastern Pennsylvania and Maryland indicate that palustrine wetland conditions consisting of small shallow channels and interconnected pools with herbaceous obligate wetland species existed in valley bottoms prior to widespread forest clearing and milldam construction (Walter and Merritts, 2008; Voli et al.,
2009, Hilgartner et al., 2010). These tussock-sedge meadows were characterized mainly by sedges (Carex spp. including C. prasina, C. crinita, C. stipata, C. stricta), as well as Polygonum spp., Eleocharis spp. and Scirpus spp. Only a few shrubs and small, scattered trees from areas adjacent to the wetlands, such as Liriodendron tulipifera (tulip tree) and Juglans cinerea (butternut), were initially recognized (Voli et al., 2009). Although it is unknown how long these wetlands persisted at any one site in particular, dating of the herbaceous fossil seeds found in Pennsylvania and Maryland indicate that these valley-bottom wetlands persisted as stable environments from ca. 11,240 ybp (Walter and Merritts, 2008) until the arrival of European settlers, approximately 300 years ago (Hilgartner et al., 2010). A single, unpublished study of leaf macrofossils provided evidence of woody, riparian wetland and non-wetland species within this system (Miller, 2010; 2011). However, leaf preservation was fragmentary, and data from non-wetland trees were especially limited. The leaf mat exposure used in this study, located at Denlingers Mill (see Methods), is exceptionally prolific and provides the first significant insights into the pre-settlement non-wetland and upland hardwood species.

i. Historical Land Use and Ecological Change

The northern and mid-Atlantic Piedmont region of the United States has a long history of anthropogenic landscape modifications, beginning with European colonial conversions of hundreds of thousands of acres of old-growth forest into agricultural fields during the 17th and 18th centuries (Costa, 1975). This region subsequently supplied the bulk of agricultural goods and other commodities to colonial port cities for trade (Lemon, 2002). Certain crops, particularly tobacco, were highly detrimental to soil quality, causing settlers to abandon fields
and clear additional land every few seasons (Gottschalk, 1945). It has been recognized since the 1700s that extensive clearing and tilling of the land led to large scale regional topsoil erosion from the uplands down into Piedmont rivers and streams, eventually causing sedimentation onto valley floodplains and lower hill slopes (Middleton, 1953; Costa, 1975). For example, even floodplains where dams were not present were typically smothered with nearly a meter of deposited sediment within the first few decades after settlement (Blankenship, 2007). Additionally, the forests of the Allegheny Plateau were intensively felled for lumber, tanning materials, and chemical wood, from which all organic chemicals, such as methanol and calcium acetate, were derived before the rise of the petrochemical industry in the early 20th century (Whitney, 1990). Expansive milldam construction amplified the influence of deforestation and upland denudation, causing extreme shifts in the regional hydrological, geomorphological, and riparian vegetation regimes (Walter and Merritts, 2008).

Sedimentological data indicate that regional geomorphology was especially altered in the Piedmont region because of the high density of milldam construction. United States census data show that at least 65,000 water-powered mills were operating in the eastern U.S. by 1840, 10,000 of which were in Pennsylvania by the mid 19th century (Walter and Merritts, 2008). Of these, there were an estimated 450+ mills built in Lancaster County alone by 1850 (Barton Collection, Lancaster County Historical Society), averaging to one dam per every two miles of stream (Blankenship, 2007). Dams stretched across entire valley bottoms and were used primarily to power mills, forges, furnaces, and mining operations. This framework significantly decreased flow velocity, causing suspended sediments to settle out of the water column and fill millpond reservoirs directly behind dams. Because dams were spaced so closely together, the alluvial deposit behind one usually stretched upstream to the last,
ultimately causing regional base level rise both along entire lengths of streams and across the entire widths of valley floors (Walter and Merritts, 2008). These accumulated, fine-grained, nutrient-rich, upland muds and silts in stream channels and on floodplains are collectively known as ‘legacy sediment’ (Walter and Merritts, 2008).

Over time, dams were abandoned and naturally breached, or intentionally removed as alternative energy sources became available. The formation of new incised channels down through the accumulated reservoir deposits after dam breaching exposed, eroded, and redistributed sediments to downstream watersheds, resulting in meandering streams with steep, elevated banks (Simon, 1989; Walter and Merritts, 2008). In stark contrast to the pre-settlement landscape of sluggish, low-gradient anabranching channels and prevailing wetland conditions, areas adjacent to the dams were converted into fast-flowing riffles with up to two times steeper gradients and nearly vertical banks, while low relief areas behind the former dams became pools, producing the hydrologic profiles seen today (Walter and Merritts, 2008; Merritts et al., 2011).

The shift in understory vegetation as a result of changing hydrogeomorphology produced secondary successional forests differing in composition from the pre-settlement old-growth forests. Northern secondary mixed forests do not provide the same type or magnitude of ecological functions associated with old-growth forests, such as snags, canopy gaps with saplings of various sizes and ages, and multiple layers of foliage (Lorimer and Frelich, 1994), as well as ecologically important in-stream habitat characteristics like the formation of debris dams and associated pools (Bilby and Likens, 1980; Keeton et al., 2007). One study focusing on riparian buffer vegetation along first and second order streams in New York State concluded that old-growth riparian forest structure is more complex than that found in modern
mature forests, and exhibits significantly greater accumulations of aboveground living and
dead tree biomass (Keeton et al., 2007).

ii. Importance of Riparian Vegetation

Riparian buffers are the interface between aquatic and terrestrial ecosystems and serve
as conduits for large fluxes of energy and materials (Ewel et al., 2001). Even though they are
typically small areas of the landscape, these critical transition zones tend to be surrounded by
intense human activity, modification, and subsequent ecological restoration challenges (Ewel
et al., 2001; Richardson et al., 2007). Riparian vegetation fulfills or influences many
important ecological functions including moderation of stream water temperatures, sediment
filtration and nutrient control, bank stabilization, and habitat and food provision for native
fauna (Correll, 1992; Federal Interagency working group, 2002; Richardson et al., 2007).
Along with disturbance, climate, animal interactions, and bedrock composition, hydro-
geomorphological processes are one of the principal determinants of riparian plant
assemblages and distribution patterns (Hupp and Osterkamp, 1996). Water availability is also
a major limiting resource, particularly to riparian woody tree species that are rooted in or near
the water table (Auble et al., 1994). Evidence suggests that the distance between the land
surface and stream base level increased so dramatically from accumulating well-drained
legacy sediments that native valley-bottom vegetation eventually lost the ability to access the
water table, effectively transforming the riparian buffer assemblage into one dominated by
weedy thistles and grasses such as *Agropyron repens* (quackgrass; Walter and Merritts, 2008;
Voli et al., 2009).
In addition to this initial stage of replacement by weedy vegetation, declining water levels after dam breaching and incision exposed nutrient-rich sediment surfaces that were previously inundated, creating prime habitat and resources for invasive species (Shafroth et al., 2002; Stanley and Doyle, 2003; Richardson et al., 2007). These disturbance-adapted, weedy species, such as Cirsium arvense (Canada thistle) and Dactylis glomerata (Orchard grass), are characterized by rapid growth, high fecundity, and efficient dispersal mechanisms (Gutshall, 2004; Doyle et al., 2005), and have a tendency to exclude native riparian vegetation (Gutshall and Oberholtzer, 2011). This altered riparian buffer has negatively impacted ecosystem function both upstream and downstream compared with the pre-settlement riparian forests.

Very few studies have documented vegetation colonization or succession following dam removals (Doyle et al., 2005), although it has been shown that pioneer communities consist of grasses and forbs, and that it can take upwards of three decades for hardwood trees to naturally colonize disturbed riparian zones (Orr, 2002). In addition to the many stream properties plants influence, including evapotranspiration, stream flow rates, groundwater levels, and local climates, long-term riparian communities along streams within former mill dam impoundments have especially important implications for channel stability (Simon and Collison, 2002). Re-establishing functional riparian vegetation, especially hardwood trees, is crucial because trees produce greater channel stabilization compared to grasses (Doyle et al., 2005), and can significantly reduce embankment erosion and subsequent downstream sediment yield. Bank stability modeling suggests that channels with riparian buffer vegetation containing a high percentage of trees can incise at least 20% deeper than channel buffers dominated by grasses before the occurrence of bank failure and mass wasting (Doyle et al.,
Furthermore, hardwood trees in the riparian buffer zone are important to both aquatic and terrestrial wildlife because leaf litter provides sustenance for in-stream biota, such as macroinvertebrates, and, in conjunction with well-vegetated wetlands, riparian hardwood tree assemblages provide prime habitat for terrestrial organisms (Gutshall and Oberholtzer, 2011).

### iii. Northern Piedmont Stream Restoration

Overall interest in restoration and management practices aimed at re-implementing the characteristics of old-growth forests is increasing (Bennet, 2005). The renewed efforts in recent years to reconstruct a proxy of the pre-European fluvial and vegetative landscape (Hilgartner and Brush, 2006; Walter and Merritts, 2007, 2008; Voli et al., 2009; Merritts, et al. 2010a, 2010b, 2011) were initiated by observations of anomalously high erosion rates in the region. Gellis et al., (2009) found that current erosional rates are between 50 and 400 times the long-term geologic average. Climatic and environmental factors such as storm and disturbance intensity, frequency of freeze-thaw cycles, and even changes in the density of riparian trees along the stream banks are not sufficient to account for the hundreds of thousands of tons of fine-grained sediments entering downstream ecosystems (Merritts et al., 2010b). Many studies conclude that modern topsoil erosion certainly contributes to the downstream sediment flux (Moss and Kochel, 1978; Douglas, 1991), but it is increasingly agreed that much, if not most, of the sediment currently being carried by rivers and streams is from the erosion of channel bank legacy sediments (Merritts and Walter, 2003; Walter et al., 2007, Blankenship, 2007). For example, in one estimate over half of the 180,000 tons of sediment transported from the Conestoga watershed into the Susquehanna River annually originates from legacy sediment, rather than contemporary farms or development sites.
These findings led Pizzuto and O’Neal (2009) to conclude that the demise of milldams has been an important influence on fluvial processes in the region and is probably mostly to blame for the accelerated rates of erosion, even more so than modern agricultural practices.

Additionally, the high chemical content of reservoir legacy sediments, especially phosphorus, causes enrichment in downstream rivers, lakes, and coastal areas (Stanley and Doyle, 2002). It has been estimated that regional legacy sediments carry approximately 135,000 pounds of phosphorus to downstream ecosystems, including the Chesapeake Bay, annually (Blankenship, 2007). Many negative effects of both pulsed and sustained inputs of sediments to stream biota are documented (Boynton et al., 1995; Waters, 1995). Even though milldams were widespread in eastern North America, the characteristics of northern Piedmont streams within the Chesapeake watershed caused them to become the largest sources of fine-grained, suspended sediment into the Bay itself (Merritts et al., 2010a). As a result, the Chesapeake Bay has a well-documented history of algal blooms and eutrophication (Pennock 1994; Boesch et al., 2001), and it is currently being affected by hypoxic and anoxic conditions (Walter and Merritts, 2008). For decades researchers have been witnessing population declines of many ecologically important organisms, including aquatic vegetation and water-filtering oysters, all at least partially caused by eutrophication (Orth and Moore, 1983; Kemp et al., 2005) stemming from the influx of legacy sediment.

Until recently, restoration efforts have been focused primarily on the water channels themselves, rather than the surrounding floodplains and deposited legacy sediment alluvium (Gutshall and Oberhotlzer, 2011). Consequently, these past hydraulic endeavors compounded the issues faced by downstream ecosystems, rather than improve ecosystem functioning.
(Walter and Merrits, 2008). For example, the forced formation of this type of “natural” meandering profile continued to eliminate the ability of streams to create their own floodplains and be in contact with the water table as they were before European settlement (Federal Interagency Stream Corridor Restoration Working Group, 2002). Additionally, this profile continued to inhibit the roots of foliage on the surface of the historical sediment from reaching the water table (Voli et al., 2009). Recently, it has been demonstrated that a more sustainable and effective approach is to remove legacy sediment completely and restore the naturally occurring riparian vegetation at stream base level wherever possible (Voli et al., 2009).

Native American influences are also well documented in North America prior to European colonization. Archaeological evidence, charcoal, and isotope analyses suggest expansive historical forest clearing and use of fire by East Coast Native American tribes (Douglas, 1991; Denevan, 1992; Springer, 2010), as well as decreases in old-growth forest taxa and increases in crop, disturbance, and early successional species (Baker et al, 1993; Black et al., 2006). According to one study of Delaware River flood deposits, maize agriculture significantly decreased upland forest cover and caused subsequent erosion and sedimentation in valley bottoms as early as 1000 C.E. (Stinchcomb, 2011).

