

**THE PALEOENVIRONMENTAL SIGNIFICANCE OF TERRESTRIAL
GASTROPOD FOSSILS FROM THE UPPER MISSISSIPPI VALLEY IN
MINNESOTA AND WISCONSIN**

by

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Terrestrial gastropod shells are common fossils within late Pleistocene sediments from the Upper Mississippi Valley (UMV) of southwestern Wisconsin and southeastern Minnesota. This thesis represents the first systematic study of the regional gastropod fauna since Chamberlin and Salisbury (1885). Results presented here provide a foundation for understanding the environmental and depositional factors affecting gastropod fossil abundance. Chapter One outlines the goals of this thesis and summarizes the important paleoenvironmental questions. Chapter Two provides a sedimentary and stratigraphic context through description of the depositional and architectural relationships of field exposures of Pleistocene deposits. Data presented here support the view that mass wasting and valley aggradation were active between 24,000 and 17,000 cal yr BP. The timing and lithology of structures and sediments related to floodplain incision do not correspond to known floods from Glacial Lake Agassiz; incision may have resulted from earlier Lake Superior Basin flood events. Chapter Three presents results of amino acid racemization analyses of 236 terrestrial gastropod shells. Shells that

are more weathered in appearance belong to Cordilleran-Boreal taxa and exhibit D/L Asp values characteristic of late Pleistocene age shells. The less-weathered shells of rare Eastern Deciduous Forest taxa exhibit D/L Asp values suggesting that these shells were introduced into the assemblage after its deposition. The small variance in succineid AAR data in conjunction with well-constrained ^{14}C ages indicate minimal time averaging (<1000 years) in these deposits. Variance within the data set may result from leaching, heat alteration, or contamination from bacteria. These results have significant implications for future gastropod-based amino acid geochronologic studies. Chapter Four is a paleoecological analyses of collections from Kulas Quarry and Hwy-JJ in Trempealeau County, Wisconsin. Most taxa from these sites have modern Cordilleran-Boreal ranges. Kulas Quarry (floodplain) samples include a larger number of rare species than do samples from Hwy-JJ (upslope). Overall similarities in gastropod rank abundance among samples suggest that the community remained stable between 21,700 and 20,000 cal yr Bp. These results indicate a tundra-like environment with minor amounts of deciduous vegetation within topographically controlled microhabitats. Chapter Five summarizes all results and provides suggestions for future work.

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; Bettis 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 interconversion 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 apertural 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 ≥ 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 reported by Chamberlin and Salisbury (1885, p. 286)

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

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

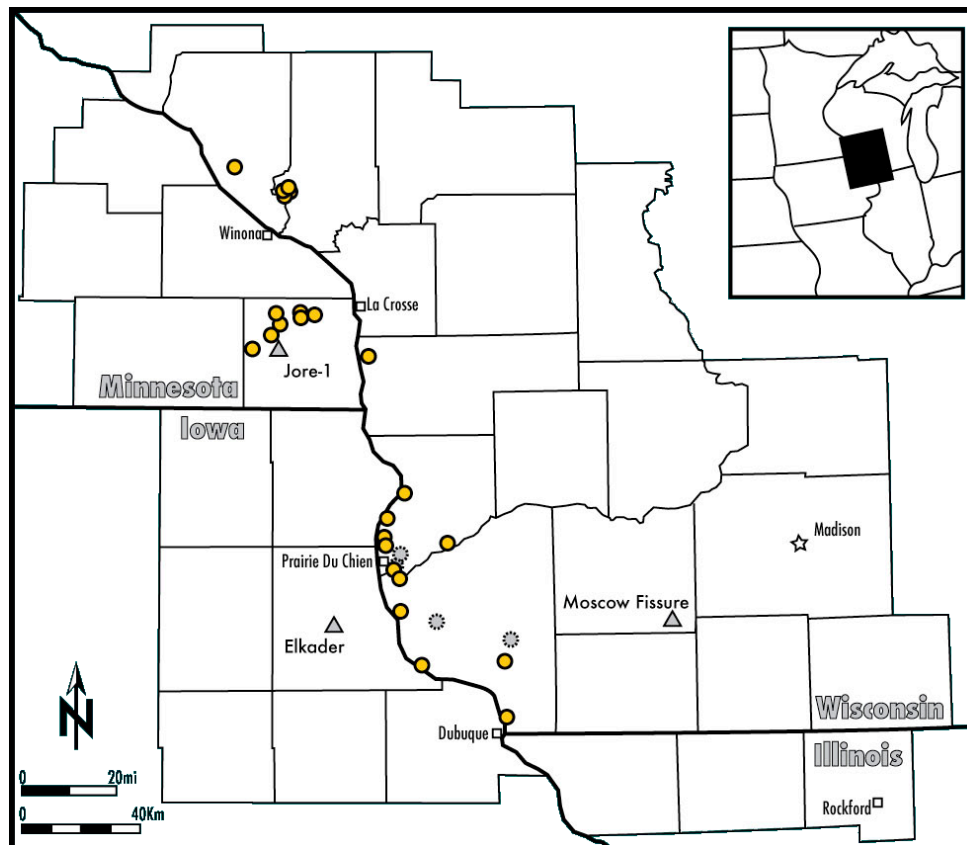


Figure 1.1. Map of study region showing gastropod localities discovered during field surveys for this dissertation (yellow dots). Gray dots represent original Chamberlain and Salisbury (1906) locations. Gray triangles represent important full-glacial fossil localities discussed in the text.

Chapter 2

Sedimentology, chronostratigraphy, and facies relationships of fossiliferous sediments in the Upper Mississippi Valley, Minnesota and Wisconsin

ABSTRACT

Several distinct, fossiliferous lithofacies are preserved within the Upper Mississippi Valley (UMV). These sediments show that several periglacial depositional mechanisms were active in this region throughout the late Pleistocene (ca. 24,000 to 16,000 cal. yr BP). Terrestrial gastropod shells are the most common fossils preserved in these sediments, but they have largely been overlooked for paleontological study. This paper describes the stratigraphic and chronologic relationships of ten fossiliferous outcrops in the UMV. The goals of this research are to: characterize fossiliferous lithofacies in the UMV, determine spatial and temporal relationships between outcrops, correlate these exposures to regional events, interpret the paleoenvironment around each site, and provide a brief report on the types of fossils commonly preserved within each section. This study will provide important context for future analyses (e.g. taphonomy) of these fossils. The typical distribution of lithofacies consists of clast- and matrix-supported diamictons along hillslopes that grade into laminated silts along the edges of the river valleys. Coarse, sandy lithofacies are commonly distributed closer to the valley axis. Radiocarbon data suggest that aggradation within river valleys was most active until about 19,000 cal. yr BP, and that hillslopes were active until at least 16,000 cal. yr BP. One site (Hideaway Lane) contained upstream dipping foresets and clay rip-up clasts characteristic of backflooding from the Mississippi River. The depth of erosion, sedimentary texture and composition are similar to backflooding deposits found elsewhere in the region. Ages from the Hideaway Lane exposure backflooding deposit do not correspond to known outburst flood events from upstream proglacial lakes. However, based on the timing (ca. 16,100 cal. yr BP) and lithology (red lacustrine clay), these may reflect drainage from either one or both of Glacial Lakes Lind and Duluth. Terrestrial gastropods were recovered from all lithofacies and were the most abundant fossils, whereas aquatic species were quite rare, comprising less than 5% of the total gastropod fauna. Most sediment was derived from local bedrock, and given the large proportion of terrestrial fossils within alluvium, terrestrial sediment input rather than glaciofluvial material was the dominant source of valley fill. This study provides important chronologic constraint on major aggradational and degradational phases within the UMV and demonstrates the importance of the gastropod fauna. Future paleontological studies in the UMV will need to consider these depositional contexts before attempting high-resolution paleoecological studies.

