Chapter 1

Paleoenvironmental significance of late Pleistocene terrestrial gastropods in the Upper Mississippi Valley of Wisconsin and Minnesota

1.1 INTRODUCTION

Fossils have always been an important proxy in Quaternary paleoenvironmental reconstruction. Most late Pleistocene species are still alive today, and they are among the most direct means of environmental interpretation. Some of the most pressing questions related to Quaternary paleoecology involve the nature of biotic response to abrupt climate change and the factors that contribute to North American fossil assemblages. The limited range of gastropod movement makes them valuable indicators of local climatic conditions and depositional settings (Miller and Bajc, 1990; Goodfriend, 1992; Rossignol, 2004). This is especially important in unique depositional settings, or regions where past environmental gradients were much steeper (e.g. Oches et al., 1996; Schwert, 1997). For example, terrestrial gastropod fossils preserved in loess were instrumental to Shimek's (1896; 1898) argument for an eolian rather than aquatic origin for loess in Iowa.

The sediments within the Upper Mississippi Valley (UMV) in Minnesota and Wisconsin contain an abundant yet overlooked fossil gastropod fauna. Gastropod shells are often the only organic material preserved in these oxidized sediments. They have been used for radiocarbon age estimates of important depositional events, but no recent systematic treatment of this fauna exists. The report by Chamberlin and Salisbury (1885) was the last survey of this fauna (Table 1.1; Figure 1.1). Gastropod fossils have the potential to provide insight into the environmental conditions present in the UMV during and immediately following the last glacial maximum.

The goal of this dissertation is to determine the potential utility of terrestrial gastropod fossils and use them to reconstruct the late Pleistocene environment within the UMV during the last "full-glacial" period (ca. 24,000 – 18,000 cal yr BP; all dates discussed in this thesis are in calibrated calendar years unless otherwise noted). By incorporating descriptive methods such as lithofacies description with quantitative analyses including amino acid racemization and multivariate statistics, I hope to provide the "groundwork" necessary to form a more detailed understanding of the paleoenvironments in the UMV based on terrestrial gastropod fossils.

1.2 PREVIOUS WORK AND RATIONALE

Péwé (1983) used the term "periglacial" to describe an environment with demonstrated evidence of non-glacial processes and features of cold. This periglacial environment covers approximately 20% of the global land surface today, but was much more widespread during glacial periods (Péwé, 1983). Geomorphic evidence such as ice-wedge casts, patterned ground, solifluction rubble, and block streams show the influence of permafrost on the landscape throughout the Driftless Area between 24,000 and 14,000 cal yr BP (Clayton et al., 2001). Permafrost developed as far south as 38°30' N in Illinois between 25,000 and 18,000 cal yr BP (Johnson, 1990). Permafrost would have hindered the growth of forests, and therefore suggests a predominantly tundra environment (Péwé, 1983). However, the insolation at mid latitudes during the last full-glacial period was greater than that near the poles. Climate patterns such as precipitation and the distribution of continuous, versus discontinuous permafrost was likely much different in the UMV at this time (Péwé, 1983).

The timing and controls on sediment deposition within the UMV have been attributed to climatically driven changes in sediment supply: mass wasting and valley aggradation during the full-glacial period, followed by late-glacial floodplain incision by draining proglacial lakes and cessation of hillslope sedimentation (Flock, 1983; Knox, 1996; Mason and Knox, 1997; Bettis et al. 2008). In contrast, Black (1969) argued for significant Holocene hillslope activity; colluvial deposits along hillslopes were not relict features from periglacial conditions.

Incision of the late Pleistocene UMV floodplain formed the Savanna Terrace, a prominent terrace surface throughout much of the study region (Flock, 1983). Relatively few radiocarbon dates have been reported from below this terrace surface in Minnesota or Wisconsin and the exact timing of this event is poorly constrained (Knox, 1996). Flock (1983) suggested the incision that formed the Savanna Terrace was a result of catastrophic drainage from glacial Lake Agassiz ca. 13,000 cal yr BP. More recent analysis, however, indicates that the initial incision was characterized by cut and fill deposits beginning much earlier, perhaps by approximately 16,500 cal yr BP (e.g. Knox, 2003; Betis et al., 2008; Loope, 2008).

An understanding of the nature and timing of depositional events within the UMV is essential to place the terrestrial gastropod fauna into a preliminary temporal context. Full-glacial, late-glacial, Holocene, or even completely mixed gastropod assemblages may have been preserved within the UMV sediments depending on when these sediments were deposited. The alluvial and colluvial architecture of the UMV will aid in designing sampling strategies for future, high-resolution paleoenvironmental studies.