Ultimately, Piedmont riparian floodplains were both hydrologically and ecologically altered by pre-historic peoples in a similar manner to colonial Europeans, but the magnitude of impact was significantly less (Asch Sidell, 2008; Stinchcomb, 2011). Therefore, the attributes of the pre-European landscape determined through sedimentological and paleontological analyses can be used as historical reference baselines, with the caveat that pre-settlement conditions were not pristine per se, simply much less degraded than now
(Palmer et al., 2005; Bennion et al., 2011). Restoration projects aimed at establishing more functional geomorphological, hydrological, and riparian communities can decrease sediment and nutrient loading downstream (Correll, 1992; Walter, 2007; Voli et al., 2009), facilitate groundwater recharge, and provide improved habitat for aquatic and terrestrial biota (Gutshall and Oberholtzer, 2011). These undertakings will be more effective with an accurate representation of the pre-settlement flora because riparian buffer vegetation is considered one of the most important drivers in restoration project success (Federal Interagency Stream Corridor Working Group, 2002). Additionally, restored wetlands have great potential as carbon sinks. Estimates of past carbon sequestration within the regional buried hydric soils is as high as 106 kg of carbon per hectare (Walter and Merritts, 2008). Therefore, restoration of upstream Piedmont habitats has additional potential regarding climate change mitigation.

iv. Benefits of Leaf Macrofossils

Plants are fundamentally different from most other organisms because they can shed material at any time (Spicer, 1989; Burnham, 1993; Work, 2005). Subsequently, plant macrofossils are globally ubiquitous within organic rich sediments in river and floodplain environments. Because plant remains capture a high-resolution record of the local environment immediately surrounding the depositional site, plant fossils discovered within stream cutbanks have been successfully used as valuable sources of Holocene paleoecological information worldwide (Chumbley, 1989; Baker et al., 1990; Miller et al., 1994; Work et al., 2005). Even though plant macrofossils tend to be used less commonly than microfossils such as pollen, they can be more effective in detailed paleoecological reconstructions because they are less prone to fluvial processes of long distance transport, spatial and temporal mixing, and
depositional sorting, and they can often be identified with greater taxonomic precision than microfossils (Bilby and Likens, 1980; Bilby, 1981; Ferguson, 1985; Burnham et al., 1992; Baker et al., 1996; 1998; 2002; Jackson et al., 1997; 2000; Work et al., 2005). Except in composite studies, most Holocene analyses have been based on wood, seeds, fruits, and pollen, instead of leaves. This is because leaves are typically less abundant than pollen or seeds at any particular locality (Birks and Birks, 2000) and also, because they are soft and encased in sediment, are fragile and often difficult to process. When used in tandem with other macrofossil and palynological data, leaves can give an accurate and realistic view of past communities (Birks and Birks, 2000) because the best paleoecological reconstructions come from a combination of all available fossil materials (Birks, 1976; Baker et al., 1993; Work et al., 2005; Hilgartner and Brush, 2006).

Leaf-dominated assemblages are produced via fundamentally different taphonomic pathways compared with fruit and seed assemblages (Behrensmeyer et al., 2000), and thus provide a different view of the pre-settlement flora. Leaves are also transported far shorter distances than other macroscopic plant remains (Birks and Mathewes, 1978; Wing and DiMichele, 1995; Davies-Vollum and Wing, 1998; Behrensmeyer et al., 2000; Birks and Birks, 2000), generally being deposited within their source habitat, oftentimes in nearly in situ (para-autochthonous) assemblages (Behrensmeyer et al., 2000). Because of this, they provide precise spatial data that cannot be supplied from other plant fossil sources (Birks and Birks, 2000). Due to their general inability to be reworked, leaves are also minimally time-averaged, having a much higher temporal resolution than seed, fruit, and pollen deposits, generally on the scale of $10^{-1}$ to $10^{2}$ years (Birks and Mathewes, 1978; Behrensmeyer et al., 2000; Birks and Birks, 2000). Because the leaf mat accumulations at Denlingers Mill are highly
concentrated, and the subfossil leaves are relatively intact, they must represent a very local signal with especially minimal transport.

**v. Research Objectives**

It is reasonable to expect that not only the valley-bottom wetland vegetation as studied previously, but also non-wetland riparian forest vegetation has been dramatically altered since European settlement. The goals of this study are to provide the first window into the facultative and facultative upland deciduous tree assemblage that grew adjacent to the pre-settlement stream bottoms, and to lend further accuracy to the regional pre-colonial old-growth forest framework, with possible implications for restoration and conservation efforts.

The deposition of large, concentrated, and generally unabraded leaves at Denlingers Mill (see Methods) indicates that the subfossil leaf material was shed locally, minimally transported as floating or suspended material, underwent minimal hydrodynamic sorting and reworking, and was deposited shortly after entering the stream (Keller and Swanson, 1979; Ferguson, 1985; Burnham et al., 1992; Burnham, 1993). The leaf mat exposure used in this study is exceptionally prolific and informative due to elevated local bedrock spurs immediately adjacent to the channel. The spur on the North side of the stream, ca. 3-4 m high, today supports a forest of tall-canopied trees that overhang and deposit large numbers of leaves into the channel. Because this area is geologically inactive and has positive relief, this small upland area would have presumably supported large overhanging trees contributing prodigious quantities of leaves to the pre-settlement deposit as it does to the altered stream today. The leaf macrofossils from this site, therefore, provide both a strong, novel, non-
wetland signal, and an opportunity to directly compare the old-growth pre-settlement forest composition with the altered secondary forest growing on the same substrate today.
II. MATERIALS AND METHODS

i. Site Description and Stratigraphy

Denlingers Mill is located on the West Branch of Little Conestoga Creek, in Lancaster County, Pennsylvania, 5 km southwest of Millersville (fossil site location 39°58’27.11’ N, 76°22’33.33’ W, Figs. 1, 2). Lancaster County is part of the Piedmont physiographic province within the Appalachian Highlands, characterized by broad rolling hills and valleys with underlying Conestoga limestone in the northern part, and schistose basement rock (Wissahickon Schist) in the southern part of the county where the study site is located (Fenneman, 1938; Merritts and Walter, 2003). The West Branch of Little Conestoga Creek is a first order stream within the Conestoga River watershed, which feeds the Susquehanna River and ultimately the Chesapeake Bay. The West Branch of the Little Conestoga itself is approximately 10 km long, and historical evidence suggests that a milldam was built every ca. 1 km along its length (data from the Lancaster County Historical Society compiled in Merritts and Walter, 2003).

![Figure 1](image_url). Location of the Denlingers Mill subfossil site on the West Branch of the Little Conestoga Creek in Lancaster County, Pennsylvania, USA.
Figure 2. Denlingers Mill leaf mat site (arrow). View is to the northeast (A) Schistose bedrock and quartz gravel composing channel bed. (B) Darker hydric soil layer containing plant macrofossils. (C) Approximately 4 m of silty legacy sediment. (D) Exposed bedrock supporting a contemporary riparian forest. Arrow points to exposure from which all subfossils for this study were collected. Each scale bar unit = 1 m. See also Figure 3.

The Denlingers Mill (DM) stratigraphic profile was measured and described at the centimeter scale during May of 2011 (Fig. 3). To ensure accuracy of descriptions, overhanging vegetation was cleared and a fresh vertical surface was exposed on a small section of the stream bank adjacent to the subfossil exposure. The entire stratigraphic section up to the base of the exposed “upland” bedrock is approximately 4.2 m thick and closely parallels the regional composite profile of mid-Atlantic streams described by Walter and Merritts (2008), as follows.
Beginning at the base of the exposure, schist bedrock and quartz gravels are overlain by a distinctive hydric soil layer ca. 80 cm thick. Regionally, this hydric soil layer contains pedologic features such as root structures and plant macrofossils (Voli et al., 2009) with an expected age range of ca. 11,500-300 ybp, terminating at colonial settlement (Walter and Merritts, 2008). The hydric soil exposure at DM is located approximately 20 m upstream from the old milldam structure, and 110 meters upstream from the confluence with the Little Conestoga Creek. The hydric soil is dense with leaf mats, seeds, twigs, and remnant herbaceous material, and it was the source of all subfossils used in this study. The remaining 3.6 meters above the hydric soil is composed of finely laminated legacy muds and silts with thin, very fine sand interbeds and lenses. Hanging roots and weedy vegetation obscure the uppermost portion of the profile. Denlingers Mill is unusual compared to other legacy sediment sites studied so far because it has upland bedrock spurs that allow a contemporary secondary riparian forest corridor to grow adjacent to the stream. This strip of forest, dominated by *Acer negundo*, is only ca. 100 m wide presently because of contiguous cultivated and developed land. Although no trees directly overhang the section described here, *Acer negundo* (Box Elder) individuals grow adjacently, and modern leaf litter from a variety of species is very abundant both on the stream bank and within the channel (Fig. 4, Tables 2, 3). The bedrock is schistose and weathered, and it tapers to a point in the northeasterly direction above the subfossil exposure.

Three leaf fragments were sent to the Center for Applied Isotope Studies at the University of Georgia for accelerator mass spectrometry (AMS) radiocarbon dating (Table 1). The “basal” and “middle” samples were taken from the typically submerged leaf mat layers, and the “top” sample was taken from the upper portion of the hydric soil unit (Fig. 3). The
returned ages in radiocarbon years BP were then calibrated using the CalPal online radiocarbon calibration package (Danzeglocke et al., 2011).

Figure 3. Stratigraphic profile of the Denlingers Mill Leaf Mat site (Fig. 2). Green blocks indicate the presence of dense leaf mat layers within the hydric soil unit. Subfossil leaves in this study were taken from all leaf mat layers. Yellow triangles indicate locations of samples taken for $^{14}$C dating.
The wedge of alluvial sediment buildup in a reservoir is typically thickest near the dam structure itself where flow velocities are lowest (Merritts et al., 2010b). The DM exposure is located at the downstream end of what was once the slackwater pond, where the majority of fine suspended sediment would have been deposited, subsequently producing the highest potential for fossil deposition and preservation. Because Denlingers Mill contains this exceptionally thick package of legacy sediment upstream of the milldam remains, but not downstream, it was among the first derelict dam sites recognized and studied sedimentologically in the region (Merritts and Walter, 2003; Fig. 3). Researchers have also previously recognized in situ tree stumps and carbonized organic debris layers below the legacy sediment deposits along the West Branch of the Little Conestoga Creek upstream of DM, interpreted as remnants of the forest floor and riverine wetlands that predated colonial settlement (Merritts and Walter, 2003). According to historical accounts, the dam at DM was built in the early 1700s, was 20 feet high, trapped sediment in a pond that extended at least 800 m upstream, and eventually breached sometime in the early 20th century (Walter et al., 2007; Merritts et al., 2010b). This study uses the previously discovered organic debris layers (Merritts and Walter, 2003) containing abundant leaf macrofossils to reconstruct the pre-settlement upland (and lowland) hardwood species assemblage for comparison with the secondary forest that exists at the site today.

ii. Sample Collection and Processing

Samples were collected from the Denlingers Mill leaf mat site five times between December 2010 and October 2011. Numerous blocks of the hydric soil layer (approximately 0.08 m³ total; see Stratigraphy) were carefully removed from the exposure using a trowel.
Portions of each hydric soil block that were evidently rich in leaves and leaf fragments were extracted and stored in stream water in either five-gallon buckets or airtight Ziploc® containers. Samples were transported to the Sedimentology and Paleobotany laboratories at Pennsylvania State University for further processing.

Methods for cleaning and mounting were modified from Miller (2011). Immediately upon arriving in the laboratory, all samples were placed in a 50-50 ethanol and high-purity deionized water solution. Individual leaves and leaf fragments were removed from the leaf mat layers by hand using metal spatulas, soft-bristled paintbrushes, and occasionally a weak solution of hydrogen peroxide, although this tended to damage leaf surfaces. Samples were placed in a 40% HCl bath (approximate pH of 1) for three to five days to remove adhered siliciclastic material. Organic debris was then removed by soaking leaves in 5% KOH for 5-15 minutes; additional time tended to destroy leaf tissue. After rinsing with high-purity deionized water, samples underwent a final brushing until the leaf surfaces were between 90-100 percent clean of debris. Generally, this procedure did not need to be repeated.

An alternative method using hydrofluoric acid was attempted. Although HF significantly reduced the time and effort needed for cleaning specimens, managing the samples during the HF bath proved unfeasible because the specimens tended to become damaged or disjointed within the small HF-rated containers, providing no benefit to compensate for the increased safety risk.

Immediately after cleaning, samples were dehydrated over the course of one week in a graded series of ethanol baths (50%, 75%, and 100%), then placed in a xylene bath for 5-10 minutes. Following dehydration, leaves were mounted using Cytoseal 280 High Viscosity Mounting Medium (Richard Allen Scientific Inc., Kalamazoo, Michigan, USA) on glass
microscope slides of varying sizes, up to 4”x6” for the largest leaves (Ted Pella Inc., Redding, California, USA), and secured with cover glasses. Before receiving specimens, slides were warmed for two to three minutes on a hot plate to minimize the quantity of air bubbles trapped in the viscous mounting medium, although it proved impossible to eliminate all air bubbles due to the irregular leaf thicknesses. Leaf specimens were positioned with abaxial sides facing up to highlight venation and increase the likelihood of observing stomata and trichomes.

Due to the extensive amount of time required for each sample preparation, statistical quantification of the subfossil assemblage was unfeasible. Instead, presence/absence and qualitative relative abundance data were collected. Actualistic studies such as Burnham et al. (1992) and Burnham (1993) show that in temperate deciduous forests, leaf litter collections spaced at canopy height or less will capture at least 70% of species, usually only excluding rare species. It has also been documented that fossil leaf assemblages often occur in correct rank abundances (Behrensmeyer et al., 2000). Therefore, it can be assumed that the fossil deposit at DM captured the dominant pre-settlement floodplain and upland tree species, potentially in accurate rank abundances. There are a total of 108 specimens identified at least to genus used in this study; 104 are mounted leaf specimens and the remaining four are macrofossil fruits and seeds (see Appendix). All specimens are deposited at the Earth and Mineral Sciences Museum, Pennsylvania State University (EMS) (See Appendix).

### iii. Imaging and Identification

A Nikon D90 (DSLR) camera and Hakuba KLV-700 Lightviewer 7000Pro were used for macrophotography of all mounted samples and reference samples. Mounted samples were examined using transmitted and epifluorescent light microscopy with a Nikon SMZ-1500
stereomicroscope and a Nikon LV100 compound microscope (Nikon, Melville, New York, USA), sharing an X-Cite 120 epifluorescence illumination unit (EXFO Electro-Optical Engineering, Quebec City, Quebec, Canada) with an Endow GFP Longpass Emission green filter (Chroma Technology Number 41018, exciter HQ470/40x, diachronic Q49LP BS, emitter HQ500LP, Chroma Technology, Rockingham, Vermont, USA). A Nikon DSRi1 CCD microscope camera and Nikon NIS Elements v.3 Basic Research Software were used for microscope photography. Composite photographs generated from images taken at multiple focal planes were assembled using Align and Blend tools in Adobe Photoshop CS5 (Adobe Systems Incorporated, San Jose, California, USA). All image adjustments, such as exposure and white balance, were performed using Adobe Photoshop CS5 Camera Raw on the entire image, and are reversible. All images were also checked for artifacts from the adjustments and blends, and none were apparent.