2.1 INTRODUCTION

Terrestrial gastropod shells are the most common fossils in late Pleistocene sediments throughout the Upper Mississippi Valley (UMV). Despite this, they have been largely overlooked as a tool for paleoenvironmental reconstruction. Previous studies have primarily focused on the geomorphology of the UMV, only using gastropod shells for radiocarbon dating (e.g. Mason and Knox, 1997). The periglacial sediments within the UMV contain a record of wind, gravity, and water-driven processes active during the last full-glacial period (ca. 24,000 to 18,000 cal. yr BP – all dates given as calibrated calendar years before present, unless otherwise noted). A general temporal framework for many of these sedimentary deposits has been developed (Knox, 1996; Mason and Knox, 1997; Bettis et al., 2008); however, the timing of significant episodes of aggradation and degradation of alluvial deposits within the UMV remains unclear (e.g. Knox, 1996; Knox, 2005). In addition, no specific attempts to place these fossil gastropods into a regional chronological and depositional context have been made since Chamberlin and Salisbury (1885). The temporal constraints on the nature of sedimentation in the UMV will determine the nature of the paleobiological data contained within the associated fossil assemblages and provide strategies for future sampling and survey efforts.

This paper describes the temporal and stratigraphic relationships of 10 fossiliferous exposures in the UMV, correlates these sites with regional events, and interprets the environments of deposition at each site. This depositional context will serve as the basis to evaluate the paleontological implications (e.g. taphonomy, paleoecology) of the fossils contained within these deposits. This work also provides important new

radiocarbon and sedimentologic data that constrain the timing of aggradation and degradation within the UMV. The aims of this chapter are threefold: 1) characterize the fossiliferous lithofacies exposed in the UMV, 2) determine the spatial and temporal associations of these lithofacies, and 3) interpret the environments of deposition at each site and correlate them with larger-scale events.

2.2 GEOLOGIC BACKGROUND

The study area is within the Upper Mississippi Valley (UMV) of southeastern Minnesota and Driftless Area of southwestern Wisconsin (Figure 2.1). Unlike much of the rest of Minnesota and Wisconsin, the last glacial advance (ca. 24,000-16,000 cal. yr BP) did not cover this region. However, earlier glacial advances covered southeastern Minnesota whereas the Driftless Area of Wisconsin remained ice-free throughout most or all of the Pleistocene (Mickelson et al., 1983; Hobbs, 1999; Syverson and Colgan, 2004). This unique landscape is characterized by bedrock-controlled topography with deep, narrow river valleys incised into the Paleozoic Plateau of Minnesota, Wisconsin, Iowa and Illinois (Syverson and Colgan, 2004). Based on magnetically reversed silts within the Bridgeport Terrace of the lower Wisconsin River, most of the valleys in the Driftless Area were eroded to their present depth before 780,000 yr BP (Knox and Attig, 1988).

Gently south-southwest dipping Cambrian and Ordovician bedrock underlies the entire region (Ostrom, 1987a, 1987b; Brown, 1988; Runkel, 1994). The oldest Cambrian units are exposed in the northern end of the study region. The oldest exposed section includes the coarse, orange arenitic sandstone of the Wonewoc Formation, which underlies the silty, micaceous, glauconitic sandstones and shales of the Lone Rock

Formation. The remaining Cambrian section, including the St. Lawrence and Jordan Formations, is generally covered. Throughout the UMV, Ordovician dolomites of the lower Prairie du Chien Group (Oneota) crop out as resistant bluff formers. The south end of the study region consists of the Prairie du Chien Group dolomites with occasional outcrops of uppermost Cambrian Jordan Sandstone along the lower reaches of larger valleys.

Along the UMV, ridgetops are covered with a thin mantle of windblown silt (loess), while the steep hillslopes are often covered by colluvium of increasing thickness downslope, where it grades into alluvial valley fill. Late Pleistocene eolian sediment, covers much of the North American Midcontinent. In Nebraska, the Peoria Silt is often more than 20 m thick; in Wisconsin it is only about 0.5-3 m thick (Hole et al., 1968; Leigh and Knox, 1994). Previous researchers have separated this loess deposition into several distinct periods (e.g. Busacca et al., 2004). Deposition of the Peoria Silt, the youngest and best-preserved loess unit in the Driftless Area began about 30,000 cal. yr BP and lasted until approximately 11,000 cal. yr BP (Bettis et al., 2003). Deposition of the Peoria Silt was not continuous, however. Weak paleosols are present in the Peoria Silt in Nebraska, Iowa, Illinois, and Indiana, indicating periods of little or no loess deposition (Ruhe et al., 1971; Bettis et al., 2003).

Thick colluvium covers many of the steep valley sides throughout the region, indicating active mass wasting along slopes. Based on radiocarbon and stratigraphic analyses, mass wasting was most active from 25,000 to 14,000 cal. yr BP as a result of climatically induced mass wasting, probably dominated by solifluction (Mason, 1995; Mason and Knox, 1997). This colluvium consists of reworked eolian silt and clay and

often contains large clasts of weathered bedrock. Along the lower footslopes in the Driftless Area, colluvial deposits often interfinger with alluvial sediments within the river valleys (Mason, 1995; Mason and Knox, 1997). This interpretation conflicts with an earlier proposal by Black (1969) that hillslopes were largely stable throughout the Pleistocene, and that colluvial activity was the result of increased Holocene precipitation. Similarly, Mills and Delcourt (1991) suggested colluvial debris at the base of footslopes in the Appalachian Blue Ridge province were triggered by intense rainfall from increased tropical storm activity in the early Holocene. Colluvial activity would have contributed a large volume of material to the fluvial systems within the UMV, affecting both general sedimentation patterns and the types of fossils preserved in colluvial and alluvial sediments.

Alluvial sedimentation in the UMV is characterized by aggrading braided streams with high sediment bedloads (Knox, 1996). Aggradation within the UMV began by approximately 25,000 cal. yr BP and ended before 13,000 cal. yr BP (Flock, 1983; Knox, 1996). Much of the alluvial sediment is thought to be glaciofluvially derived (Flock, 1983; Knox, 1996). However, in river valleys not directly affected by glacial melt water, much of the valley fill consists of weathered bedrock and reworked silt and clay (Mason, 1995). Bettis and Halberg (1985) characterized the alluvial sediments in eastern Iowa as planar bedded, gray-silty clay and yellow-brown silt with rare red clay beds – a description that also applies to exposures in southeastern Minnesota and southwestern Wisconsin (Knox, 1996).

In many locations, the topmost late Pleistocene alluvial sediments consist of 30-50 cm of red clay and silt, which are interpreted as slackwater deposits from large flood

events. Minor cut-and-fill deposits, characterized by sandy red clay and upstream-dipping foresets, can be seen along many tributaries in Wisconsin (Knox, 1996; Knox 2005). Following this period of valley aggradation, drainage of sediment-poor water from large glacial lakes cut into the late Pleistocene floodplain, creating a system of terraces throughout the UMV. Downcutting was likely completed by about 13,000 cal. yr BP when outburst floods from Glacial Lake Agassiz drained south via the Mississippi River for the last time (Knox, 1996). The highest terrace surface not covered by loess is referred to as the Savanna Terrace (Flock, 1983). This surface can be traced for more than 1,000 km along the length of the UMV from central Wisconsin to southern Illinois and several km upstream into major tributaries. Remnant high terrace surfaces can be followed from the Mississippi River into tributary valleys throughout the study region; therefore, I consider these tributary surfaces as part of the Savanna Terrace (*sensu* Mason, 1995).