Amino acid racemization (AAR) is the study of the introconversion of biologically produced L-amino acids to their D-isomeric configuration. The rate of racemization is time and temperature dependent and is generally used as a relative-dating tool or calibrated using other numerical dating techniques. AAR is applicable to many different types of fossils and stratigraphic problems (e.g. correlations and reworking). Development of analysis using high-performance liquid chromatography has enabled an increase in temporal resolution and reduction in sample size requirements compared to previous methods (see Kaufman and Manley, 1998). If a specimen's age can be independently estimated, AAR is often used for paleothermometry studies (e.g. Oches et al., 1996; Kaufman, 2000). It is also a cost-effective method for dating the many specimens needed for time-averaging studies (e.g. Carroll et al., 2003; Yanes et al., 2007). However, the methods necessary to assess the quality of AAR data and identify spurious results are not well developed. Thus, before the gastropod fossils in the UMV can be used for detailed chronologic, taphonomic, or paleothermometry studies, the sources of error and uncertainty (e.g. age-mixing and contamination) need to be assessed.

In addition to the aforementioned lack of study of Wisconsin gastropods, there are relatively few full-glacial biotic sites within the UMV. Faunas from Elkader and Conklin Quarry in Iowa contain a rich assemblage of tundra and boreal forest taxa (Baker et al., 1986; Woodman et al., 1996). These authors suggested that the fauna was indicative of an environment dominated by open ground near the limit for tree growth with topographically controlled areas of stunted boreal forest vegetation. In addition, Jore-1 in southeastern Minnesota contained numerous well-preserved plant macrofossils of tundra plants (Baker et al., 1999). In contrast, the microvertebrate fauna from Moscow Fissure in southwestern Wisconsin was dominated by boreal taxa and contained few tundra dwelling species (Foley, 1984). The gastropods were not identified to the species level, but the genera that were reported, like the vertebrates, are those that are found within Boreal and Eastern deciduous forest habitats today. Foley (1984) suggested the topography of southwestern Wisconsin provided suitable conditions to support a diverse and comparatively temperate vertebrate fauna.

1.3 TERRESTRIAL GASTROPODS AS ENVIRONMENTAL PROXIES

Most gastropod species that occur as late Pleistocene fossils can be referred to extant species; however, identification of the fossil organisms is limited to their hard shells (Miller and Bajc, 1990). In general, the taxonomic assumptions based on hard parts is reasonable for most taxa, because shells of living snails can be identified to species based on their hard parts (Pilsbry, 1948; Burch, 1962; La Rocque, 1970; Miller and Bajc, 1990). However, some taxa cannot be attributed to species (or in some cases even to genus) based on hard parts and require genetic or soft tissue dissection (Miller and Bajc, 1990).

Such a problem exists for succineid gastropods, whose taxonomic identification often requires the study of their genitalia (e.g. Pilsbry, 1948). The phenotypic ambiguity of this group has likely resulted in an overestimation of their fossil diversity. I recognize two distinct morphotypes of succineid shells in the study region. I designate "*Succinea* cf. *bakeri*" as representing large (length > 1 cm), ovate succineids whose aperatural height is more than twice the apertural width and a body whorl that accounts for more than 90% of the total size of the shell. "*Catinella* cf. *gelida*" refers to the smaller form (length $\geq$ 0.5 cm) with an apertural height less than twice the width and a body whorl that accounts for about 75-50% of the total length of the shell (see Chapter 3). These distinctions can be observed in deposits that contain both morphotypes, and are similar to those species described by Baker et al. (1986) and Woodman et al. (1996) in full-glacial gastropod assemblages from Iowa. The taxonomy used for this dissertation follows Turgeon et al. (1997) with suggestions by Hubricht (1985), Barthel and Nekola (2000), and Nekola (2003, 2004).

Our knowledge regarding the distribution and abundance of modern land snails necessarily forms the basis of paleoenvironmental interpretation (Goodfriend, 1992; Lowe and Walker, 1997). This uniformitarian approach has limitations, since it assumes that no evolutionary change has occurred: their environmental requirements have remained constant. However, because abundance is linked to environmental factors, there are likely selective pressures acting on these populations. Therefore long-term evolutionary trends that are not directly connected to environmental factors can also occur (Goodfriend, 1992). In the Quaternary, environmental instability has been thought to encourage stability in faunal groups such as beetles (e.g. Ashworth, 2001) and gastropods (e.g. Miller and Bajc, 1990). Nekola (2003) noted that gastropods presented an interesting paradox: at large spatial scales, terrestrial gastropods appeared to act as specialists, but generalists at small scales.

Another problem related to this uniformitarian approach to environmental reconstruction can arise if the relationship between organisms and environmental variables has no direct modern analog. For example, changes in Earth's climate parameters will result in different relationships between the mean annual and mean seasonal temperatures (Kutzbach, 1981). Thus modern faunal environmental associations may not allow for a direct comparison of fossil assemblages.