Methods outlined in The Manual of Leaf Architecture (Ellis et al., 2009) were used to describe the characteristic leaf architecture of individual specimens, including venation patterns, margin type, and tooth shape. These descriptions were eventually pooled for recognized species (see Systematics). Because leaves were generally incomplete, usually not all characters could be determined for most samples.

Preliminary identifications were based on reference images and general morphological features described from many sources. Those used most often were Fernald (1950); Symonds (1958); Gleason and Cronquist (1963); Little (1980); Rhoads and Block (2005, 2007); Sibley (2009); mounted leaves from P. Wilf’s York County and Allegheny National Forest, Pennsylvania collections (Wilf, 1997); cleared leaf images from the Jack A. Wolfe USGS Cleared Leaf Collection, housed at the Smithsonian Institution National Museum of Natural
Preliminary identifications based on morphology and leaf architecture were followed by more rigorous comparisons using the sources above, also taking into account epidermal features such as foliar trichomes and stomatal configurations. Trichome types were characterized using the nomenclature from the *Atlas of foliar surface features in woody plants* I, VIII, and IX (Hardin, 1979; Hardin and Johnson, 1985; Hardin and Bell, 1986). Especially within family Betulaceae and the genus *Quercus*, certain trichome types, such as multiradiate and stellate, seemed to be preferentially lost before or during deposition, although all trichomes seemed to be lost from *Quercus* samples. With the one exception of *Quercus* cf. *alba*, which is characteristically glabrous, when using foliar trichomes to identify species, only the presence, not absence, of specific trichome types was used to increase taxonomic resolution. When possible, cuticle characters were also compared with images from The Cuticle Database Project (Barclay et al., 2012; http://cuticledb.eesi.psu.edu/).

Given the low likelihood that the pre-settlement assemblage contained non-native or invasive species, only those species historically native to the Northeastern region of the U.S. were considered here. Because the leaf-mat layers were deposited during the Little Ice Age (1550-1850 CE), during which time the average climate cooled by 0.6 °C (Mann 2002), species ranges may have extended outside of modern boundaries. Therefore, native species of Pennsylvania, as well as all surrounding states in the region, were considered.
iv. Modern Forest Study and Leaf Litter Collection

A contemporary forest stand and leaf litter study was conducted nearing the end of maximum leaf fall during October 2011 in order to quantify the modern forest assemblage for comparison to the subfossil assemblage. Using methods modified from Burnham et al., (1992), a half hectare was measured and mapped around the Denlingers Mill exposure site, extending 50 m across the stream and 100 m upstream (Fig. 4). Due to cultivated and agricultural land abutting the riparian zone on both sides, this was the largest possible mappable area at the site. Within the plot, all stems >10 cm dbh (1.4 m) were measured for circumference and identified to species. Relative abundance and total basal area (m²) data were calculated for all identified hardwood species within the plot (Table 2).

Additionally, a leaf litter summary was conducted for comparison to, and quantification of, the contemporary stand assemblage. As per Burnham et al. (1992), 16 wooden bushel baskets were placed evenly around the site at a distance less than or equal to the height of the canopy, ca. 15-25 m apart (Fig. 4). The baskets collected leaf litter fall for one week; attempts to collect litter in the stream over the course of the same week were unsuccessful. The data from one basket (9) were discounted because the basket overturned during the course of the collection period. Litter from the remaining baskets was collected, sorted, counted, and weighed by species (Table 3). Some of the leaf litter was not clearly identifiable to species; therefore some species of white oaks were lumped into two groups; “white oak group 1” is most likely Quercus alba or Q. michauxii, whereas “white oak group 2” is most likely composed of Q. prinus or Q. muehlenbergii.
Figure 4. Schematic diagram of 50 m x 100 m half hectare plot in the contemporary riparian forest. Diamonds denote the 16 leaf litter collection baskets. The relative locations of all identified trees within the plot are coded by the first letter of the genus and species. There were a total of 92 trees >10 cm dbh. Codes followed by an asterisk (*) were not counted in the stand summary because their stems were <10 cm dbh. Codes followed by a caret (^) denote trees that fell due to flooding from Hurricane Irene in the fall of 2011, and were also not counted. All species are native to North America except *Morus alba*, which is native to China.

Spearman’s rank-order correlations were calculated using the R statistical package (R, 2010) in order to compare the stand and leaf litter data (Table 4, Fig. 5). Both the stand and leaf litter data were transformed using arcsin-transformation for percentage data and log-transformation for all other data. Spearman’s rank-order correlation is the nonparametric alternative to the Pearson product-moment correlation. Correlation coefficients (ρ) are based on covariance and measure the strength of association between two ranked variables. Rho values were tested for statistical significance using critical value tables, as well as a Spearman’s rank significance graph. With df=21, P-values were calculated using the AS89 algorithm specifically designed for Spearman’s rank-order correlation data within the R statistical package. All methods indicate 99% confidence for all rho values.
III. RESULTS: DATING AND CONTEMPORARY FOREST COMPOSITION

i. Radiocarbon Dating

Based on three radiocarbon dated leaf fragments, the leaf mat deposit at Denlingers Mill accumulated between ca. 1697 - 1899 C.E. (Table 1). The sample taken from the upper portion of the hydric soil unit had an older $^{14}$C date than the middle and basal samples, indicating some sort of mixing event among the leaf mat layers within the unit. Because of this temporal displacement, all specimens from within the hydric soil unit were considered to be one lumped sample. Considering that there were no permanent settlements in this part of Pennsylvania until almost the mid 17th century (Weslager, 1955), these radiocarbon dates are consistent with the historical data concerning the construction of the dam at DM sometime in the early 18th century. The subfossil leaf mat deposits are therefore presumed to represent the subsequent leaf accumulation in the slackwater pond behind the dam. Similar hydric soil layers in the region have been carbon dated as far back as ca. 11,500 ybp (Walter and Merritts, 2008), but given the recent age range of this deposit, the subfossil species assemblage identified from DM can be considered representative of the last stages of old-growth forest at this locality.
Table 1. Leaf macrofossils from Denlingers Mill with radiocarbon ages in uncalibrated years BP and calibrated cal AD. See also Fig. 3.

<table>
<thead>
<tr>
<th>Sample Number</th>
<th>Years BP</th>
<th>Cal AD</th>
</tr>
</thead>
<tbody>
<tr>
<td>UGAMS 09414 (DM#1 - Basal)</td>
<td>110±20</td>
<td>1806 CE ±94</td>
</tr>
<tr>
<td>UGAMS 09415 (DM#3 - Middle)</td>
<td>100±20</td>
<td>1805 CE ±94</td>
</tr>
<tr>
<td>UGAMS 09416 (DM#5 - Top)</td>
<td>150±20</td>
<td>1810 CE ±113</td>
</tr>
</tbody>
</table>

**ii. Contemporary Riparian Forest Composition**

A total of eighteen species were identified in the half hectare (Table 2). Of these, two species of maple, *Acer negundo* and *Acer saccharum*, clearly dominate the assemblage in terms of abundance and basal area. It has been demonstrated that in a temperate, homogeneous forest containing approximately twenty arborescent species per hectare, 12-15 leaf litter collection samples will recover 70% of species (Burnham et al., 1992). Interestingly, this leaf litter study captured 88% of species identified in the stand study, as well as five additional hardwood species not seen in the half hectare. These included two species of *Carya, Alnus serrulata, Nyssa sylvatica*, and *Prunus* sp. (Table 3). Rho was highest between percent leaf weight (leaf biomass), and both abundance and basal area, similar to earlier studies (Burnham et al., 1992). The strong correlations between the stand and leaf litter data suggest that an accurate portrayal of the modern day species richness and abundances were captured by this study, thus reinforcing the forest classification type assigned to the contemporary forest. All statistical results are summarized in Table 4 below.
Table 2. Denlingers Mill half hectare stand summary. Eighteen identified species are listed in order of abundance. Data was collected from 92 trees total.

<table>
<thead>
<tr>
<th>Species</th>
<th>No. Stems &gt;10 cm diam.</th>
<th>Relative Stem #</th>
<th>Total Basal Area (m²)</th>
<th>Relative Basal Area</th>
</tr>
</thead>
<tbody>
<tr>
<td>Box Elder (Acer negundo)</td>
<td>30</td>
<td>32.61</td>
<td>4.95</td>
<td>35.68</td>
</tr>
<tr>
<td>Sugar Maple (Acer saccharum)</td>
<td>20</td>
<td>21.74</td>
<td>2.33</td>
<td>16.81</td>
</tr>
<tr>
<td>White Oaks 1 (Q. alba/Q. michauxii)</td>
<td>6</td>
<td>6.52</td>
<td>0.3</td>
<td>2</td>
</tr>
<tr>
<td>Walnut (Juglans nigra)</td>
<td>6</td>
<td>6.52</td>
<td>0.35</td>
<td>2.53</td>
</tr>
<tr>
<td>Black Cherry (Prunus serotina)</td>
<td>4</td>
<td>4.35</td>
<td>0.33</td>
<td>2.41</td>
</tr>
<tr>
<td>Tulip (Liriodendron tulipifera)</td>
<td>4</td>
<td>4.35</td>
<td>0.6</td>
<td>4.31</td>
</tr>
<tr>
<td>American Elm (Ulmus americana)</td>
<td>4</td>
<td>4.35</td>
<td>0.88</td>
<td>6.34</td>
</tr>
<tr>
<td>Red Oak (Quercus rubra)</td>
<td>3</td>
<td>3.26</td>
<td>0.45</td>
<td>3.25</td>
</tr>
<tr>
<td>White Oaks 2 (Q. muehlenbergii/prinus)</td>
<td>2</td>
<td>2.17</td>
<td>0.4</td>
<td>2.92</td>
</tr>
<tr>
<td>American Beech (Fagus grandifolia)</td>
<td>2</td>
<td>2.17</td>
<td>0.05</td>
<td>0.33</td>
</tr>
<tr>
<td>Sycamore (Platanus occidentalis)</td>
<td>2</td>
<td>2.17</td>
<td>1.5</td>
<td>10.83</td>
</tr>
<tr>
<td>Hackberry (Celtis occidentalis)</td>
<td>2</td>
<td>2.17</td>
<td>0.42</td>
<td>3.06</td>
</tr>
<tr>
<td>White Willow (Salix alba)</td>
<td>2</td>
<td>2.17</td>
<td>0.75</td>
<td>5.43</td>
</tr>
<tr>
<td>Yellow Birch (Betula alleghaniensis)</td>
<td>1</td>
<td>1.09</td>
<td>0.15</td>
<td>1.08</td>
</tr>
<tr>
<td>Sweet (Black) Birch (Betula lenta)</td>
<td>1</td>
<td>1.09</td>
<td>0.1</td>
<td>0.72</td>
</tr>
<tr>
<td>Pecan (Carya illinoiensis)</td>
<td>1</td>
<td>1.09</td>
<td>0.17</td>
<td>1.2</td>
</tr>
<tr>
<td>Slippery Elm (Ulmus fulva)</td>
<td>1</td>
<td>1.09</td>
<td>0.09</td>
<td>0.62</td>
</tr>
<tr>
<td>White Mulberry (Morus alba)</td>
<td>1</td>
<td>1.09</td>
<td>0.07</td>
<td>0.48</td>
</tr>
</tbody>
</table>

Totals                  | 92   | 100                   | 13.89                | 100                 |

Table 3. Leaf litter summary. A total of 23 species were identified.

<table>
<thead>
<tr>
<th>Species</th>
<th>Frequency</th>
<th>Mean Leaf #</th>
<th>% Leaf No.</th>
<th>Mean Leaf Wgt</th>
<th>% Leaf Wgt</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acer negundo</td>
<td>93.3</td>
<td>23.73</td>
<td>43.89</td>
<td>3.00</td>
<td>29.2</td>
</tr>
<tr>
<td>Acer saccharum</td>
<td>80.0</td>
<td>10.53</td>
<td>19.44</td>
<td>1.91</td>
<td>18.6</td>
</tr>
<tr>
<td>Q. alba/Q. michauxii</td>
<td>20.0</td>
<td>0.27</td>
<td>0.49</td>
<td>0.06</td>
<td>0.6</td>
</tr>
<tr>
<td>Juglans nigra</td>
<td>6.7</td>
<td>0.33</td>
<td>0.62</td>
<td>0.05</td>
<td>0.47</td>
</tr>
<tr>
<td>Prunus serotina</td>
<td>40.0</td>
<td>1.33</td>
<td>2.47</td>
<td>0.32</td>
<td>3.06</td>
</tr>
<tr>
<td>Liriodendron tulipifera</td>
<td>46.7</td>
<td>2.93</td>
<td>5.43</td>
<td>1.62</td>
<td>15.69</td>
</tr>
<tr>
<td>Ulmus americana</td>
<td>40.0</td>
<td>2.47</td>
<td>4.57</td>
<td>0.78</td>
<td>7.57</td>
</tr>
<tr>
<td>Quercus rubra</td>
<td>53.3</td>
<td>2.33</td>
<td>4.31</td>
<td>1.00</td>
<td>9.74</td>
</tr>
<tr>
<td>Q. muehlenbergii/Q. prinus</td>
<td>20.0</td>
<td>0.60</td>
<td>1.11</td>
<td>0.19</td>
<td>1.88</td>
</tr>
<tr>
<td>Fagus grandifolia</td>
<td>13.3</td>
<td>0.20</td>
<td>0.37</td>
<td>0.03</td>
<td>0.27</td>
</tr>
<tr>
<td>Platanus occidentalis</td>
<td>20.0</td>
<td>0.67</td>
<td>1.24</td>
<td>0.71</td>
<td>6.86</td>
</tr>
<tr>
<td>Celtis occidentalis</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Salix alba</td>
<td>13.3</td>
<td>1.20</td>
<td>2.22</td>
<td>0.03</td>
<td>0.31</td>
</tr>
<tr>
<td>Betula alleghaniensis</td>
<td>33.3</td>
<td>0.87</td>
<td>1.61</td>
<td>0.09</td>
<td>0.9</td>
</tr>
<tr>
<td>Betula lenta</td>
<td>20.0</td>
<td>0.53</td>
<td>0.99</td>
<td>0.06</td>
<td>0.58</td>
</tr>
<tr>
<td>Carya illinoiensis</td>
<td>20.0</td>
<td>2.33</td>
<td>4.32</td>
<td>0.11</td>
<td>1.11</td>
</tr>
<tr>
<td>Ulmus fulva</td>
<td>6.7</td>
<td>0.07</td>
<td>0.12</td>
<td>0.04</td>
<td>0.36</td>
</tr>
<tr>
<td>Morus alba</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Carya glabra</td>
<td>26.7</td>
<td>3.00</td>
<td>5.56</td>
<td>0.23</td>
<td>2.23</td>
</tr>
<tr>
<td>Unknown Carya sp.</td>
<td>13.3</td>
<td>0.20</td>
<td>0.37</td>
<td>0.02</td>
<td>0.19</td>
</tr>
<tr>
<td>Alnus serrulata</td>
<td>6.7</td>
<td>0.07</td>
<td>0.07</td>
<td>0.01</td>
<td>0.08</td>
</tr>
<tr>
<td>Nyssa sylvatica</td>
<td>6.7</td>
<td>0.27</td>
<td>0.49</td>
<td>0.01</td>
<td>0.14</td>
</tr>
<tr>
<td>Unknown Prunus sp.</td>
<td>6.7</td>
<td>0.07</td>
<td>0.12</td>
<td>0.09</td>
<td>0.18</td>
</tr>
</tbody>
</table>

Totals                      | 54.0      | 100.00      | 10.36      | 100.00        |
Table 4. Spearman’s rank order correlations between stand and leaf litter data.