2.3 METHODS

2.3.1 Field Methods

The locations discussed in this chapter (Figure 2.2) were discovered during field surveys in 2005 and 2006. I first identified potential outcrops from air photos and topographic maps, and located specific sites by driving systematically along highways looking for exposures of late Pleistocene sediments. I chose sites with abundant gastropod fossils, distinct sedimentary structures, and lithofacies characteristics for detailed study. I also reexamined sites mentioned by Mason (1995), who noted several gastropod-bearing exposures within the Root River Valley of Minnesota.

The location for each site was recorded using a handheld GPS and verified using air photos and digital elevation models available online from the USGS (<http://seamless.usgs.gov>). I also used these online maps to determine elevations of the Savanna Terrace, local tributaries, and Mississippi River near each location. I described a generalized stratigraphic column for each exposure to illustrate the vertical relationships between associated sedimentary lithofacies. In addition, I took photographs to illustrate the geographic context, horizontal relationships, and associations of prominent sedimentary structures. I used the “photomerge” function in Adobe Photoshop ® to assemble composite photographs of larger outcrops. These field observations, previous reports, airphotos, and digital elevation models were used to create an idealized cross section at selected time intervals.

I followed the lithofacies designations described by Miall (1977). This method designates major lithofacies groups with a capital letter followed by a lower case letter indicating unique sedimentary structures or other physical properties: e.g. “Fl” for fine-grained, laminated sediments; “Sp” for sandy, planar bedded sediments, etc. These designations are most often used for describing much older sediments, but are increasingly applied to Quaternary studies (e.g. Mason, 1995). The codes used to designate lithofacies described in this study are explained in Table 2.1.

My strategy was to differentiate between colluvial diamictons, sand-dominated, and silt-dominated lithofacies because they constituted the majority of sediment types in the study region. I subdivided these lithofacies based on associated sedimentary structures, but did not attempt to further differentiate these lithofacies based on smaller scale fabrics. Fine-grained **Silts (F)** contained less than 50% sand-sized grains. **Clays**

were differentiated from silts by their smooth versus gritty texture and plastic behavior.

Sands (S) were well to poorly sorted sediments containing at least 50% sand-sized particles. **Diamictons (D)** were poorly sorted and contained at least 10% pebble-sized or larger clasts (most often dolostone).

2.3.2 Lab Methods

For grain size analysis, I separated selected field samples into smaller ca. 100 g portions using a sample splitter. Clumps were either disaggregated by hand or gently crushed in a mortar and pestle to facilitate dry sieving. I used a sonic sifter and a standard series of sieves to determine the relative proportions of sand (2 mm – 0.063 mm) in each sample. For matrix processed to obtain fossils, I compared the mass of the wet-sieved residuum retained within the largest sieve (>2 mm) to the mass of sample that passed through all sieves (<0.425 mm).

I followed standard wet-sieve methods (e.g. Frest and Dickson, 1986) to recover fossils for analysis. Samples were first air-dried, then soaked for several hours to disaggregate the sediment. This material was washed through a series of ASTM sieves (smallest opening = 0.425 mm). Fossils were picked from the residuum and assigned to taxonomic group (terrestrial and aquatic gastropods, bivalves, fish scales, mammal teeth and bones, and ostracods) as present or absent from each sample/site.

2.3.3 Radiocarbon Analysis

I obtained radiocarbon dates from succineid gastropod shells. Succineid gastropods are abundant in many late Pleistocene deposits, and are often the only organic material available for radiocarbon dating (Pigati et al., 2004). There are two primary sources of error in radiocarbon dates obtained from gastropod shells. The first is

recrystallization of aragonite to calcite, which can yield younger-than-actual ages. This error can be avoided by using shells without visibly recrystallized, “chalky” shell material and by pre-etching the sample in acid before analysis (Goodfriend and Stipp, 1983; Goodfriend and Hood, 1983). The second problem is harder to detect and occurs when the snail ingests ^{14}C -depleted carbonate, which can yield anomalously old radiocarbon ages (Goodfriend and Hood, 1983; Goodfriend and Stipp, 1983, Pigati et al., 2004). Succineid gastropods do not appear to ingest these “old” carbonates, even when in a ^{14}C -depleted carbonate environment (Pigati et al., 2004; J. Rech and J. Nekola personal communication, 2007). Radiocarbon ages were converted to calendar years using the “CalPal” online calibration software (Danzeglocke et al., 2009). Fossil material is cataloged in the University of Wisconsin-Madison Geology Museum under UW1987.

2.4 RESULTS

The data represent 10 sites within the UMV of Minnesota and Wisconsin (Figure 2.2). These sites are located both above and below the Savanna Terrace (Figure 2.3) and consist of both fine- and sandy-grained alluvial sediments and colluvial diamicts and silts (Figure 2.4). The results are presented in the following order: 1) general lithofacies descriptions for all of the sites studied; 2) grainsize characteristics for selected lithofacies; and 3) site-specific data including sedimentology, radiocarbon data, and observed fossils.

2.4.1 *Lithofacies*

The F, S, and D lithofacies observed at each site can be subdivided into individual lithofacies based on primary sedimentary structures (e.g. laminations, cross-bedding). All

sediment samples from this study were calcareous and showed mild to strong effervescence with the addition of dilute HCl. Terrestrial gastropod fossils are preserved within all lithofacies, and were often the only biotic material recovered.

2.4.1.1 Fine-grained lithofacies (F)

Silt-dominated lithofacies in the study region consisted of poorly sorted, calcareous silt and clay with trace amounts of very fine to medium sand and pebble to cobble size clasts of local bedrock. Root traces and rhizcretions were common. Gastropod fossils were generally rare, however some samples contained more than 20 shells per kg.

F1: Laminated silt. This lithofacies was characterized by alternating layers of reddish brown and buff to gray poorly sorted, calcareous silt and clay with occasional fine to medium sand. Root traces, halos, and rhizoconcretions are common. Where this lithofacies contacted bedrock, it often contained weathered, rounded to angular bedrock clasts. The F1 lithofacies was the most common lithofacies encountered below the Savanna Terrace. It also occurred along lower hillslopes above this terrace. Along valley floor margins, the F1 facies often interfingered with hillslope diamictons.

Fc: Convolute silt. This lithofacies can be differentiated from the laminated silts due to prominent soft sediment deformation structures, light gray color, and lack of internal lamination. Convolute and slumped bedding, root casts, and vugs with iron oxide halos were common within this unit. The contact between this and other lithofacies was complex. The Fc unit contained irregular and sometimes overturned beds with apparent load casts or flame structures. Large (5-30 cm) clasts of underlying lithofacies

were often incorporated within the convolute silt. Iron oxide bands were formed around these incorporated sediments.

Fm: Massive silt. Massive silts below the Savanna Terrace surface occur as 10-30 cm thick interbeds within laminated silts. Above the terrace at Big Platte, this massive silt consisted of dark brown silt with minor amounts of sand and angular dolomite bedrock fragments. Gastropod fossils were abundant within this lithofacies. Root traces and rhizcretions are also common. In outcrops, recent animal burrows (usually cliff swallow colonies) were most often found in the massive or thickly bedded silts compared to other sediments.

2.4.1.2 Sandy lithofacies (S)

Sand-dominated lithofacies contained abundant rounded lithic fragments and medium to fine grains of well-rounded quartz, glauconite, and muscovite. The texture and mineralogy of the sandy valley fill was nearly identical in composition to that of the local Cambrian-aged bedrock. The structures associated with these lithofacies were either **planar-bedded** with current and climbing ripples, or **trough-cross bedded** channel and channel fill bedforms. Gastropods were found throughout these lithofacies, especially in trough cross-bedded sands, where individual troughs contained several hundred shells per kg. In some troughs, gastropods formed shell-supported coquina-like beds within foresets.