The concept of a "non-analog" fauna has been observed for many fossil groups including plants (Overpeck et al., 1993), vertebrates (Graham and Meade, 1987; Semken, 1988), beetles (Ashworth, 1996), and gastropods (Goodfriend, 1989; Miller et al., 1994). These have been variously described as disharmonious (Semken, 1988), intermingled (Graham, 1985), extraprovincial (Roy et al., 1995), and allopatric (Webb et al., 2004). These terms are generally too ambiguous, or have specific evolutionary meaning (e.g. allopatric); therefore I refer to stratigraphically associated taxa whose extant species do not currently live together as non-analog (*sensu* Graham and Mead, 1987).

Another problem related to gastropod paleoecology is the limited knowledge of many species' current distributions (Hubricht, 1985; Goodfriend, 1992; Jass, 2004). For example, Nekola (2009) suggested that the ranges for most species in the genus *Vertigo* were more widespread than previously thought. This lack of knowledge is especially evident in the upper Midwest in Minnesota, Wisconsin, and Iowa (Hubricht, 1985; Jass, 2004).

Despite these issues, there are well-documented patterns in late Pleistocene gastropod biogeography. Many glacial fossil assemblages consist of taxa whose ranges are currently centered over the Rocky Mountains or north in the Canadian Taiga and Tundra regions. These ranges have been described as Rocky Mountain and Northern (Baker et al., 1986; Frest and Dickson, 1986; Woodman, 1996), Cordilleran-Boreal

(Wells and Stewart, 1987). Burch (1962) referred to these, respectively, as Western and Northern. Frest and Fay (1980) proposed the “Midwest Biome” to describe the unique fossil land snail associations found in Iowa. This assemblage consisted of Cordilleran-Boreal (e.g. *Vertigo hannai*) and Eastern Deciduous Forest taxa (e.g. *Hendersonia occulta*). Some of these taxa, (e.g. *H. occulta*, *Catinella gelida*) exist in the UMV as relict populations, and others (e.g. Succinea bakeri) are thought to be extinct (Frest and Dickson, 1986).

For the purposes of this dissertation, I refer to gastropods whose range extends West through the Rocky Mountains at high elevations and north into the Taiga and Tundra as “Cordilleran-Boreal,” while gastropods whose range is associated with deciduous forests, especially east of the Mississippi River are described as “Eastern Deciduous Forest.” These labels do not account for all the individual variations, but they sufficiently separate the distribution patterns observed in fossil land snail assemblages throughout the Midwest (e.g. Leonard, 1950, 1952; Bequart and Miller, 1973; Wells and Stewart, 1987).

Terrestrial gastropods offer a wealth of untapped paleoenvironmental information. Their shells can be directly dated with radiocarbon and amino acid racemization analyses, making it possible to objectively study problems with transport and mixing. Paleoenvironmental reconstruction is further enhanced when combined with additional independent lines of evidence such as sedimentary structures and facies patterns. The gastropod fossils recovered from the sites discovered during this research were deposited in a unique periglacial environment; the abundance of taxa preserved in these sediments is a function of both ecological and sedimentary mechanisms. This paleoenvironment can be more readily interpreted by integrating analytical and sedimentological techniques.

1.4 PROJECT DESCRIPTION

A detailed paleoenvironmental study of the UMV gastropod fauna provides the opportunity to test hypotheses related to the habitats found within the region. By first establishing a depositional and chronologic framework, it will be possible to compare the habitat preferences of the gastropod faunas in Minnesota and Wisconsin to those from previous studies. The concept of a cold, tundra-vegetated environment throughout the UMV has been well documented by previous authors (e.g. Birks, 1976; Baker et al., 1986; Woodman et al., 1996; Baker et al., 1999). The fossils described in this thesis offer the opportunity to examine this interpretation in greater detail.

This dissertation consists of three primary research chapters. Each chapter is presented as a manuscript intended for publication. Chapter Two is a description of the sedimentology, stratigraphy, and chronology of fossiliferous sediments from selected sites in the UMV. This provides a chronologic and depositional framework for the gastropod assemblages. Chapter Three presents the results of AAR analysis in order to characterize the age relationships between individual shells from two sites. These AAR data are analyzed with a combination of univariate and multivariate statistical methods to determine potential sources of error and uncertainty that might affect the AAR results (e.g. age mixing, amino acid diagenesis, etc.). Chapter Four utilizes the insights gained earlier to interpret the paleoenvironmental significance of shells recovered from the two northernmost gastropod fossil localities in the midwest. This reconstruction is based on modern gastropod autecology and standard statistical analysis and a new application for a multivariate comparison method, MRPP (multi-response permutation procedure; McCune and Grace, 2002). Chapter Five provides a summary of the results from the previous chapters and suggests avenues for future work. Some of the results from this suggested work are briefly described within the appendices along with supplementary data.