<table>
<thead>
<tr>
<th>Transformed Data</th>
<th>Rho</th>
<th>Significance (99% confidence)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abundance vs. mean leaf no.</td>
<td>0.49</td>
<td>P=0.0089</td>
</tr>
<tr>
<td>Abundance vs. mean leaf weight</td>
<td>0.56</td>
<td>P=0.0031</td>
</tr>
<tr>
<td>Abundance vs. % leaf weight</td>
<td>0.63</td>
<td>P=0.0007</td>
</tr>
<tr>
<td>Basal area vs. mean leaf no.</td>
<td>0.59</td>
<td>P=0.0014</td>
</tr>
<tr>
<td>Basal area vs. mean leaf weight</td>
<td>0.63</td>
<td>P=0.0009</td>
</tr>
<tr>
<td>Basal area vs. % leaf weight</td>
<td>0.69</td>
<td>P=0.0002</td>
</tr>
</tbody>
</table>

Figure 5. Histogram showing positively correlated rho values for all contemporary forest data. For both abundance and basal area (m), rho is highest for percent leaf weight (i.e. leaf biomass) indicating a strong correlation between these values.
IV. RESULTS: DENLINGERS MILL FOSSIL FLORA

In addition to abundant herbaceous remains found in the hydric soil from DM, eleven species or morphotypes of hardwood trees were identified from preserved leaves or fruits. All species in the subfossil assemblage are currently native to Pennsylvania and are classified as facultative upland, meaning they occur in non-wetland settings 67-99% of the time, facultative, meaning they are equally likely to occur in wetlands or non-wetlands, or facultative wetland, meaning they inhabit wetlands 67-99% of the time (United States Department of Agriculture Plants Database, 2011). Complete descriptions are presented below.
ORDER Fagales
FAMILY Betulaceae
GENUS *Betula* L.
SPECIES *Betula lenta* L.

**Referred Material**
DM2; DM11; DM12; DM16; DM19

**Distinguishing Features**

*Betula lenta* (Sweet birch, Fig. 6) is ovate or elliptic with a finely and sharply singly, or doubly, toothed margin, a round or cordate base, and an acute to acuminate apex (Fernald, 1950; Little, 1980). Sweet birch has 9-12 pairs of lateral veins with compound agrophic veins that branch near the leaf margin (Rhoads and Block, 2007) and tends to be pubescent on veins and in vein axils on the abaxial surface (Fernald, 1950; Hardin and Bell, 1986). This species commonly exhibits the short, stiff, tapered subulate trichomes (30-100 um) along the midvein and secondary veins that are characteristic of family Betulaceae (Hardin and Bell, 1986). The petiole is often pubescent as well (Virginia Tech Forest Resources and Environmental Conservation Tree ID database, 2010).

**Description**

Laminar sizes of these 5 subfossils range from nanophyll to mesophyll. The laminae are elliptic in shape, and when preserved, show medial and basal symmetry with a marginal blade attachment. Apices are either straight and acute, or acuminate. All preserved bases are cordate with an obtuse basal angle. Naked basal veins can be present. Laminae surfaces are pubescent and sometimes have scattered surficial glands. Margins are sharply serrate with angular sinuses and either one order of regularly spaced teeth, or two orders of irregularly
spaced teeth that can be crowded and overlapping. Depending on the lamina size there are between 4 and 7 teeth per cm. Common tooth shapes (apical/basal) are flexuous/flexuous, flexuous/convex, straight/convex, straight/flexuous, convex/convex, convex/straight, concave/convex, concave/flexuous, and rarely flexuous/retroflexed. Principal veins terminate at teeth apices with straight or concave accessory veins. Primary venation is pinnate with 3 basal veins and compound agrophic veins. Major secondaries are craspedodromous to semicraspedodromous with regular and uniform spacing. They are mainly excurrent on the midvein, but sometimes become decurrent towards the base. Costal secondary veins exhibit a smoothly increasing vein angle proximally. Minor secondary veins are usually craspedodromous, but can be semicraspedodromous. Intercostal tertiary veins are sinuous or convex opposite percurrent to mixed percurrent, are obtuse to the midvein, and have a proximally increasing vein angle. Intercostal tertiaries can also decrease in vein angle exmedially. Epimedial tertiaries are opposite, alternate, or mixed percurrent. Proximal vein course is usually perpendicular to the midvein but can also be slightly obtuse or parallel to the intercostal tertiaries. The distal course is parallel to the intercostal tertiaries. Exterior tertiary veins terminate at the margin, and some tertiary veins originate outside of the teeth and terminate at the sinus. Quaternary and quinternary vein fabric is irregular reticulate. Sixth order veins are random reticulate. Freely ending veinlets are absent and areolation exhibits good development. Subulate trichomes are evident on almost all costal veins of all specimens. Solitary and acicular trichomes are evident fringing the midveins, as well as in primary and secondary vein axils. Rarely, single trichomes can be seen scattered on the laminar surfaces.
Discussion

Betula lenta appears similar to other species of Betula, especially B. alleghaniensis (yellow birch). Betula alleghaniensis has distinctive papery bark, whereas the bark of B. lenta remains smooth and shiny with many horizontal lenticels (Little, 1980; Rhoads and Block, 2005; Sibley, 2009). Because these species are usually differentiated based on bark (Sibley, 2009), distinguishing between these two species based on subfossil leaves alone was difficult. Leaves of B. alleghaniensis lack the branching agrophic veins seen in B. lenta, and are persistently more pubescent. Also, yellow birch exhibits many long, straight, filiform trichomes on the abaxial cuticle surface, whereas sweet birch typically exhibits long acicular trichomes along the sides of the midvein and in vein junctions only (Little, 1980; Hardin and Bell, 1986; Rhoads and Block, 2005). The subfossils exhibit features not seen in B. alleghaniensis, including compound agrophic veins (Fig. 6, A,D), a puberulent cuticle surface (Fig. 6, C), subulate trichomes on costal veins (Fig. 6, C, E), and dense trichomes in vein junctions only (Fig. 6, E), and were therefore classified as B. lenta.

Betula lenta is native to the northeastern United States, occurring from southern Maine, west to Ohio and Kentucky, and south to Alabama. Isolated populations also occur in south Quebec and southeast Ontario (Little, 1980). Sweet birch is an aromatic tree with a rounded crown of spreading branches, growing between 15 and 24 m tall. This species prefers moist upland forests, usually along streams and on rocky slopes, and is classified as facultative upland (United States Department of Agriculture Plants Database, 2011). Sweet birch commonly forms associations with other hardwoods and conifers (Little, 1980; Rhoads and Block, 2005).
Figure 6. *Betula lenta* (A) Whole subfossil DM16 showing doubly serrated margin. Arrows point to compound agrophic veins. (B) DM12 (left) showing acute apex and DM11 (right) showing acuminate apex. Both subfossils also exhibit a doubly serrated margin. (C) DM11 cuticle and stomata configuration. Epifluorescent image, 100x mag. Inset image is a closeup of subulate trichomes from DM2. Epifluorescent image, 500x mag. (D) Whole subfossil DM16 showing cordate base, doubly serrate margin, and compound agrophic veins (arrows). (E) Axillary trichomes from DM16. Subulate trichomes are also evident on primary and secondary veins (arrows). Epifluorescent image, 100x mag.
GENUS *Ostrya* Scop.
SPECIES *Ostrya virginiana* (Mill.) K. Koch

**Referred Material**
DM7; DM40; DM63

**Distinguishing Features**

The leaves of *Ostrya virginiana* (eastern hophornbeam, Fig. 7) are distinguished by their sharply, unevenly, and doubly serrate margins, abruptly acuminate apex, and many nearly straight, parallel secondary veins (Little, 1980). The petioles of *Ostrya virginiana* are short and pubescent, and abaxial veins and leaf margins have subulate and acicular trichomes (Hardin and Bell, 1986). Primary surface relief is formed by distinctly convex or dome-shaped epidermal cells (Hardin and Bell, 1986).

The fruits of *Ostrya virginiana* form involucres up to 5 cm long (Little, 1980). Individual seeds are acute, cuspidate, ¼” nutlets within inflated, papery, pubescent bracts (Fernald, 1950; Little, 1980; Rhoads and Block, 2005). The bracts are parallel veined and finely reticulated, and are villous with bristly trichomes around the base, as well as on veins (Fernald, 1950).

**Description**

The laminar size is microphyll and a L:W ratio (extrapolated to include the distal portion of the subfossil) is 4.1:2.3 cm. The lamina is elliptic with medial and basal symmetry, and a pubescent petiole has marginal blade attachment. The apex is acuminate. Basal shape is obtuse to the midvein, and potentially convex or cordate in shape, but is not fully preserved. Laminar surfaces are pubescent with dense, scattered surficial glands. The margin is irregularly doubly serrate with angular sinuses and 7-10 teeth per cm. Principal tooth shapes
(apical/basal) include flexuous/retroflexed, flexuous/flexuous, straight/flexuous, and concave/flexuous. The principal veins terminate at tooth apices and accessory veins are straight or concave. The primary veination is pinnate, with three basal veins and simple agrophic veins. Major secondary veins are craspedodromous and have uniform vein angles. Spacing is regular but can slightly decrease proximally. Costal secondary vein attachment is distally excurrent and gradually becomes deflected, creating a sympodial midvein proximally. Intercostal tertiary vein fabric is mixed percurrent, with veins ranging from straight, convex, and sinuous to alternate with regular offsets. Tertiaries are obtuse to the midvein and can maintain a consistent vein angle or slightly increase proximally. Epimedial tertiaries are opposite percurrent to mixed percurrent. The proximal course is either slightly obtuse or perpendicular to the midvein, while the distal course becomes parallel to the intercostal tertiaries. Exterior tertiary veins terminate at the margin. Quaternary and quinternary vein fabric is irregular reticulate. Freely ending veinlets are absent, and areolation exhibits moderate to good development. Small acicular trichomes can be seen on margins of both subfossils. Longer solitary trichomes are evident on costal veins.

The preserved seed (nutlet) is 0.6 cm long within a 1.4 cm bract. The bract of the fruit exhibits many long parallel veins surrounded by a smaller-gauge, reticulated vein network.

Discussion

The leaves of *O. virginiana* (eastern hophornbeam) are very similar to *Carpinus caroliniana* (eastern hornbeam), therefore the hophornbeam is usually distinguished instead by its shaggy bark and fruit involucres (Fernald, 1950; Sibley, 2009). The leaves of *Carpinus caroliniana* are very similar to those of *Ostrya virginiana*, but are overall less pubescent
(Fernald, 1950; Rhoads and Block, 2007). The subfossil leaves exhibit straight parallel secondary veins and simple agrophic veins (Fig. 7, A, B), a doubly serrate margin (Fig. 7, A, B, C), a pubescent petiole (Fig. 7, D), and marginal trichomes and long solitary trichomes on veins (Fig. 7, D, E). The combination of these features, especially the pubescent petiole and higher density of trichomes on veins and margins, led to the classification of the fossils as *Ostrya virginiana*, as opposed to *Carpinus caroliniana*. The preserved, but not affiliated, fruit (DM7) reinforces this conclusion because it is a parallel-veined, thin, papery bract (Fig. 7, F) with various types of trichomes (Fig. 7, G), whereas *C. caroliniana* fruits are ribbed nutlets surrounded by 3-lobed leafy bracts (Virginia Tech Forest Resources and Environmental Conservation Tree ID database, 2010).