Sp: Planar-bedded sand. This lithofacies consisted of poorly sorted gray to tan fine quartz sand with planar beds, as well as climbing and current rippled cross beds less than five centimeters in ripple height. It was most prominent at Kulas Quarry where it

occurred in laterally continuous beds up to 1.5 m thick and more than 20 m wide. At other sites below the late Pleistocene terrace surface, thin 5-10 cm beds of the Sp lithofacies were interbedded within the laminated silts.

St: Trough cross-bedded sand. The trough cross-bedded lithofacies were exposed at Kulas Quarry and Hideaway Lane. This lithofacies was characterized by poorly sorted fine to medium grained, brown and tan sand with abundant rounded to well-rounded clasts of local bedrock. Bedrock clasts range in size from granules to cobbles and tabular clay rip-ups were less than 1 cm in diameter. Troughs ranged in size from 10 to 150 cm in height and fined upward from a coarse gravel lag at the base to fine grained sand at the top. Some troughs were filled with current and climbing ripple cross beds, while others were filled with massive fine sand to silt. At Kulas Quarry, the troughs were bound by laterally accreting foresets.

2.4.1.3 Diamict lithofacies (D)

Diamictons were either **clast-supported** or **matrix-supported**. In general, the diamictons were poorly sorted with silty tan to brown matrix and angular, gravel to boulder size clasts of dolomite bedrock. Most large clasts were oriented with the long axis parallel to slope. Gastropod fossils occurred within both lithofacies; other biotic material and root traces were rare or absent. Contacts between diamictons and other lithofacies were approximately parallel to slope. Along slopes near the valley floor, these diamictons interfingered with alluvial sediments and often were lenticular in cross-section.

Dm: Matrix-supported Diamictons. This lithofacies consisted of brown to tan silt with minor amounts of angular bedrock clasts. Bedrock clasts were predominantly

dolomite, with some chert or sandstone, depending on location. This lithofacies was often found well above the Savanna Terrace surface (Figure 2.4). Below the terrace at Root River, the Dm lithofacies was interbedded with the laminated silts. Terrestrial gastropod fossils were common within this unit, and abundance exceeded 100 shells per kg. Occasionally, unbroken gastropod eggs and root traces such as rhizcretions were encountered within this lithofacies.

Dc: Clast-supported Diamictons. Clast-supported diamictons were mineralogically similar to matrix-supported diamictons, but differed in the proportion of large clasts. Fossils and root traces were generally rare within this lithofacies, although gastropod fossils were sometimes preserved within the interstitial matrix of even the coarsest diamictons.

2.4.2 Grain Size Analysis

In addition to the expected differences between sandy and silty sediments, grain size analyses of selected samples showed that the trough cross-bedded sands (St) were coarser than the planar-bedded sands (Sp). The St lithofacies contained a larger proportion of coarse sand and pebble-sized clasts compared to the Sp samples (Figure 2.5). Within silt-dominated sediments, the laminated silt (Fl) lithofacies were similar to one another, while the convolute silt (Fc) lithofacies from Kulas Quarry was finer, and contained a much smaller proportion of sand-sized material.

2.4.3 Sites

The locations of the sites described in this study are shown in Figure 2.2, Figure 2.3 and described in Table 2.2. The radiocarbon age data from each site are shown in Figure 2.4 and summarized in Table 2.3. These sites covered an area approximately 200 km North-South and 50 km East-West. Five sections (Kulas Quarry, Kulas-2, Kulas-1, Hwy-JJ, and JX) were described from the Latch Valley, a small tributary valley of the Trempealeau River. Two sections (Storer Creek and Root River) were described along the Root River in Minnesota. The remaining sections were located along tributary valleys in southern Wisconsin: Coon Creek (Hideaway Lane), Limery Creek (Limery Coulee), and the Platte River (Big Platte). Three of these sites (Hwy-JJ, Limery Coulee, Big Platte) were located along hillslopes above the Savanna Terrace, while the rest were located within the paleo-floodplain at or below this surface (Figure 2.3, Figure 2.4).

2.4.3.1 Kulas Quarry

Kulas Quarry is a large borrow pit approximately 7 m high by 21 m wide, located in the Latch Valley (Figure 2.6A). The top of this exposure correlates with the Savanna Terrace. Much of the Kulas Quarry section consisted of either trough cross-bedded (St) or planar-bedded (Sp) sands (Figure 2.6B). A prominent scour surface is visible along the base of the upper St lithofacies, separating the exposure into two individual fining upward packages of sediment (Figure 2.4; Figure 2.6A). The upper meter consists of laminated silt (Fl) that was weathered down to about 50 cm. Numerous fish scales, vertebrate teeth and post-cranial bones were present throughout the exposure, often within discrete, fossiliferous lenses or as plaster deposits along foreset surfaces within St lithofacies. Terrestrial gastropod shells were abundant; individual samples contained as many as 500 shells per kg of sediment. Aquatic gastropods were present, but much less

common than terrestrial shells. Rare, disarticulated valves of bivalves and ostracods were also recovered. Succineid gastropod shell material (ca. 3 shells of *Catinella* cf. *gelida*) from the trough-bedded sand (KQ-15) 2.75 m below the top of the exposure yielded radiocarbon ages of $16,670 \pm 60$ RCYBP (BETA-223641; $19,929 \pm 295$ cal. yr BP). An additional sample (ca. 3 shells of *Catinella* cf. *gelida*; KQ-05) 4.5 m below the exposure surface yielded an age of $17,550 \pm 70$ RCYBP (BETA-223642; $20,961 \pm 314$ cal. yr BP). Charcoal and additional *Catinella* c.f. *gelida* shells from these two horizons were analyzed by Jason Rech et al. (in prep):

- KQ-15 (depth = 2.75 m)
 - Shell: $16,840 \pm 120$ (AA-83090; $20,059 \pm 296$ cal yr BP)
 - Shell: $16,890 \pm 120$ (AA-83092; $20,122 \pm 288$ cal yr BP)
 - Shell: $17,180 \pm 130$ (AA-83091; $20,617 \pm 330$ cal yr BP)
 - Charcoal: $31,400 \pm 120$ (AA-77831; $35,310 \pm 362$ cal yr BP)
- KQ-05 (depth = 4.5 m)
 - Shell: $17,990 \pm 200$ (AA-82558; $21,673 \pm 448$ cal yr BP)
 - Charcoal: $28,720 \pm 320$ (AA-82587; $33,190 \pm 478$ cal yr BP)

These shells yielded similar dates to those analyzed by Beta Analytic, Inc within the same horizon, however the charcoal is likely reworked, since radiocarbon results from these small wood samples were much older than the shell dates.

2.4.3.2 Kulas-1 and Kulas-2

Kulas-1 and Kulas-2 were located within the Latch Valley, about 500 m downstream from Kulas Quarry (Figure 2.7A). These exposures were less than 250 m apart and are described together. The top of the exposure at Kulas-2 correlated to the Savanna Terrace, while the top of the exposed section at Kulas-1 was approximately 3 m

lower. Both exposures were dominated by laminated silt lithofacies. A few thin beds of planar-bedded sand occurred near the base of Kulas-1. Other root traces such as rhizocretions and root haloes were present at both Kulas-1 and Kulas-2. Numerous 0.5-1 m long vertical cracks were exposed at Kulas-1. These probably represent root traces due to the downturned laminae and bifurcation of these wedge-shaped features (Figure 2.7B). Ice wedges create upturned laminae of the surrounding sediment as the ice expands and forces the sediments upward and outward (e.g. Clayton et al., 2001).