The aim of this dissertation is to provide a link between earlier paleoecological studies from throughout North America and future research. This project will contribute significantly to our understanding of the late Pleistocene environment and provide a historical perspective to understand the factors that influence the distribution of gastropods today. All specimens referenced in this dissertation are in the collections of the Department of Geology and Geophysics, University of Wisconsin-Madison, under the file number UW1987. A reference that describes the Sample Field numbers and their corresponding UW catalog numbers is provided in Appendix E.

Gastropod taxa repored by Chamberlin and Salisbury (1885, p. 286)

Site Description	Taxa	Remarks
Grant County:		
Sw1/4 Sec26 Bloomington	*Succinea avara* SAY	*S. avara* = *Catinella avara*; morphologically similar to *Catinella* cf. *gelida*
Sec34 Ellenton TWP	*S. avara* SAY	No record of any "Ellenton" township in WI: may be Ellenboro
Terrace along Platte R.	*Succinea obliqua* SAY *Pupa muscorum* LINN	*S. obliqua* may by synonymous with *Succinea ovalis*; morphologically similar to *Succinea* cf. *bakeri; Pupa muscorum* = *Pupilla muscorum*
Crawford County:		
East of Prairie du Chein, 425' above Mississippi R.	*S. avara* SAY *Lymnophysa humilis* SAY	*Lymnophysa humilis* = *Fossaria humilis*, an aquatic species.
Higher Terraces at Bridgeport	*S. avara* SAY *L. humilis* SAY *Patula striatella* ANTHONY *Vertigo simplex* GOULD	*P. striatella* = *Discus whitneyi*; *V. simplex* = *Columella simplex*

Table 1.1. Sites and gastropod taxa described by Chamberlin and Salisbury (1885).

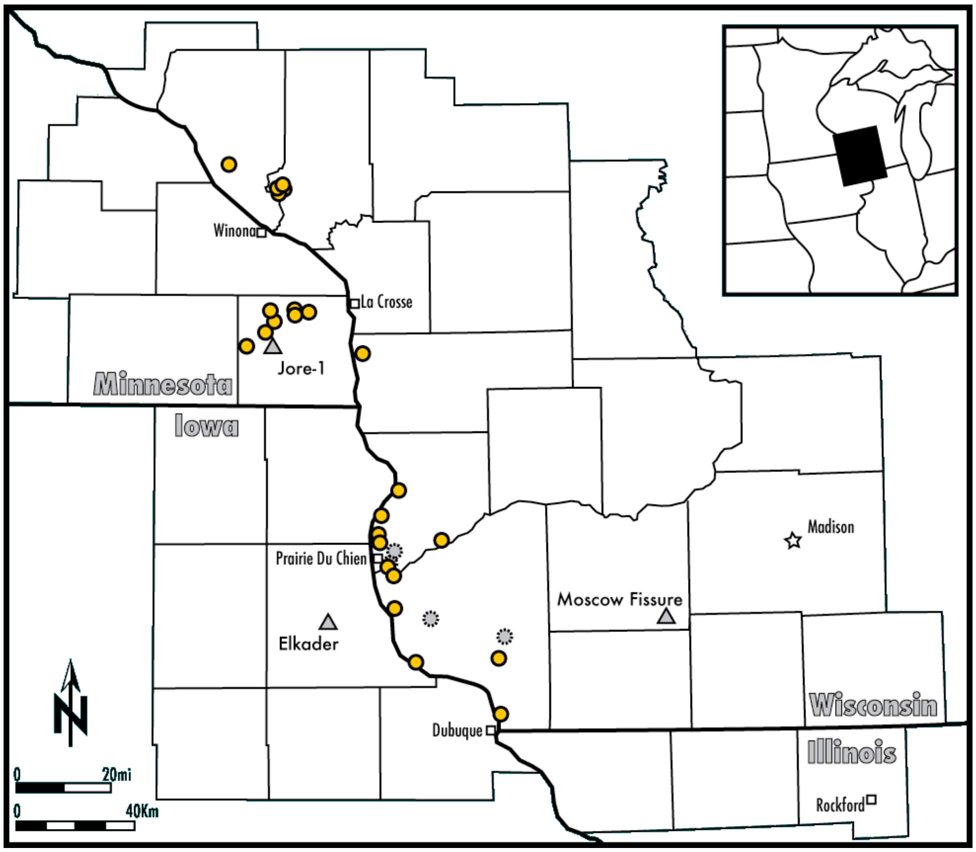

Figure 1.1. Map of study region showing gastropod localities discovered during field surveys for this dissertation (yellow dots). Gray dots represent original Chamberlain and Salisbury (1906) locations. Gray triangles represent important full-glacial fossil localities discussed in the text.