*Ostrya virginiana* is native to North America and ranges along the east coast from southeast Manitoba to northern Florida, and west through the eastern half of Texas (Little, 1980). The eastern hop hornbeam forms a rounded crown of slender, spreading branches (Little, 1980) and usually grows between 6-15 m tall, sometimes reaching heights of 20 m (Gleason and Cronquist, 1963). This species inhabits moist soils in the understory of upland hardwood forests, and is considered a facultative upland species (Little, 1980; United States Department of Agriculture Plants Database, 2011). The hop hornbeam also frequents dry, wooded slopes often on calcareous soils (Rhoads and Block, 2007).
**Figure 7. Ostrya virginiana** (A) Whole subfossil DM63 exhibiting straight parallel secondary veins. (B) Closeup of DM63 doubly serrated margin and simple agrophic veins (arrows). (C) Whole subfossil DM40 showing acuminate apex with doubly serrated margin. (D) Pubescent petiole and marginal trichomes of DM63. Epifluorescent image, 100x mag. (E) Arrows point to acicular trichomes on vein and subulate trichome in marginal sinus on DM40. Epifluorescent image, 100x mag. (F) DM7 fruit with enclosed seed. (G) Arrows point to various trichome types on fruit (DM7). Epifluorescent image, 50x mag.
**Family** Fagaceae  
**Genus** Fagus L.  
**Species** Fagus grandifolia Ehrh.

**Referred Material**  
DM1; DM21; DM25; DM48; DM50  

**Distinguishing Features**

*Fagus grandifolia* (American beech, Fig. 8) leaves are most notably characterized by straight, regular, and parallel secondary veins each ending in a single rounded tooth. The cuticle surface is puberulent between sericeous veins, and petioles are usually short. Trichomes are mostly unicellular solitary, or multicellular filiform, and occur primarily along the midvein and secondary veins, with the highest density in vein junctions (Hardin and Johnson, 1985). The apex is typically follicate, i.e. concave on one side and convex on the other. Adaxial epidermal cells are highly buttressed (Barclay et al., 2012: The Cuticle Database Project).

**Description**

The scored *Fagus grandifolia* specimens are notophyll to microphyll in size after extrapolating to include the non-preserved portions of the laminae, and range from 4.6-12.5 cm long by 2.2 to 6.3 cm wide. Laminar shape is elliptic, with medial and basal symmetry and marginal blade attachment. Apices are acute, convex, or follicate. Base shape ranges from convex, with an acute angle, to cordate, with an obtuse angle. The laminar surface is pubescent with surficial glands. The margin is unlobed and serrate, with regular tooth spacing occurring one per secondary vein, with 2-3 teeth per cm. Sinuses are generally rounded, and prominent tooth shapes (apical/basal) are concave/convex, concave/retroflexed, flexuous/convex, straight/convex, and convex/convex. Principal veins are present and
terminate at tooth apices; accessory veins are convex. Primary venation is pinnate with 1-3 basal veins. Major secondary veins are craspedodromous, and rarely semicraspedodromous, with uniform vein angles. Attachment is mostly excurrent, but it is sometimes deflected, creating a sympodial midvein along a portion of the lamina. Major spacing is regular, but can decrease proximally. Intercostal tertiary veins are highly variable, ranging from sinuous, straight, or convex opposite percurrent, to alternate percurrent, and sometimes irregular reticulate. They are consistently obtuse to the midvein, and vein angle increases proximally. Epimedial terciaries are mixed, exhibiting opposite and alternate percurrent trends, as well as reticulated fabric. Proximal course is either perpendicular or slightly obtuse to the midvein, while the distal course is parallel to the intercostal tertiary veins. Exterior tertiary course is variable. Quaternary vein fabric is irregular reticulate and quaternary vein fabric is regular reticulate. Areolation exhibits good development, and marginal ultimate venation is either looped or terminates at the margin. Costal veins are pubescent with solitary and filiform trichomes, especially in vein junctions.

Discussion

This species appears similar to other northeastern species of Fagaceae, including *Quercus muehlenbergii* (chinkapin oak) and *Castanea dentata* (American chestnut), but it is distinguishable mainly by tooth shape and trichome types. The leaf surface of *Q. muehlenbergii* generally lacks the long solitary trichomes seen in *F. grandifolia* in favor of short, tufted fasciculate and multiradiate trichomes (Hardin and Johnson, 1985). *Quercus muehlenbergii* and *C. dentata* also have more acute, incurved teeth, versus the generally rounded teeth on *F. grandifolia* (Rhoads and Block, 2007). The subfossils exhibit straight parallel secondary veins each ending in a rounded tooth (Fig. 8, A), short petioles with
cordate or convex bases (Fig. 8, A), dense trichomes in vein junctions (Fig. 9, B), and a buttressed adaxial surface (Fig. 9, C), and were therefore classified as *F. grandifolia*

This species is native to the northeastern United States, and it ranges from southern Ontario and Michigan down into northern Florida, extending west to Texas and Oklahoma. Isolated, high altitude populations of *F. grandifolia* have also been found in New Mexico and Utah (Little, 1980; United States Department of Agriculture, 2011), but in the northeast, *F. grandifolia* generally grows at lower altitudes (Colodonata, 1991). The American beech is a large tree, growing 20-24 m in height, with a rounded crown and many spreading horizontal branches (Little, 1980). It inhabits moist rich soils of uplands or well-drained lowlands, and is considered a facultative upland species (Little 1980; Colodonata, 1991; Rhoads and Block, 2007; United States Department of Agriculture Plants Database, 2011). The American beech sometimes forms either dense patches or larger, pure stands due to asexual reproduction (Little 1980; Rhoads and Block, 2007).
Figure 8. *Fagus grandifolia* (A) Whole subfossils from left to right DM1, DM48, and DM25 with regularly spaced, straight, parallel secondary veins, each ending in one rounded tooth. Arrows indicate well-preserved teeth; brackets signify extent of preserved margin exhibiting these features. Specimens also exhibit short petioles and convex (DM1) and cordate (DM48, DM25) base shapes. (B) Image shows dense solitary and filiform axillary trichomes, as well as the puberulent cuticle surface of (DM1). Epifluorescent image, 100x mag. (C) Highly buttressed adaxial epidermal cells (DM1). Epifluorescent image, 100x mag.
GENUS *Castanea* (Mill.)
SPECIES *Castanea dentata* (Marsh.) Borkh.

**Referred Material**

DM6

**Distinguishing Features**

Leaves of *Castanea dentata* (American chestnut, Fig. 9) have distinctly curved or hooked, awned teeth, and deep rounded sinuses (Little, 1980; Flora of North America, 2008). These distinctive teeth are regularly spaced, each occurring at the end of a straight parallel secondary vein (Little, 1980). Diagnostic cuticle features include protruding epidermal cell walls, and a puberulent abaxial leaf surface with a variety of trichomes including solitary, fasciculate, and bulbous. Trichomes occur on costal veins and sometimes margins (Hardin and Johnson, 1985).

**Description**

This subfossil is a marginal fragment with a L:W ratio of 1.8:0.6 cm, and therefore many characters could not be scored. The margin is unlobed and serrate with first order teeth and rounded sinuses. Tooth spacing is regular with 2 teeth per cm. Tooth shape is apically concave and basally retroflexed, creating a characteristically hooked curve, and principal veins terminate in tooth apices. The laminar surface texture is fairly smooth with only a few trichomes on or near the veins. Primary venation is not visible. Major secondaries are craspedodromous. Intercostal tertiary veins are straight or sinuous opposite percurrent; there are some alternate percurrent veins exmedially. Exterior tertiary veins terminate at the margin. Quaternary and quinternary vein fabric is regular reticulate. Freely ending veinlets are absent, and areolation exhibits good development.
Discussion

Like the American Beech, the American chestnut also closely resembles other members of Fagaceae, including the chinkapin oak (*Quercus muehlenbergii*) and the Allegheny chinkapin (*Castanea pumila*), but it can be distinguished based on leaf morphology and tooth characteristics. American Chestnut leaves are oblong with curved, awned teeth, whereas *Q. muehlenbergii* leaves are typically obovate with wavy edges and rounder teeth (Little, 1980). Unlike the leaves of *C. dentata*, *C. pumila* leaves have coarser, more irregularly toothed margins and are tomentose beneath on the abaxial cuticle (Hardin and Johnson, 1985; Virginia Tech Forest Resources and Environmental Conservation Tree ID database, 2010). The subfossil exhibits characteristic awned, hooked teeth at the end of parallel veins (Fig. 9, A) as well as solitary trichomes on veins (Fig. 9, C) and is therefore classified as *C. dentata*.

This species is native to the northeastern United States, and was historically ubiquitous, ranging from southern Ontario and Maine, south to Florida, and west to Mississippi and Indiana (Little, 1980; United States Department of Agriculture, 2011). The American chestnut has a massive trunk and naturally grows upwards of 30 m, forming a broad, rounded crown. Due to the effects of the chestnut blight fungus introduced to North America in the early 20th century, any wild trees today are usually small, multi-stemmed resprouts, ca. 5-10 m tall, growing from the bases of dead trees (Little, 1980; Flora of North America, 2008). The American chestnut prefers moist upland soils in mixed forests (Little, 1980), and because it is an upland species, it is not assigned a wetland indicator status (United States Department of Agriculture, 2011).
Figure 9. *Castanea dentata* (A) Whole subfossil DM6 showing margin with hooked teeth. (B) *Castanea dentata* reference image from sample Y1-4 of the York County Collection from Wilf (1997). (C) DM6 epifluorescent image, 100x mag. Arrow points to solitary trichomes on veins.
GENUS *Quercus* L.
SPECIES *Quercus cf. alba* L.

**Referred Material**
DM15; DM26; DM27; DM29

**Distinguishing Features**

*Quercus cf. alba* (white oak, Fig. 10) is characterized by elliptic leaves that have a triple-lobed apex and a decurrent, cuneate base (Gleason and Cronquist, 1963). Leaves have entire margins composed of 5-11 rounded lobes ending in retuse, asymmetrical apices (Rhoads and Block, 2005; 2007). A fimbrial vein is present along the margin. Lobes have moderate to deep rounded sinuses (Sibley, 2009). *Quercus alba* leaves are essentially glabrous (Gleason and Cronquist, 1963), although this species sometimes has simple or fasciculate trichomes (Hardin, 1979).

**Description**

The largest *Quercus cf. alba* specimen scored is microphyll in size with a L:W ratio of 7:3.7 cm; all other samples were fragments. Shape is elliptic with medial symmetry, a pinnately moderately lobed margin, and a smooth, glabrous surface texture. The very distal portion of the terminal apex is not preserved, although all other lobes on the specimen end in retuse apices. Primary venation is pinnate. Major secondaries are craspedodromous and arched, with irregular spacing, inconsistent vein angles, and basally decurrent attachment. A fimbrial vein is present on all samples with preserved margin. Intersecondary veins are present usually within the distal portion of the leaf. Proximal and distal intersecondary courses are parallel to major secondaries. Intersecondaries are <50% of subjacent secondary veins and occur at < 1 per intercostal area. Intercostal tertiaries are mostly straight and convex.
opposite percurrent, with some alternate percurrent veins. They are obtuse to the midvein, with an exmedially increasing vein angle. Epimedial tertiaries are opposite percurrent, with a proximal course perpendicular to the midvein, and a distal course parallel to the intercostal tertiaries. Most exterior tertiary veins are looped, although some terminate at the margin.

Quaternary vein fabric is mixed percurrent to irregular reticulate, and quinternary vein fabric is consistently irregular reticulate. Sixth order veins are sometimes random reticulate, but mostly end in simple, unbranched, or singly branched, freely ending veinlets. Areolation is good to moderate.

**Discussion**

Native species within the white oak group (*Quercus* subgenus *Quercus*) generally have rounded lobe apices, differentiating them from the acute, bristle-tipped red oak group (*Quercus* subgenus *Lobatae*). The only native white oak species lacking these characteristics is *Quercus muehlenbergii* (chinkapin oak), which has a serrate margin with regularly spaced, curved teeth (Rhoads and Block, 2007; Sibley, 2009). The leaf surfaces of the *Quercus* cf. *alba* subfossils from DM are glabrous, lacking any identifiable trichomes, which is a distinguishing characteristic of this species, but could also be taphonomic. Additionally, the subfossils exhibit arched secondary veins (Fig. 10, A), rounded lobes with retuse and asymmetrical apices (Fig. 10, A-C), fimbrial veins tracing the leaf margins (Fig. 10, B), and a triple-lobe apex (Fig. 10, C).

The eastern White Oak is native to North America, and ranges from southern Ontario and Quebec, east to Maine, south to northern Florida, and west to Minnesota and Texas (United States Department of Agriculture Plants Database, 2011). *Quercus alba* forms a large rounded crown with wide-spreading, stout, horizontal branches (Little, 1980). This species
usually grows between 24-30 m, but has been known to grow taller (Little, 1980). The white oak prefers moist, rich upland soils often on ridges or slopes, or well-drained lowlands (Sibley, 2009) and is classified as a facultative upland species (United States Department of Agriculture Plants Database, 2012). *Quercus alba* often forms pure stands (Little, 1980) and is possibly the most abundant native hardwood tree species in North America (Sibley, 2009).

**Figure 10.** *Quercus cf. alba.* (A) Whole white oak subfossil DM15 with arched secondary veins (arrow). (B) Lobe of DM15 with retuse apex and fimbrial vein (arrow), 25x mag. (C) DM26 showing triple crown feature of a true leaf apex. (D) DM27 showing variation in lobe morphology and insect damage.
GENUS Quercus L.
SPECIES Quercus subgenus Lobatae

Referred Material
DM14; DM20; DM22; DM28; DM77; DM78; DM80; DM90; DM91; DM92; DM99

Distinguishing Features

Unlike the white oak group, the majority of Quercus subgenus Lobatae (red oaks, Fig. 11) are characterized by elliptical leaves with oblong, acute, asymmetrical lobes, sometimes ending in irregular bristle tips. These lobes can be distally expanded, and are separated by shallow sinuses. Red oak margins also contain a fimbrial vein. Although there are species belonging to the red oak group with entire margins, they still possess bristled teeth. Leaf surfaces also contain a high density of randomly orientated stomata whose guard cells form evident T-shapes at their junctions.