Two 20 cm thick layers of dark brown, clay-rich sediment were present at each site, approximately 1 m below the top of both exposures. These beds were not correlative with each other. Based on the dark color, cementation, clayey texture, and lateral continuity, these horizons may represent weakly developed paleosols or early pedogenic textures. Samples of laminated silt from both Kulas-1 and Kulas-2 contained terrestrial and aquatic gastropod fossils. Interestingly, despite being located along the valley floor, these sections did not contain large channel features or other evidence of active fluvial transport apart from small 5-10 cm thick tabular cross-bedded sands and silts. This finding contrasts with Kulas Quarry, where large trough beds are visible throughout the exposure.

2.4.3.3 Hwy-JJ

Hwy-JJ was a 3 m tall scarp exposure of laminated silt located along a footslope within the Latch Valley, approximately 1 km downstream from Kulas Quarry (Figure 2.8). The base of this exposure was approximately 2.5 m above the Savanna Terrace surface. The Fl lithofacies exposed at this site contained millimeter-scale tan to buff silt and interbedded sub-millimeter red clay bands. These laminations were oriented parallel

to the slope of the surface. Root traces and rhizcretions were common throughout the exposure. Weathered bedrock clasts were increasingly abundant near the base of this exposure, but the concentration of large clasts was less than 5%. Hwy-JJ samples contained terrestrial gastropod fossils. Three shells of *Catinella* c.f. *gelida* from a sample approximately 2 m below the top of the exposure yielded an age of 16,120±60 RCYBP (BETA-243248; 19,236±236 cal. yr BP). Terrestrial gastropod fossils were common throughout this exposure, along with occasional gastropod eggs.

2.4.3.4 JX

JX is a 3.6 m roadcut exposure of laminated tan silt with interbedded sand and massive silt, located at the mouth of the Latch Valley (Figure 2.9A). The top of the exposed section at JX was approximately at the same elevation as the Savanna Terrace. Rare gravel-sized clasts of sandstone bedrock and several thin, planar sand horizons are present at the base of the section. About 100 m to the East, the Fl lithofacies can be observed lying disconformably atop the Cambrian Wonewoc Formation (Figure 2.9B). The section fines upward into laminated silt with a thin 20 cm soil horizon developed at the top of the exposure. Root traces and rhizcretions were increasingly abundant towards the top of the exposure. Samples from JX contained both aquatic and terrestrial gastropod shells.

2.4.3.5 Storer Creek

Storer Creek is a 10.7 m tall by 200 m wide roadcut exposure of tan to buff, laminated silt in the Root River Valley, Houston County, Minnesota (Figure 2.10). The top of this exposure correlated to the Savanna Terrace. Shells of *Catinella* cf. *gelida* 2.5 m below the top of this exposure yielded an age of 15,800±50 RCYBP (Beta-223643;

19,019±221 cal. yr BP). Sandy trough cross-beds were exposed near the base of the section. Small rhizocretions were encountered throughout the exposure. Several samples contained abundant terrestrial gastropod shells, but few shells of aquatic taxa. Two samples did not yield gastropod shells, but did contain numerous ostracod valves.

2.4.3.6 Root River

Root River is a 4-7 m tall roadcut exposure of laminated silt and interbedded, clast-supported diamicton located approximately 5 km downstream from the Storer Creek section (Figure 2.11). This section was studied by Mason (1995) and data published by Mason and Knox (1997) provided ages of 15,983±136 RCYBP (AA-17787; 19,140±238 cal. yr BP) 1 m below the top of the exposure, and 16,925±351 RCYBP (AA-17786; 20,256±543 cal. yr BP) 5 m below the top of the section. Both of these dates were obtained from gastropod shells. The types of snails were not recorded, although *Catinella* cf. *gelida* or *Discus shimaki* were the most likely species analyzed (J. Mason personal communication, 2005). Both aquatic and terrestrial gastropods were recovered from this locality.

2.4.3.7 Hideaway Lane

Hideaway Lane is located approximately 20 km south of La Crosse, Wisconsin in the Coon Valley, Vernon County, Wisconsin (Figure 2.12A). This small roadcut exposure consisted of 80 cm of cross-bedded sand and silt with abundant red and gray clay rip-up clasts. Gastropod shells and shell fragments were also common. The thinly bedded foresets at Hideaway Lane were approximately 50 cm high, with an upstream dip direction (Figure 2.12B). The upper sediments at this location were covered. The elevation of the exposed St lithofacies was about 7 m below the high terrace, which may

correlate to the younger Bagley Terrace (Knox, 2005), which is about 10 m lower than the Savanna Terrace. About 20 cm of massive, tan to gray silty clay is exposed below the St unit. The contact between these units is irregular, but distinct. Both aquatic and terrestrial gastropod species were abundant with occasional disarticulated bivalves and ostracods. A few badly eroded rodent teeth were also recovered. Two individual shells of *Succinea* cf. *bakeri* from the lower 20 cm yielded ages of 13,180±40 RCYBP (Beta-223640; 16,106±387 cal. yr BP) and 13,780±40 RCYBP (Beta-223639; 16,959±147 cal. yr BP).

2.4.3.8 Limery Coulee

Limery Coulee is located approximately 10 km north of the city of Prairie du Chien in Clayton County, Wisconsin (Figure 2.13). This 5.3 m tall exposure of clast- and matrix-supported diamicton was located on a steep hillslope more than 40 m above the Savanna Terrace Surface. Clasts consisted of large angular fragments of cherty, dolomite bedrock. The contacts between lithofacies and the orientation of the long-axis of larger bedrock clasts were roughly parallel to the slope. Few rhizcretions or root traces were found, but samples of the matrix-supported diamicton contained abundant terrestrial gastropod fossils and unbroken gastropod eggs. Shells of *Catinella* cf. *gelida* 1.3 m below the top of the exposure yielded an age of 13,460±50 RCYBP (Beta-243247; 16,415±409 cal. yr BP), while shells 40 cm below this sample yielded an age of 13,430±70 RCYBP (Beta-242905; 16,377±416 cal. yr BP).

2.4.3.9 Big Platte

Big Platte was a 1.5 m tall by 4 m wide scarp exposure of massive silt in the Platte River valley of southwestern Grant County, Wisconsin (Figure 2.14). Bulk samples

from throughout this exposure contained abundant terrestrial gastropod fossils and gastropod eggs. A thin 20 cm thick bed of barren, massive sand outcropped below the fossiliferous Fm lithofacies and below this, a massive sandy silt contained rare terrestrial gastropod shells. Individual shells of *Succinea* cf. *bakeri* yielded ages of $15,710 \pm 60$ (Beta-223638; $18,964 \pm 228$ cal. yr BP) and $15,890 \pm 50$ RCYBP (Beta-223637; $19,075 \pm 215$ cal. yr BP) from approximately 30 cm below the top of the exposure. A shell of *Succinea* cf. *bakeri* from 65 cm below the top of the section yielded an age of $15,800 \pm 100$ RCYBP (Beta-231781; $19,021 \pm 229$ cal. yr BP). Large, spherical rhizocretions 2-3 cm in diameter were abundant throughout the Fm lithofacies at Big Platte. The contact between the sand and silt was roughly parallel to bedding, but no distinct sedimentary structures were observed at this location.

2.5 DISCUSSION

2.5.1 Depositional Environment

Figure 2.15 represents a generalized cross section showing the relationships between the lithofacies described above. The relationships are based on the observations from this study as well as data presented by Mason (1995), Knox (1996), and Mason and Knox (1997). The colluvial diamictos mantle the hillslopes, thickening downslope where they laterally grade into the silty lithofacies. Silty lithofacies are concentrated along lower footslopes (as colluvium) and valley edges (reworked colluvium or distal floodplain sediments), while the sandy lithofacies deposited within the active channel belt occupy the central valley fill.

Both the clast-supported (Dc) and matrix-supported (Dm) diamictons are indicative of gravity-driven colluvial deposits, based on the location of these sediments along hillslopes and the slope-parallel orientation of large clasts. Massive and laminated silts above the Savanna Terrace are likely colluvial or reworked colluvial deposits. The absence of root traces and rhizcretions within the Dm and Dc lithofacies suggests little well-established vegetation atop these deposits. Radiocarbon age data from sites in this study suggest downslope movement of sediment was active between 19,000 and 16,000 cal. yr BP. These dates agree with the findings of Mason and Knox (1997), who suggested permafrost-induced solifluction was active between 25,000 and 13,000 cal. yr BP. The presence of unbroken gastropod eggs suggests that movement of these lithofacies may have been relatively slow and gradual or large blocks of colluvium remained intact during transport; higher energy mechanisms would likely have crushed these fragile fossils.

Based on the location of the silt-dominated lithofacies along the edges of valley floodplains and presence of aquatic and terrestrial gastropod species within these lithofacies, laminated silts are primarily a result of alluvial sedimentation outside the active river channels either as slackwater deposits or reworked colluvial and eolian silt. The presence of root traces and rhizcretions suggests that these sediments were sufficiently stable and exposed to allow extensive vegetation to develop. Root traces at Kulas-1 are up to 50 cm in length suggesting some of these plants possessed a long, well-developed root system. In addition, the dark brown clay-rich horizons at Kulas-1 and Kulas-2 suggest sufficient subaerial exposure to create a weathering profile. Flame structures and other fluid escape features at sites such as Kulas-1 suggest that some of the

silt deposition was rapid, but the low amplitude cross stratification indicates relatively small sheet floods. Some of these soft sediment deformation structures are capped by more clay-rich sediment characteristic of slackwater deposits. The presence of aquatic gastropods and ostracods indicates that some of these areas retained sufficient moisture to support aquatic animals, perhaps as seasonal ponds adjacent to the active floodplain. However, the well developed root traces and thin clay-rich horizons argue against numerous large, permanent pools. Hwy-JJ is located above the Savanna Terrace and probably represents distal gravity-driven silts and slopewash marginal to the floodplain. This interpretation is supported by the presence of small angular bedrock fragments, slope-parallel laminations and lack of aquatic gastropods.

The sand-dominated lithofacies at Kulas Quarry are characteristic of a braided stream depositional environment with trough cross-bedded channel and braid bar deposits within the active channels and thin, planar cross-bedded sands typical of overbank and splay deposits. Alternately, these deposits from a simple, rather than complex, network of braided streams. The active channel belt was relatively narrow; the width of the thickest trough cross-bedded sand lithofacies at Kulas Quarry is less than 10 m wide. The sediments at Kulas Quarry show two well-developed fining-upward architectural successions (Figure 2.4; Figure 2.7A). These sandy lithofacies represent a complex succession of coarse, laterally accreting trough cross-bedded sands capped by thin, vertically accreting planar sands and silts. Lower trough cross-bedded sands (St) transition upward into planar-bedded sands (Sp), which are then covered by convolute silt (Fc). This fining upward pattern is characteristic of active channel migration away from the section exposure. Finer-grained overbank sediments are deposited atop these channel

sediments. Loess was probably deposited on the inactive floodplain during this hiatus.

The large proportion of silt and clay-sized sediment within the Fc lithofacies compared to laminated silts supports the interpretation of an eolian origin for these sediments (Figure 2.5). When the active channel belt returned to the Kulas Quarry exposure, the underlying fine sediments were partially scoured. Large clasts of intact St lithofacies occur within the Fc lithofacies. Irregular lobes of convolute silt have intruded into the overlying trough cross-bedded sands, apparently following bedding surfaces in some locations, suggesting the silt was “injected” into the overlying sands under pressure (Figure 2.6C).

Deformation of the Fc lithofacies could be a result of cryoturbation and/or deformation by the weight of the overlying sands deposited as the active channel belt migrated back into the Kulas Quarry location.

The cross-bedded sand at Hideaway Lane is likely a result of backflooding from the Mississippi River. The large foresets, abundant clay rip-ups, and shell fragments are characteristic of high-energy flood deposits. The foreset height (ca. 30 – 50cm), incision depth (> 7 m), and abundance of red and gray clay rip-up clasts are similar to descriptions of backflooding deposits found elsewhere in the UMV such as Sandy Creek and Mill Coulee (Knox, 1996). At Onalaska, Wisconsin, about 22 km north of Hideaway Lane, a basal peat beneath a large cut-and-fill exposure on the Bagley Terrace yielded an age of $16,506 \pm 399$ cal. yr BP ($13,545 \pm 85$ RCYBP, AA-23384; Knox, 2005). The ages from gastropod shells at Hideaway Lane closely match this observation. The relative stratigraphic position and radiocarbon data indicate that the incision and backflooding at Hideaway Lane occurred by approximately 16,100 yr BP, as the youngest dated shell must already have been formed before this flooding event occurred. These cut and fill

features have been interpreted as a result of outburst floods from proglacial lakes further north (Flock, 1983; Knox, 1996; Knox, 2005). The red clay is characteristic of lacustrine clays from the Lake Superior Basin draining south along the Bois Brule and St. Croix Rivers (Flock, 1983; Knox, 1996; Figure 2.1). It is possible these sites are coeval, or reflect a general period of minor cutting and filling along the UMV floodplain prior to the final incision.

2.5.2 Chronology of events in the UMV

Based on the results of this study, multiple transport and depositional mechanisms were responsible for accumulating abundant gastropod fossils within the UMV between 22,000 and 16,000 cal. yr BP. Colluvial diamictons along hillslopes represent gravity-driven sediments moving downslope and grade laterally into alluvial sediments. Alluvial sediments consist of either silt-dominated lithofacies along valley margins that represent lower energy floodplains, or sand-dominated lithofacies along valley centers representing higher energy active channel belts within a braided stream environment (Figure 2.15).

Colluvial activity appears to have been active until at least 16,400 cal. yr BP, based on the radiocarbon data from Limery Coulee (Figure 2.4; Table 2.2). This agrees with the results of Mason (1995) and Mason and Knox (1997), who suggested hillslope sedimentation was a result of permafrost-induced solifluction.

Most of the valley aggradation occurred before 17,000 cal. yr BP based on the numerous ages within a few meters of the terrace surface that are clustered between 19,000 to 20,000 cal. yr BP (Kulas Quarry, Storer Creek, Root River; Figure 2.3; Table 2.2). Mason and Knox (1997) reported two radiocarbon dates between 17,300 and 18,000

cal yr BP ($14,090 \pm 60$, Beta-82840; and $14,650 \pm 210$ RCYBP, Beta-82841) from wood within fluvial sediment about 4.5 m below the Savanna Terrace in Crystal Creek, a tributary of the Root River. Knox (2005) observed a gastropod shell lag beneath red clay-rich silt, about 4 m below the Savanna Terrace at Boice Creek in southwestern Wisconsin, which yielded an age of approximately 17,500 cal. yr BP ($14,300 \pm 80$ RCYBP; Beta-92064). Cutting and filling into the late Pleistocene surface is recorded at locations such as Hideaway Lane (see also Knox, 1996; Knox, 2005), with upstream dipping foresets in an exposure of cross-bedded, red clay-rich sandy silt. It is not clear if the high terrace surface is directly correlative with the Savanna Terrace at this location, as the younger Bagley Terrace complex is a prominent intermediate terrace surface along this stretch of the Mississippi River. The Bagley Terrace north of Hideaway Lane is a few meters lower in elevation, however, this terrace surface is quite variable (Knox, 1996) and Hideaway Lane may correspond to one of these intermediate surfaces. The radiocarbon data from Onalaska and Hideaway Lane suggests incision was underway by 16,500 cal. yr BP.