Description

No specimens have preserved apices, therefore laminar sizes extrapolated to include the missing distal portions range from notophyll, example L:W ratio of 11.2:8.6 cm, to microphyll-sized specimens that are obviously juvenile, example L:W ratio 6.2:3 cm. Because apices are not preserved, laminar shape cannot precisely be determined, but could be elliptic or oblong. Specimens exhibit medial symmetry and a marginal, asymmetrical basal insertion onto the petiole. Margins are pinnately, moderately to deeply lobed and entire, except for bristle-tips at lobe apices. Sinuses are usually angular and somewhat v-shaped, but can also be rounded. Base angles are obtuse, and base shape can be rounded, slightly cordate, or asymmetrically decurrent. Primary venation is pinnate with one basal vein. Major secondaries are craspedodromous, arched, and have basally decurrent attachment. Vein spacing can be roughly regular or slightly decrease proximaly, and vein angles range from uniform to
smoothly decreasing proximally. A fimbrial vein is present in all specimens with preserved margins. Intersecondaries are <50% of subjacent secondaries and occur at < 1 per intercostal area. Intersecondary proximal courses can be perpendicular to the midvein or parallel to the major secondaries, and distal courses are either parallel to the subjacent major secondary or reticulating. Intercostal tertiary veins are straight or sinuous opposite percurrent to alternate percurrent, are obtuse to the midvein, and exhibit proximally increasing vein angles. Epimedial tertiaries range from mixed percurrent to reticulate, have a proximal course that is either perpendicular or obtuse to the midvein, and a basiflexed distal course. Exterior tertiary veins are variable. Quaternary vein fabric is alternate percurrent or regular reticulate. Quincternary vein fabric is regular reticulate. Sixth order veins are regular reticulate, or end in simple freely ending veinlets. FEV’s are mostly singly branched, but can also be unbranched or dichotomous. Areolation exhibits good development. Cuticle surface texture is essentially smooth with laminar glands and no observable trichomes.

**Discussion**

Identifying the DM red oak specimens to species level based on leaves alone was unfeasible for multiple reasons, including the substantial amount of interspecies morphological similarity, the ample amount of intraspecies morphological variation, and the fact that species within this subgenus commonly hybridize (Rhoads and Block, 2007). Furthermore, no trichomes were found on any red oak morphotype samples. The red oak subfossils are distinguishable by their acute, bristle-tipped lobes (Fig. 11, A) and their distinctive T-shaped guard cell junctions around stomata (Fig. 11, B, inset).
Species belonging to the red oak subgroup vary widely in their environmental preferences (Rhoads and Block, 2007; United States Department of Agriculture, 2011). Because other taxa identified within the subfossil assemblage from DM exhibit a range of habitats, the red oak morphotypes from DM could be a number of species, even after eliminating all members of this group that do not exhibit acute-lobed morphology. Species such as *Quercus shumardii* (shumard oak) and *Q. palustris* (pin oak) are facultative to facultative wetland and are associated with a variety of riverine and wetland communities (Carey, 1992a; Rhoads and Block, 2007; United States Department of Agriculture, 2011). Based on the other species present in the subfossil assemblage, the majority of red oak specimens from DM probably represent facultative upland and upland species such as *Q. rubra* (red oak) and *Q. coccinea* (scarlet oak), which prefer dry to moist woodlands on upland ridges and slopes (Little, 1980; Sander, 1990; Carey, 1992b Rhoads and Block, 2007). However, it is also possible that purely upland species such as *Q. velutina* (black oak) and *Q. ilarifolia* (bear oak) are represented, even though they are extremely unlikely to be found associated with wetland communities (United States Department of Agriculture, 2011). All species within the red oak subgroup are large trees, growing to between 20 and 30 m (Rhoads and Block, 2007). The one exception is *Q. ilicifolia*, which is a shrub that grows up to 6 m in height (Little, 1980).
Figure 11. *Quercus* subgenus *Lobatae* morphotypes (A) DM14 (B) DM20 (C) DM28 (D) DM78. Arrows point to preserved acute, bristle-tipped lobes. (E-G) Examples of cuticle variation amongst morphotypes. Epifluorescent images, 100x mag. Inset in middle image shows distinctive t-shaped guard cell junctions; inset scale bar = 30 microns.
ORDER Salicales  
FAMILY Salicaceae  
GENUS *Salix* L.  
SPECIES *Salix* sp. L.

**Referred Material**  
DM33

**Distinguishing Features**  
Most *Salix* spp. (willows, Fig. 12) are shrubs or small trees that grow in dense thickets along streams and in other wet areas (Sibley, 2009). Leaf surfaces of this genus are generally pubescent, at least two times longer than they are wide, and have characteristic salicoid teeth with dark, round, setae attached to teeth apices (Hickey and Wolfe, 1975; Rhoads and Block, 2007). This morphotype can be assigned to the genus *Salix* based on the presence of salicoid teeth, which are unique to family Salicaceae, but it cannot be identified to species level based on the leaf fragment available.

**Description**  
This subfossil fragment is a distal portion of the apex and is medially symmetrical. The laminar margin is minimally serrate with rounded sinuses. Teeth are salicoid with spherulate apices. They are regularly spaced with approximately 5 teeth per cm. Principal veins are present and terminate at the margin. The apex angle is acute. Primary venation is pinnate. Major secondary veins are simple brochidodromous with irregular spacing and decurrent attachment. Vein angles smoothly increase proximally. Intersecondary veins are approximately half the length of the subjacent secondary and occur at < 1 per intercostal area. Proximally they are parallel to the major secondaries and distally they dichotomize to join super- and subjacent secondary veins. Intercostal tertiary veins are convex to sinuous opposite percurrent, and irregular reticulate. They are consistently obtuse to the midvein. Epimedial
tertiaries are mixed percurrent. Proximally they are either perpendicular or acute to the midvein and distally they are parallel to the intercostal tertiaries. The majority of exterior epimedial tertiaries are looped, although some terminate at the margin. Quaternary vein fabric is mixed percurrent, and quinternary vein fabric is freely ramifying. Freely ending veinlets are mostly one branched with simple termination. Marginal ultimate venation is looped. Areolation exhibits poor development. The laminar surface is rugose due to high vein relief, and is essentially glabrous probably due to taphonomic processes.

**Discussion**

Identifying willows to species level based on leaves alone proves difficult because in addition to common hybridization between species, branching patterns, leaf attachment, and catkin morphology are the typical diagnostic features (Argus, 2006). Only two genera within family Salicaceae, *Salix* and *Populus*, are native to Pennsylvania (Rhoads and Block, 2007). *Populus* leaves can be distinguished from *Salix* leaves because they are about as wide as they are long (Rhoads and Block, 2007). Because the morphotype presented here has salicoid teeth (Fig. 12 A, C) and is also longer than it is wide, it is assigned to genus *Salix*. Species in this genus are found worldwide, with around 100 species native to North America (Rhoads and Block, 2007). Of the species that are native to Pennsylvania, all except one (*Salix humilis*, the prairie willow) are either wetland obligate or wetland facultative species (United States Department of Agriculture, 2012). *Salix humilis* has an entire margin and is frequently tomentose on the abaxial leaf surface (Argus, 2006; Rhoads and Block, 2007). The *Salix* morphotype described here does not have these characteristics, and it is therefore considered to have a wetland obligate or wetland facultative affiliation.
Figure 12. *Salix* sp. (A) Characteristic salicoid tooth from left margin (as viewed) of whole subfossil. (B) Complete specimen DM33. (C) Well-defined salicoid tooth from right margin (as viewed) of subfossil also showing well preserved stomata. Epifluorescent image, 100x mag.
ORDER Sapindales  
FAMILY Aceraceae  
GENUS Acer L.  
SPECIES Acer spicatum Lam.

**Referred Material**  
DM9

**Distinguishing Features**

*Acer spicatum* (mountain maple, Fig. 13) leaves are broadly ovate or orbicular with 3-5 short, broad lobes forming v-shaped sinuses, and a coarsely serrated margin (Little, 1980; Rhoads and Block, 2005; Virginia Tech Forest Resources and Environmental Conservation Tree ID database, 2010). Leaves of *A. spicatum* exhibit palmate venation with 5-7 main basal veins. The mountain maple has a pubescent petiole and abaxial surface with scattered acicular and solitary trichomes. Vein junctions are densely villous with acicular, filiform, and aduncate trichomes, as is the petiole attachment (Little, 1980: Virginia Tech Forest Resources and Environmental Conservation Tree ID database, 2010).

**Description**

The subfossil laminar size is microphyll, orbicular in shape, and palmately lobed. The petiole is 3 cm long and pubescent with a marginal blade attachment. The true margin is not preserved. Primary venation is basal actinodromous with 7 basal veins. Base shape is lobate with a reflex base angle. The apex is not preserved. Surface texture is highly pubescent, especially in vein junctions. Major secondary veins are excurrent with regular and uniform spacing. Interior secondaries are present but poorly preserved. Minor secondary veins occur at < 1 per intercostal area and are < 50% of the length of subjacent secondaries. The proximal course is parallel to the major secondary veins; distal course is perpendicular to the subjacent major secondary. Intercostal tertiary veins are obtuse to the midvein, are alternate percurrent and sinuous opposite percurrent, and increase in angle exmedially. Epimedial tertiaries are
reticulate. Both quaternary and quaternary vein fabric is irregular reticulate. Areolation shows good development

**Discussion**

*Acer spicatum* is similar to other species of maple, namely *A. pensylvanicum* (striped maple) and *A. pseudoplatanus* (sycamore maple). Both of these species have 3-5 broad lobes, similarly to *A. spicatum*, but are considerably more finely serrated (Little, 1980). Additionally, the striped maple tends to have pointed lobes and only 3 basal veins, and the sycamore maple has distinctive protruding veins and is glabrous on the abaxial surface (Rhoads and Block, 2005). The subfossil has an extremely pubescent abaxial surface and dense, villous vein junctions (Fig. 13, B, C), unlike *A. pseudoplatanus*, and has 7 basal veins (Fig. 13, A), which is considerably more than *A. pensylvanicum* typically exhibits. Therefore, it is classified as *A. spicatum*.

*Acer spicatum* is native to northeastern North America, and ranges from Saskatchewan to Newfoundland, south to Iowa and east through Pennsylvania. The mountain maple also occurs in the southern Appalachians through Georgia and Alabama (Little, 1980). Unlike the other species identified in the DM subfossil assemblage, which are mostly large trees, *A. spicatum* is a small tree or shrub, usually growing no larger than 7-8 m in height, with a crown of slender, upright branches (Virginia Tech Forest Resources and Environmental Conservation Tree ID database, 2010). This species prefers moist rocky uplands, especially on mountains, and is a common understory tree of hardwood forests (Little, 1980).
Figure 13. *Acer spicatum* (A) Whole subfossil DM9. (B) DM9 axillary tufts of acicular, aduncate, and filiform trichomes. Epifluorescent image, 100x mag. (C) Dense acicular, aduncate, and filiform basal trichomes of sample DM9. Epifluorescent image, 100x mag. (D) and (E) *Acer spicatum* reference image from sample M5-2 of the Allegheny National Forest, Pennsylvania collection from Wilf (1997). Epifluorescent images, 50x mag. (D) Image shows axillary tufts with the same types and configuration of trichomes as (B), while (E) exhibits the same dense basal trichomes seen in (C).
GENUS *Acer*
SPECIES *Acer rubrum* L.

**Referred Material**
DM5; DM13; DM32

**Distinguishing Features**

*Acer rubrum* (red or swamp maple, Fig. 14) leaves are broadly ovate with 3-5 lobes and a compoundly serrated margin composed of coarse and irregular teeth. Leaves typically have 5 primary veins (Little, 1980), as well as an obvious perimarginal vein and dichotomizing minor secondary and tertiary veins near the margin. The abaxial surface is glabrous to puberulent on primary veins and in vein junctions (Little, 1980; Rhoads and Block, 2007; Virginia Tech Forest Resources and Environmental Conservation Tree ID database, 2010).

**Description**

*Acer rubrum* is represented by three fragments depicting various areas of the laminar surface, including a lobe apex (L:W ratio 2:0.8 cm), a segment of mid-leaf margin (L:W ratio 2.8:1.3 cm), and the central portion of a lobe (L:W ratio 3.6:2.3 cm). Combining all of the characteristics, the apex is straight and acute, the leaf surface is generally smooth with a serrated margin. Tooth spacing is irregular, with one or two orders of teeth, and 3-4 teeth per cm. Depending on teeth shape and crowding, the sinuses are mostly angular but can be rounded. Principal tooth shapes (apical/basal) include concave/convex, concave/straight, concave/retroflexed, flexuous/retroflexed, and flexuous/concave. Principal veins are present and terminate in tooth apices. Accessory veins are usually convex, but can rarely be concave depending on the size and shape of the tooth. Primary venation is not preserved. Agrophic veins are simple, and minor secondary veins are craspedodromous to simple.
brochidodromous. Major secondary veins are craspedodromous with excurrent attachment, but accurate spacing could not be determined from these fragments. Variation in secondary vein angles could be either uniform or smoothly increasing proximally. The intramarginal secondary vein is the same gauge as the intersecondaries and minor secondaries.

Intersecondary veins are >50% of subjacent secondaries and occur at ~ 1 per intercostal area, but can be up to two. Proximal course is either parallel with the major secondaries, or perpendicular to the midvein, and the distal course is either perpendicular to the subjacent major secondary or reticulating. Intercostal tertiary veins are mixed percurrent, and are either straight or sinuous opposite percurrent, or alternate percurrent, and are obtuse to the midvein. Epimedial tertiaries are either alternate percurrent or reticulate. Exterior tertiary course is looped. Quaternary vein fabric is usually regular reticulate, but can be irregular. Quinternary veins freely ramify. Areolation is moderate to good. Freely ending veinlets are mostly unbranched, although some have one branch, with simple termination. Marginal ultimate venation is looped. Preservation quality of these three specimens was low, and therefore the majority of the actual cuticle surfaces were missing. A few remaining trichomes were found on one specimen within vein junctions.