The red clay rip ups at Hideaway Lane are characteristic of lacustrine clay derived from the Lake Superior Basin via the St. Croix River Valley (Flock, 1983). Radiocarbon ages from Hideaway Lane and Onalaska predate the formation of Glacial Lakes Grantsburg and Agassiz (e.g. Johnson and Halmstead, 1998; Fisher, 2004). Knox (2005) suggested these flood deposits did not correspond directly to well-documented deglaciation events, but instead were from Glacial Lake Duluth. Another possibility is Glacial Lake Lind. Although it is relatively small, Johnson et al. (1999) noted convolute bedding within the lacustrine silt and sands of Lake Lind characteristic of rapid drops in

water level. The backflooding events preserved at Hideaway Lane and elsewhere may represent periodic, low-magnitude outbursts from the Lake Superior Basin. In northeast Iowa, incision of the late Pleistocene floodplain was completed by approximately 15,000 cal. yr BP, based on a radiocarbon age from wood within tributary valley sediment fill below the Savanna Terrace (Bettis and Hallberg, 1985). Between approximately 14,000 and 12,700 cal. yr BP, outburst floods from Lake Agassiz into the UMV likely contributed to downcutting, although the latest floods from this lake did not overtop the Savanna Terrace surface or backflood into tributary valleys (Knox, 1996; Fisher, 2004). The sediment bypass that characterizes the last phase of downcutting contrasts with the initial flooding events that left numerous backflood and slackwater deposits throughout the UMV.

During the aggradational phase, most sediment input to the UMV has been thought to be glacial in origin (e.g. Flock, 1983; Knox, 1996). However, the sections below the Savanna Terrace within the Latch Valley (Figure 2.1) consist almost entirely of weathered bedrock and do not show any influence of glaciofluvially-derived sediment. There are no backflooding structures or red clay sediments, and the observed sedimentary structures indicate downstream and lateral flow. The lack of extrabasinal sediment within the Latch Valley is probably due in part to the protected nature of the Trempealeau River drainage basin. Glaciofluvial outwash sediment would have been directed either to the north along the Chippewa River, or to the south, via the Black River (Figure 2.1). In addition, Mason (1995) noted the lack of backflooding or glaciofluvial sediment within the Root River Valley and suggested alluvial sediment consisted of weathered bedrock and reworked loess as a result of terrestrial input from permafrost induced mass wasting

of hillslope material. The lack of backflooding evidence in some tributaries may relate to the dynamics of the tributary system or simply because of erosion.

The influence of terrestrial sediment input on valley aggradation is supported by the presence of bedrock-derived sediment throughout exposures in the Latch and Root River Valleys. In the Latch Valley, the radiocarbon dates are separated by 1,000 years and approximately 2 m of sediment. Assuming the total valley is about 10 km² and the middle of the valley is filled with sediment (about 25% of the total area; fill volume = 2 m * 2500 m² = 5000 m³), it would require a 67 cm-thick layer of material from the sides of the valley to fill the center with 2 m of material (5000m³ ÷ 7500m² = 0.67 m). This suggests a hillslope erosion rate of approximately 0.6 mm/yr. In addition, terrestrial gastropods are the dominant fossil remains at all sites; aquatic gastropods account for less than 5% of the total number of shells obtained from any location (Table 2.2). In addition to the rates of erosion and sedimentation, assuming a constant lateral migration rate for the Latch Valley creek channel belt, and that the succession exposed at Kulas Quarry represents one complete back and forth cycle across the valley (2 * 400 m) yields a lateral migration rate of approximately 0.8 m/yr.

2.5.3 Conclusions and implications for future work

Despite being underutilized for more than 100 years (Chamberlin and Salisbury, 1885), the gastropod fauna from late Pleistocene sediments in the UMRV shows tremendous potential for future paleoenvironmental studies. It is not the intent of this study to explain the complex dynamics of the entire Mississippi River/Laurentide glacial meltwater system, but by outlining the temporal constraints on the dominant sedimentary

mechanisms and depositional characteristics found within the UMV, it is possible to discuss the potential implications of these results and suggest avenues for future work.

Based on stratigraphic and radiocarbon age data from the sections described in this study, deposition of fossiliferous sediments in the UMV began before 22,000 yr BP and continued throughout the late-glacial period, approximately 16,000 yr BP. These findings agree with those of Mason (1995), Knox (1996), and Mason and Knox (1997). What is interesting to note is that many of the fossiliferous deposits immediately below the Savanna Terrace are roughly synchronous, generally none is older than 22,000 cal. yr BP and none is younger than 16,000 cal. yr BP. These dates are well before major climatic shifts, such as the Younger Dryas or Mid Holocene thermal maximum. Studies into the response of biotic groups to large climate changes will benefit from locating younger deposits (such as younger, intermediate terraces or along the modern floodplain) to establish a longer local chronologic record. Alternately, the contemporaneous nature of these deposits offers the possibility of studying latitudinal environmental gradients during the last full-glacial period (ca. 24,000 to 18,000 cal. yr BP).

While aggradation dominated the depositional characteristics of sediments below the Savanna Terrace, cutting and filling from outburst flooding events suggests the potential for mixing shells of disparate ages and locations. Care should be taken to characterize the age structure (see Chapter 4) of faunas within locations. For example, based on the sedimentary characteristics, unbroken gastropod eggs, and overlapping radiocarbon ages, it may be reasonable to assume that little age-mixing has occurred within the massive silt at Big Platte (Figure 2.4; Figure 2.14). However, given the mechanics of backflood deposition and widely separated radiocarbon results, it would be

problematic to assume less than a thousand years age difference between shells preserved within the deposit at Hideaway Lane (Figure 2.4; Figure 2.12).

The dominance of terrestrial gastropods in all sediment samples indicates a high proportion of terrestrial sediment input. Sources such as weathered bedrock and loess were likely brought down into valleys via solifluction or other gravity-driven mechanisms. This has implications for local, gastropod-based environmental interpretations due to the potential to mix similarly aged taxa with widely differing habitat preferences as sediments travel downslope and into the stream valleys. Sites deposited during periods of high stream velocity such as Kulas Quarry and Hideaway Lane present the possibility of hydrodynamically sorted assemblages, with easily transported shells separated from less mobile forms. In addition, compaction of fine, clay rich sediment will tend to crush fragile shells more than coarse sediments. Groundwater movement through sandy sediments may allow for a higher degree of oxidation and diagenetic alteration compared to silt and clay rich lithofacies.

Finally, the potential for gastropods to inform future studies related to the dynamics of UMV aggradation and degradation cannot be understated. Gastropods are often the only organic material preserved within these sediments and they have proved invaluable in establishing a regional radiocarbon chronology for major sedimentary episodes within the UMV. Multiple shell radiocarbon dates from discrete horizons often overlap within one sigma, whereas the minute charcoal fragments are significantly older suggesting that reworked charcoal may persist within the environment for much longer periods (e.g. Figures 2.4, 2.6A). The inverted ages of the charcoal may reflect gradual “unroofing” of the surrounding basin soils and infilling of the basin. When coupled with

other techniques such as optically stimulated luminescence (OSL) or amino acid racemization (AAR), it might be possible to further constrain the principal sedimentary episodes within smaller-order tributaries. Data from the Latch Valley suggests weathered bedrock was an important source of sediment in the Driftless Area during the aggradational phase of the UMV. This aggradational phase has preserved a rich, but underutilized fossil assemblage from a dynamic periglacial environment.

2.6 ACKNOWLEDGEMENTS

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Table 2.1. Lithofacies codes used in this study.