Discussion

*Acer rubrum* is morphologically similar to other species of maple including *Acer saccharum* (sugar maple) and *Acer nigrum* (black maple). Both of these species also have 3-5 palmate lobes and coarsely serrated margins, but usually have deeper, more pointed lobes than *A. rubrum* (Little, 1980; Rhoads and Block, 2007). These species can also be differentiated based on trichome configurations. Unlike *A. rubrum*, which is glabrous to mildly puberulent,
A. nigrum and A. saccharum are commonly sericeous with long trichomes, especially on or near veins (Rhoads and Block, 2007; Sibley, 2009). The subfossils exhibit coarse, compoundly serrated margins (Fig. 14, A,B,C), dichotomizing tertiary veins that rejoin subjacent secondary veins instead of terminating at the margin (most clearly seen in Fig. 14 C), and puberulent vein junctions with aduncate trichomes on otherwise essentially glabrous cuticle surfaces (Fig. 14, E). Because A. nigrum and A. saccharum are consistently pubescent to sericeous, these subfossils were classified as A. rubrum.

Acer rubrum is native to North America and is widespread in eastern Canada and throughout the United States east of Texas, Oklahoma, and Minnesota, south to the tip of Florida (Little, 1980; United States Department of Agriculture, 2011). The red maple is a tall tree, up to 24-27 m in height, and forms a narrow or rounded crown (Little, 1980; Virginia Tech Forest Resources and Environmental Conservation Tree ID database, 2010). This species is characterized as an obligate or facultative wetland species (United States Department of Agriculture, 2011), but it is adaptive to a wide array of climatic and environmental conditions. In Pennsylvania, A. rubrum is commonly associated with moist or wet soils of stream banks, swamps, and valleys, but it may also grow on upland slopes and dry ridges in mixed hardwood forests (Little, 1980; Rhoads and Block, 2007).
Figure 14. *Acer rubrum* (A) Subfossil DM5 showing coarse, compoundly serrated margin. (B) Subfossil DM13 showing a middle portion of a lobe. (C) Subfossil DM32 showing a lobe apex. (D) *Acer rubrum* reference image from sample M9-1 of the Allegheny National Forest, Pennsylvania collection from Wilf (1997). Letters correspond to the probable areas of a lobe represented by DM5, DM13, and DM32. Arrows in (A-D) point to dichotomizing veins. (E) Epifluorescent image showing puberulent vein junctions with aduncate trichomes and stomata configuration on DM13, 100x mag.
ORDER Scrophulariales  
FAMILY Oleaceae  
GENUS *Fraxinus* L.  
SPECIES *Fraxinus nigra* Marsh.

**Referred Material**

DM8

**Distinguishing Features**

*Fraxinus nigra* (black ash, Fig. 15) is the only species from the DM fossil assemblage to be represented by its fruit only, rather than by leaves or a combination. The samara of the black ash is elongated, typically 2.5-4 cm in length, with a broad, oblong wing that has a retuse apex and extends back to the base of the flat-bodied seed (Little, 1980). A midvein runs down the entire length of the wing.

**Discussion**

Fruits of the Black ash are similar to fruits of other ash species, as well as the fruit of *Liriodendron tulipifera* (tulip tree). *Fraxinus nigra* samaras differ from those of *L. tulipifera* because they lack the thickened basal ridge and also have flat wings compared with the curved wings of the tulip tree fruit (Rhoads and Block, 2007). *Fraxinus nigra* is native to North America, extending from Manitoba and Newfoundland south to Virginia and Iowa (Virginia Tech Forest Resources and Environmental Conservation Tree ID database, 2010; United States Department of Agriculture, 2011). The black ash forms a narrow, rounded crown of upright branches and usually grows 9-15 m tall (Little, 1980), sometimes up to 25 m (Rhoads and Block, 2007). This species occurs in both coniferous and hardwood forests, preferring wet soils near streams, swamps, and peat bogs (Little, 1980), and it is classified as a facultative wetland species (United States Department of Agriculture, 2011).
Figure 15. *Fraxinus nigra* (A) Whole subfossil DM8 showing flat, elliptical seed body with extended wing containing midvein (arrow) and retuse apex. (B) Close up of midvein and retuse apex with small projection (arrow), 25x mag.
ORDER Hamamelidales  
FAMILY Platanaceae  
GENUS *Platanus* L.  
SPECIES *Platanus occidentalis* L.

**Referred Material**
DM42

**Distinguishing Features**

The leaves of *Platanus occidentalis* (American sycamore, Fig. 16) are highly variable, but are typically very large and broadly ovate in shape (Sibley, 2009). They have palmate veination with 3-5 offset primary basal veins that are decurrent onto the petiole. American sycamore leaves also have 3-5 lobes that are often wider than they are long, forming shallow concave sinuses (Flora of North America, 2008). *Platanus occidentalis* margins are entire or coarsely toothed, sometimes with short-awn (bristle) tips on acuminate tooth apices (Little, 1980; Rhoads and Block, 2005; Flora of North America, 2008). Veins are persistently tomentose on the abaxial surface (Flora of North America, 2008), sometimes with multiradiate trichomes with whorls of arms (Carpenter et al., 2005). Characteristic trichome bases of the genus *Platanus* are compound, exhibited by a rounded scar on the junction of two or more modified underlying epidermal cells (Carpenter et al., 2005).

**Description**

The margin is palmately lobed and entire except for bristle tips, and the blade attachment is marginal. The apex is not preserved. The base is lobate with a reflex angle. The surface texture is pubescent with scattered surficial glands. Primary venation is basal actinodromous with 3 basal veins and compound agrophic veins. Both major and minor secondary veins are semicraspedodromous. Intercostal tertiary veins are straight or sinuous
opposite percurrent, are obtuse to the midvein, and increase in angle exmedially. Epimedial
tertiaries are mixed percurrent, with a proximal course perpendicular to the midvein and a
distal course that is basiflexed. Exterior tertiary veins terminate at the margin. Quaternary
vein fabric is mixed percurrent. Quaternary vein fabric is irregular reticulate. Freely ending
veinlets are absent and areolation shows good development.

Discussion

The American Sycamore (*Platanus occidentalis*) is very similar to two non-native
species, the London Planetree (*Platanus × acerifolia*), a hybrid species originating in Europe,
and the Sycamore maple (*Acer pseudoplatanus*), a tree from Europe and western Asia (Sibley,
2009). Both these species are commonly cultivated in Pennsylvania and surrounding states
today, but it is highly unlikely that these species were present during the formation of the
subfossil assemblage. Leaves of the London Planetree can be differentiated from the
American sycamore because they are typically smaller, with deeper lobes and fewer teeth
(Sibley, 2009). *Acer pseudoplatanus* is usually distinguishable by its dangling clusters of
flowers and fruit compared with the hanging spherical fruit of the American sycamore
(Sibley, 2009). The leaves of *A. pseudoplatanus* can be distinguished from *P. occidentalis*
because they consistently have 5 lobes and protruding veins on the abaxial surface (Rhoads
and Block, 2005). Besides the fact that both of these species are non-native to the U.S., the
subfossil is classified as the American Sycamore because it exhibits characteristic multiradiate
(aka candelabraform) trichomes in vein junctions (Fig. 16, B).

This species is native to the northeastern U.S. and extends from Ontario and southwest
Maine down to Florida, and west to central Texas and Nebraska (United States Department of
Agriculture, 2011). Isolated populations also occur in northeastern Mexico (Little, 1980). *P. occidentalis* has a straight trunk with enlarged base and large, crooked branches that spread to form a broad, open crown (Little, 1980). The American sycamore grows between 18 and 30 m tall, sometimes up to 50 m (Gleason and Cronquist, 1963), and has the largest trunk diameter of any native hardwood species (Little, 1980). This species prefers wet soils of streambanks and floodplains, as well as the edges of lakes and swamps (Sibley, 2009) and is classified as a facultative wetland or wetland species (United States Department of Agriculture, 2011). The American sycamore is commonly dominant in mixed forests (Little, 1980).

**Figure 16. Platanus occidentalis** (A) Whole subfossil DM42 showing a bristle-tipped tooth, slightly offset, decurrent basal veins (black arrows), and compound agrophic veins (white arrows). (B) Arrows point to characteristic multiradiate (tall and branched) trichomes in vein junctions. Epifluorescent image, 100x mag.
V. DISCUSSION

The pre-settlement flora recovered from DM has a high proportion of upland woody species, but it also represents the adjacent associated wetland and floodplain communities. It was expected that the majority of species would be facultative or facultative upland because of local topography around the subfossil site, but the presence of lowland trees and herbaceous remains implies that a true wetland ecosystem was also in close proximity during pre-colonial times.

There are a total of eleven identified woody species and morphotypes, all of which are associated with wetlands at least part of the time. The exception is *Castanea dentata*, which is a purely upland slope hardwood species. The subfossils with the highest relative abundances are *Fagus grandifolia*, *Quercus* spp. subgenus *Lobatae*, and *Betula lenta*. All these species have facultative upland associations throughout the northeast. Other minor facultative upland constituents of the subfossil assemblage include *Acer spicatum* and *Ostrya virginiana*. The remaining four subfossil species represent the transitional community from valley-bottom wetlands to the facultative upland assemblage just described. These species, *Platanus occidentalis*, *Acer rubrum*, *Fraxinus nigra*, and *Salix* sp., are commonly either facultative or facultative wetland.

The Denlingers Mill site is unusual in that it has presumably continuously harbored an upland slope community, at least throughout the recent Holocene. Even though there are species shared between the subfossil assemblage and modern community, the dominant components of the pre- and post-settlement forests vary significantly. Furthermore, even though the source of this transition is anthropogenic in origin, DM is distinct from other
previously studied subfossil sites because the vegetation shifts are most likely attributable to deforestation and land clearing more so than milldam construction and accumulation of legacy sediments. Based on average longevity of certain species identified both in the modern forest and the subfossil assemblage, such as *Quercus* spp., *F. grandifolia*, and *P. occidentalis*, it is possible that some of the large hardwood trees around the field site today may be the descendants of the pre-colonial trees that deposited the subfossil leaf mats at Denlingers Mill.

**i. Classification of the Contemporary Forest**

According to a compendium of modern terrestrial and palustrine plant communities of Pennsylvania (Fike, 1999), the extant forest surrounding Denlingers Mill could be considered a river bed-bank-floodplain complex, which characteristically supports mixed forest vegetation of wetland and upland species, as well as high structural, community, and species diversity due to variations in substrate, disturbance, and hydrologic regimes. Vegetation of this type is driven primarily by stream water levels and often contains a continuum of intermediate forest classification types.

Based on the results from the modern stand and leaf litter studies (Tables 2, 3), the contemporary forest surrounding Denlingers Mill is a combination of multiple forest types. A rich red oak-sugar maple forest inhabits the uppermost slopes. This forest type is blended with a northeastern modified successional forest, which then grades into a box elder floodplain forest in closest proximity to the stream. The red oak-sugar maple forest is typically found on moist slopes in Pennsylvania and is dominated by *Acer saccharum*, *Quercus* spp., *Liriodendron tulipifera*, *Carya* spp., and *Nyssa sylvatica*. Other constituents include *Betula* spp., *Fagus grandifolia*, *Ostrya virginiana*, and *Carpinus caroliniana* (Westervelt et al.,
Evidence suggests that *Castanea dentata* may once have been an important component in this forest type as well, before its demise from chestnut blight (Fleming and Van Alstine, 1999). Northeastern modified successional forests are highly variable in physiognomy, but are usually mesic and are typical of disturbed sites that have been cleared for agriculture, or otherwise heavily modified in the past (Westervelt et al., 2006). This forest type includes *L. tulipifera, Prunus serotina, Juglans nigra, Ulmus* spp., *Quercus* spp., *Betula* spp., and various maples including *Acer negundo*. The box elder floodplain forest found closest to the West Branch of the Little Conestoga Creek is an early successional palustrine community that arises from either natural or anthropogenic floodplain disturbances (Westervelt et al., 2006). It is dominated by *Acer negundo* (box elder) and *Platanus occidentalis* (American sycamore), as well as other *Acer* spp. and *Salix* spp. (Fike, 1999; Westervelt et al., 2006). These three forest types contain many overlapping taxa, and when taken together, represent all the major canopy forming trees identified in the field around DM, as well as the majority of the subcanopy species present today.

**ii. Paleocommunity Interpretation and Comparisons**

Qualitative abundance data indicate that *F. grandifolia* (American beech) and *Quercus* spp. (red and white oaks) were the dominant species in the upland portion of the fossil old-growth forest. Because forest classifications are based on dominant species, the pre-settlement upland forest was most likely similar to a modern red oak-mixed hardwood forest, which is a broadly defined community that occurs on mesic sites and is rather variable in composition (Fike, 1999). The dominant canopy species are *Quercus* spp., *F. grandifolia*, and *A. rubrum*, while typical subcanopy species are *B. lenta, L. tulipifera*, and *O. virginiana*. This forest
classification contains all the facultative upland species found in the DM subfossil deposit except *A. spicatum*, and *C. dentata*, which is no longer included in forest classifications following its eradication due to chestnut blight.

Precise fitting of the fossil assemblage into a modern day forest classification was unexpected due, in part, to taphonomic biases including temporal and spatial averaging, stature and distance of the paleovegetation from the sampled area, preservational quality of the vegetation such as cuticle thickness, and differential abundances and biomass production of the source community (Wing and DiMichele, 1995). Additionally, this assemblage probably represents multiple communities, some of which have been previously described (Table 5). Macrofossil fruits and seeds from Big Spring Run (Voli et al., 2009) and fragmentary leaf macrofossils from White Clay Creek (Miller, 2011) have supplied information about the pre-settlement herbaceous wetland and lowland tree components, respectively. The tussock sedge meadow community proposed to have inhabited saturated valley-bottoms was composed of a variety of obligate wetland species including *Carex* spp., *Scirpus* spp., and *Eleocharis* spp. The subfossil leaf assemblage from White Clay Creek contained mostly facultative and facultative wetland species such as *A. rubrum*, *A. negundo*, *Alnus serrulata*, and *Salix* spp., as well as some facultative upland species including *F. grandifolia*, *Quercus* spp., and *L. tulipifera*. Miller (2011) interpreted these results as most likely being a red maple-black ash deciduous swamp forest, which is commonly present on floodplains. This swamp forest usually has a sedge-dominated (*Carex* spp.) understory, and is also sensitive to changes in hydrology (Westervelt et al., 2006). In addition to the two dominant species *A. rubrum* and *F. nigra*, this community frequently contains
<table>
<thead>
<tr>
<th>Site</th>
<th>Denlingers Mill</th>
<th>White Clay Creek</th>
<th>Big Spring Run</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Data Source</strong></td>
<td>Leaf macrofossils, fruit macrofossil <em>(F. nigra, O. virginiana)</em></td>
<td>Leaf macrofossils, fruit macrofossil <em>(L. tulipifera)</em></td>
<td>Fruit and Seed Macrofossils</td>
</tr>
<tr>
<td><strong>Location</strong></td>
<td>West Branch of the Little Conestoga Creek, Lancaster Co., PA</td>
<td>White Clay Creek, Chester Co., PA</td>
<td>Big Spring Run, Lancaster Co., PA</td>
</tr>
<tr>
<td><strong>Age</strong></td>
<td>113 to 295 Cal BP</td>
<td>217 to 368 Cal BP</td>
<td>690 to 3200 Cal BP</td>
</tr>
<tr>
<td><strong>Herbaceous Species</strong></td>
<td>Remnant herbaceous material recovered but none identified</td>
<td>Remnant herbaceous material recovered but none identified</td>
<td><em>Carex stricta, C. crinita, C. stipata, Polygonum spp., Eleocharis spp., Scirpus spp., Najas flexilis, Brasenia scherberi</em></td>
</tr>
<tr>
<td><strong>Woody Species</strong></td>
<td><em>Fagus grandifolia,</em> <em>Quercus subgenus</em> Quercus, <em>Quercus subgenus Lobatae,</em> <em>Betula spp., Ostrya virginiana,</em> <em>Fraxinus nigra,</em> <em>Acer rubrum,</em> <em>Acer spicatum,</em> <em>Castanea dentata,</em> <em>Platanus occidentalis,</em> <em>Salix sp.</em></td>
<td><em>Acer rubrum,</em> <em>A. negundo,</em> <em>Alnus serrulata,</em> <em>Salix spp., Fagus grandifolia,</em> <em>Quercus subgenus Quercus,</em> <em>Quercus subgenus Lobatae,</em> <em>Liriodendron tulipifera</em></td>
<td><em>Liriodendron tulipifera</em> <em>Juglans cinerea</em></td>
</tr>
<tr>
<td><strong>Community Type</strong></td>
<td>Rich red oak-mixed hardwood forest and red maple-black ash forested swamp</td>
<td>Potential red maple-black ash forested palustrine swamp</td>
<td>Palustrine wet meadow wetland with herbaceous obligate emergent species and adjacent upland community</td>
</tr>
</tbody>
</table>

**Table 5.** Comparison of the White Clay Creek flora (Miller, 2011) and the Big Spring Run flora (Voli et al., 2009) with the Denlingers Mill subfossil flora.
Betula spp., Quercus spp. and Salix spp. (Fike, 1999), all of which are also found in the subfossil assemblage at DM (Table 5).

Big Spring Run and White Clay Creek are in close proximity to Denlingers Mill, and are also located in areas highly influenced by milldams. Both locations now support altered, incised, single-channel streams lined by weedy vegetation, opposed to the many small anabranching channels bordered by hydrophytic trees, shrubs, and sedges hypothesized to have prevailed in the past. The results of these two studies have species in common, such as L. tulipifera, but come from neighboring counties, suggesting that these two associated pre-settlement communities are not isolated occurrences, but are instead regionally widespread.

Integrating the results from all three sites, I propose that the pre-settlement landscape consisted of three distinct communities, but with a continuum of overlapping species. The pre-settlement landscape would have transitioned from saturated wetlands with obligate emergent species occupying valley-bottoms into bordering maple and ash swamp forests, finally transitioning into oak and beech-dominated mixed hardwood forests on valley slopes and other upland areas. This landscape model is represented on the modified diagram of a palustrine and upland setting from Cowardin (1979) below. Consequently, even though the red oak-mixed hardwood forest type assigned to the subfossil assemblage from Denlingers Mill does exclude A. spicatum, C. dentata, and P. occidentalis, it is possible that these species represent a different community association not found today, or nearby pre-settlement communities that have not yet been investigated. For instance, Acer negundo, found at White Clay Creek, and Platanus occidentalis, found at DM, frequently occur together on contemporary floodplains, as evidenced in the modern forest at DM (Fike, 1999; Westervelt et al., 2006). Therefore, even though these two species were found at different fossil sites, the
association of the two may represent an alternative floodplain community other than those described here.

Figure 17. Diagram of palustrine and upland vegetation in proximity to stream base level, illustrating a potential model of the pre-settlement landscape interpreted using plant macrofossils from 3 sites around SE Pennsylvania. (A) Palustrine persistent emergent wetlands with tussock sedge vegetation as described in Voli et al., (2009). (B) Red maple-Black ash deciduous swamp forest described in Miller (2011) and here. (C) Slope and upland communities interpreted from the Denlingers Mill subfossil assemblage representing a potential red oak-beech mixed hardwood forest dominated by *Quercus* spp., *F. grandifolia*, and *A. rubrum*. The highlighted box represents an area in which all species found in the subfossil assemblage at Denlingers Mill could potentially occur. Modified from Cowardin (1979), not to scale.
iii. Implications for Restoration

As discussed above, the pre-settlement landscape consisted of low, frequently inundated floodplains with riparian vegetation capable of reaching the water table. As continued sediment deposition in streams and on floodplains caused base level rise throughout the Piedmont region, it became increasingly difficult for this historic vegetation to access the water table, thereby causing a regional shift from predominantly valley-bottom vegetation to a weedy assemblage capable of surviving on the xeric legacy sediments (Walter and Merritts, 2008). Current restoration methods include legacy sediment removal with an assumption that at least some buried seeds are still viable and will germinate, thereby initiating the creation of a natural riparian buffer (Marris, 2008; Gutshall and Oberholtzer, 2011). Floodplain reconnection projects at Lilitz Run in Lancaster County, for example, have demonstrated that buried seeds from historical native vegetation can sprout after exposure of the pre-settlement hydric wetland soils (Blankenship, 2007; Gutshall and Oberholtzer, 2011 courtesy of LandStudies Inc.). Even though this is a successful technique for the natural exclusion of invasives, such as purple loosestrife and multiflora rose, it so far has resulted in a purely herbaceous buffer, excluding hardwood trees.

Successful restoration entailing the reestablishment of stream-accessible floodplains, the creation of a self-sustaining riparian buffer flora, and subsequent reduced erosion and nutrient loading downstream necessitates a basic understanding of the pre-European settlement plant communities. A native and functional riparian flora could consist of *Acer rubrum*, *Fraxinus nigra*, *Platanus occidentalis*, and *Salix* spp., and would ideally be planted on floodplains along with the native herbaceous wetland taxa described by Voli et al., (2009).
Additionally, to replicate the pre-settlement environment as closely as possible, an appropriate native upland assemblage planted on the surrounding slopes could consist of *Fagus grandifolia*, species of red and white oak (*Quercus* spp.), *Betula lenta*, *Ostrya virginiana*, *Acer spicatum*, and *Liriodendron tulipifera* as described in Miller (2011). Ultimately, the floral communities described here can be used to aid stream restoration regarding the re-establishment of wetland, riparian, and upland communities along Piedmont reaches. Furthermore, increased restoration success is not only ecologically advantageous; it is also economically beneficial considering that restoration often costs hundreds of thousands of dollars per stream mile (Blankenship, 2007).
VI. CONCLUSIONS

The pre-settlement flora from DM is a diverse mix of species ranging from herbaceous wetland plants to hydrophytic and upper slope woody taxa, and contains representative species from at least three different communities. These communities grade from valley-bottom wetlands represented by remnant herbaceous material, to transitional wetland and riparian floodplain communities represented by *Acer rubrum*, *Fraxinus nigra*, *Platanus occidentalis*, and *Salix* spp., into a facultative upland slope community dominated by *Fagus grandifolia*, *Quercus* spp., and *Betula lenta*. Minor upland community constituents include *Acer spicatum*, *Castanea dentata*, and *Ostrya virginiana*. Although the riparian and upland forest at Denlingers Mill today has some species in common with the subfossil assemblage, including various *Quercus* spp., *Fagus grandifolia*, *Betula lenta*, and *Platanus occidentalis*, the modern forest at this site is dominated by *Acer negundo* and *Acer saccharum*, which are characteristically disturbance and successional species. Incorporating all the aforementioned woody species into interpretations of the pre-settlement communities can help refine and enhance our understanding of a past complex and dynamic landscape. Leaf deposits contain data not available from other macrofossil sources, especially in revealing local signals, and should therefore be used in tandem with all available data sources in order to facilitate a more accurate paleoecological reconstruction.

Stream restoration efforts in the Piedmont have shown limited success when the effects of historical sediments are not considered (Gutshall and Oberholtzer, 2011). Effective restoration techniques, such as legacy sediment removal and the reconnection of streams with their floodplains and the groundwater supply, have the potential to significantly improve
Piedmont stream function. An increasingly accurate and comprehensive view of historic plant communities throughout the region has important implications for restoration because riparian plant assemblages affect fluvial hydrology, geomorphology (Richardson et al., 2007), and channel bank stability (Doyle et al., 2005). Additionally, a functional riparian buffer provides many positive ecological and economic benefits including decreased sediment and nutrient loading, increased groundwater recharge, and increased healthy habitat for important stream and wetland biota.
REFERENCES CITED


Comparison of multiple proxy records of Holocene environments in Midwestern USA.  
*Geology.* 26: 1131-1134.


The Earth and Environmental Systems Institute of Pennsylvania State University, University Park, PA 16801, USA.

Barton, Harold, R., Unknown. Mills and Bridges of Lancaster County, PA. Lancaster County Historical Society. (Compiled in Merritts and Walter, 2003).

*Paleobiology.* 26: 103-147.


Blankenship, K. 2007. Restorers banking on reconnecting streams to their flood plains.

Boesch D.F., Brinsfield, R. B., Magnien, R.E. 2001. Chesapeake Bay eutrophication:
   Scientific understanding, ecosystem restoration, and challenges for agriculture.
   *Journal of Environmental Quality* 30: 303-320.

Boynton W.R., Garber, J.H., Summers. R., Kemp, W.M. 1995. Inputs, transformations and
   transport of Nitrogen and Phosphorus in Chesapeake Bay and selected tributaries.

   Communities in Leaf Litter: Implications for Autochthonous Litter Assemblages from
   the Fossil Record. *Paleobiology* 18: 30-49.


Chumbley, C.A. 1989. Late-glacial and Holocene vegetation of the Roberts Creek Basin, northeast Iowa. Ph.D. dissertation University of Iowa, Iowa City, IA.


Cowardin, L. M., V. Carter, F. C. Golet, E. T. LaRoe. 1979. Classification of wetlands and


Gottschalk, L.C. 1945. Effects of soil erosion on navigation in Upper Chesapeake Bay. 

*Geographical Review* 35: 219-238.


Hilgartner, W.B., Brush, G.S. 2006. Prehistoric habitat instability and post-settlement habitat change in a Chesapeake Bay freshwater tidal wetland, USA. *The Holocene*. 16: 479-494.


APPENDIX

All Subfossil Samples from DM

<table>
<thead>
<tr>
<th>Species ID</th>
<th>Sample #</th>
</tr>
</thead>
<tbody>
<tr>
<td>Identified Samples:</td>
<td></td>
</tr>
<tr>
<td><em>Salix sp.</em></td>
<td>DM33</td>
</tr>
<tr>
<td><em>Acer spicatum</em></td>
<td>DM9</td>
</tr>
<tr>
<td><em>Acer rubrum</em></td>
<td>DM32, DM5, DM13</td>
</tr>
<tr>
<td><em>Platanus occidentalis</em></td>
<td>DM42</td>
</tr>
<tr>
<td><em>Fraxinus nigra</em></td>
<td>DM8 (samara)</td>
</tr>
<tr>
<td><em>Quercus cf. alba</em></td>
<td>DM26, DM27, DM15, DM29, DM36, DM37, DM38, DM39</td>
</tr>
<tr>
<td><em>Quercus subgenus Lobatae</em></td>
<td>DM14, DM91, DM99, DM22, DM28, DM92, DM77, DM78, DM20, DM90</td>
</tr>
</tbody>
</table>
DM80
DM89
DM102
DM94
DM105
DM107
DM17
DM23
DM30
DM79
DM81
DM82
DM83
DM84
DM85
DM86
DM87
DM88
DM93
DM95
DM96
DM97
DM98
DM100
DM101
DM103
DM104
DM106
DM108 (acorn)

*Castanea dentata*  
DM6

*Fagus grandifolia*  
DM1
DM50
DM48
DM21
DM25
DM31
DM44
DM45
DM46
DM47
DM49
Betula lenta

DM2
DM3
DM4
DM11
DM12
DM16
DM18
DM19
DM64
DM65
DM66
DM67
DM68
DM69
DM70

Ostrya virginiana

DM40
DM63
DM7 (seed)

Unidentified samples and fragments:

DM10
DM24
DM35
DM34
DM62
DM71
DM72
DM73
DM74
DM75
DM76
DM41
DM43
DM109
DM110
DM111
DM112
DM113
DM114
DM115
DM116
DM117
DM118
DM119
DM120
DM121
DM122
DM123
DM124
DMP1
DMP2