<u>Facies descriptions</u>	
Fm	Massive Silt
Fl	Laminated Silt
Fc	Convolute Silt
St	Troug cross-bedded Sand
Sp	Planar bedded Sand
Sm	Massive Sand
Dc	Clast-supported Diamicton
Dm	Matrix-supported Diamicton

Table 2.2. Location, elevation, and fossil types at sites discussed in text. Note: aquatic gastropods represent less than 5% of the total number of shells recovered in any sample.

Site	Lat	Lon	Terrace	Elev (m)	Ht (m)	F	Sh/Kg	N	TG	AG	BV	OS	FS	RT
Kulas Quarry (KQ)	44.1731	-91.5483	0	231.6	7.4	Sp, St	79.7	21	x	x	x	x	x	x
Kulas-2 (K2)	44.1693	-91.5454	0	231.6	2.5	Fl	NA		x	x				
Kulas-1 (K1)	44.1687	-91.5427	-3.4	231.6	4	Fl	NA		x	x				
Hwy-JJ (JJ)	44.168	-91.5573	4.1	235.7	2.5	Fl	17.7	8	x					
JX	44.1564	-91.5542	0	227.3	3.3	Fl	NA		x	x				
Storer Creek (SC)	43.7918	-91.4233	0	219.5	10.7	Fl	19.1	5	x	x		x		
Root River (RR)	43.787	-91.4831	-2.5	217	7	Fl	35.8	2	x	x				
Hideaway Lane (HL)	43.6664	-91.1978	-6.9	206.5	0.8	St	NA		x	x	x			x
Limery Coulee (LC)	43.0888	-91.1155	49.5	258.3	5.3	Dm	192.1	2	x					
Big Platte (BP)	42.6944	-90.6433	13.7	211.8	1.5	Fm	49.4	20	x					

Notes: "Terrace" = Elevation of section top relative to late Pleistocene terrace surface; "Elev" = height of section top above sea level; "Ht(m)" = height of measured section; "F" = Facies present in section; "Sh/Kg" = Average no. shells per Kg of sample matrix; "N" = no. of samples; "TG" = Terrestrial gastropods; "AG" = Aquatic gastropods; "BV" = Bivalves; "OS" = Ostracodes; "FS" = Fish Scales; "RT" = Rodent Teeth

Table 2.3. Radiocarbon and calibrated age data for sites from this study. Note the discordance between shell and charcoal (char) radiocarbon results.

Site	Lab#	¹⁴C Age	Cal Age	Depth (m)
Kulas Quarry	Beta-223641	16,670±60	19,929±295	2.75
Kulas Quarry**	AA-83090	16,840±120	20,059±296	2.75
Kulas Quarry**	AA-83091	17,180±130	20,617±330	2.75
Kulas Quarry**	AA-83092	16,890±120	20,122±288	2.75
Kulas Quarry**	AA-77831(char)	31,400±120	35,310±362	2.75
Kulas Quarry	Beta-223642	17,550±70	20,961±314	4.5
Kulas Quarry**	AA-82558	17,990±200	21,673±448	4.5
Kulas Quarry**	AA-82587(char)	28,720±320	33,190±478	4.5
Hwy-JJ	Beta-243248	16,120±60	19,236±236	2
Storer Creek	Beta-223643	15,800±50	19,019±221	1.5
Root River*	AA-17787	15,983±136	19,140±238	1
Root River*	AA-17786	16,925±351	20,256±543	4
Hideaway Lane	Beta-223639	13,780±40	16,959±147	0.6
Hideaway Lane	Beta-223640	13,180±40	16,106±387	0.6
Limery Coulee	Beta-243247	13,460±50	16,415±409	1.7
Limery Coulee	Beta-242905	13,430±70	16,377±416	2.5
Big Platte	Beta-223638	15,710±60	18,964±228	0.2-0.5
Big Platte	Beta-223637	15,890±50	19,075±215	0.2-0.5
Big Platte	Beta-231781	15,800±100	19,021±229	0.7

Notes: "**Depth (m)**" indicates depth below top of section where ¹⁴C date obtained; all dates obtained via AMS ¹⁴C analysis of gastropod shell carbonate unless noted; site locations shown in Figure 1; radiocarbon calibration via **calpal online**; *dates from Mason and Knox (1997); **dates from Rech et al. (in prep).

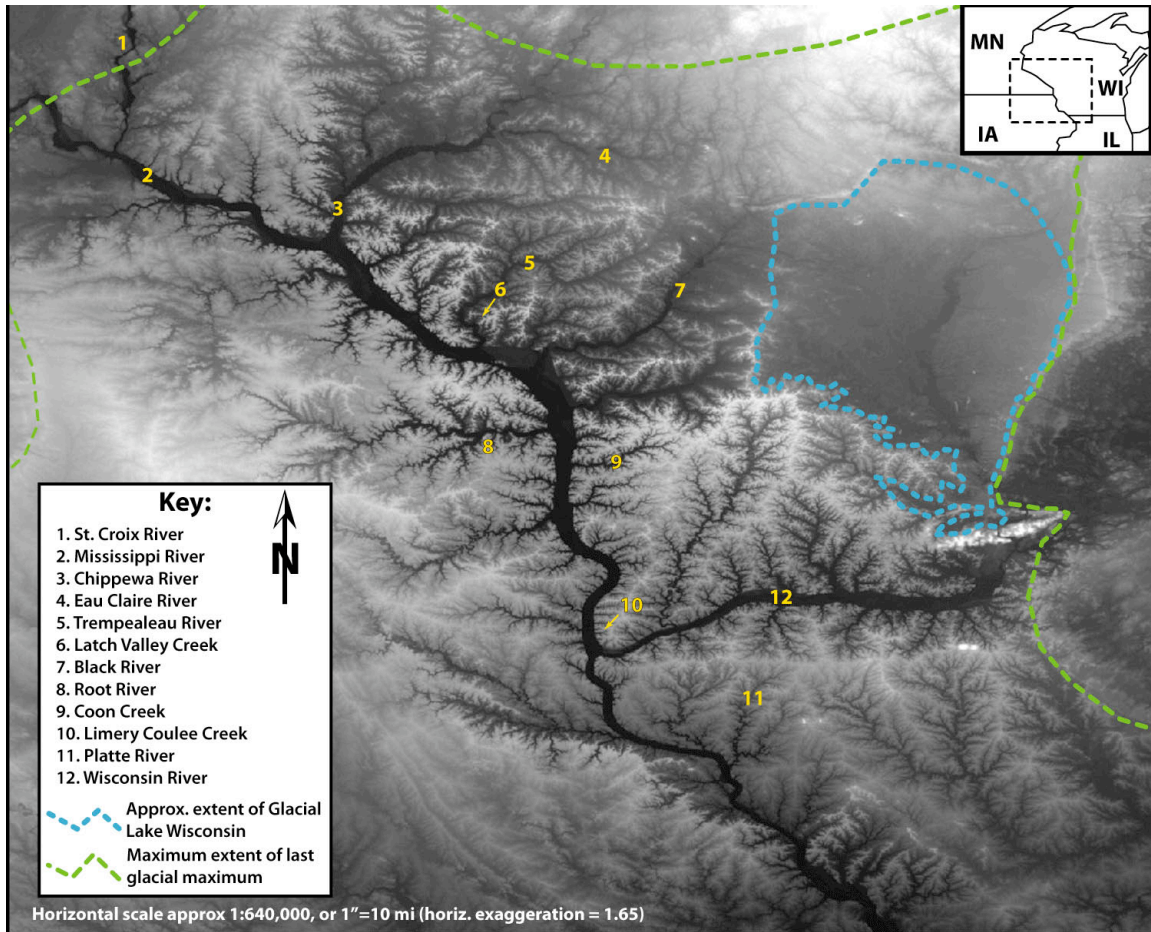


Figure 2.1 Shaded (white=high elevation) relief map of the study region. Primary tributaries and sites discussed in the text are indicated.

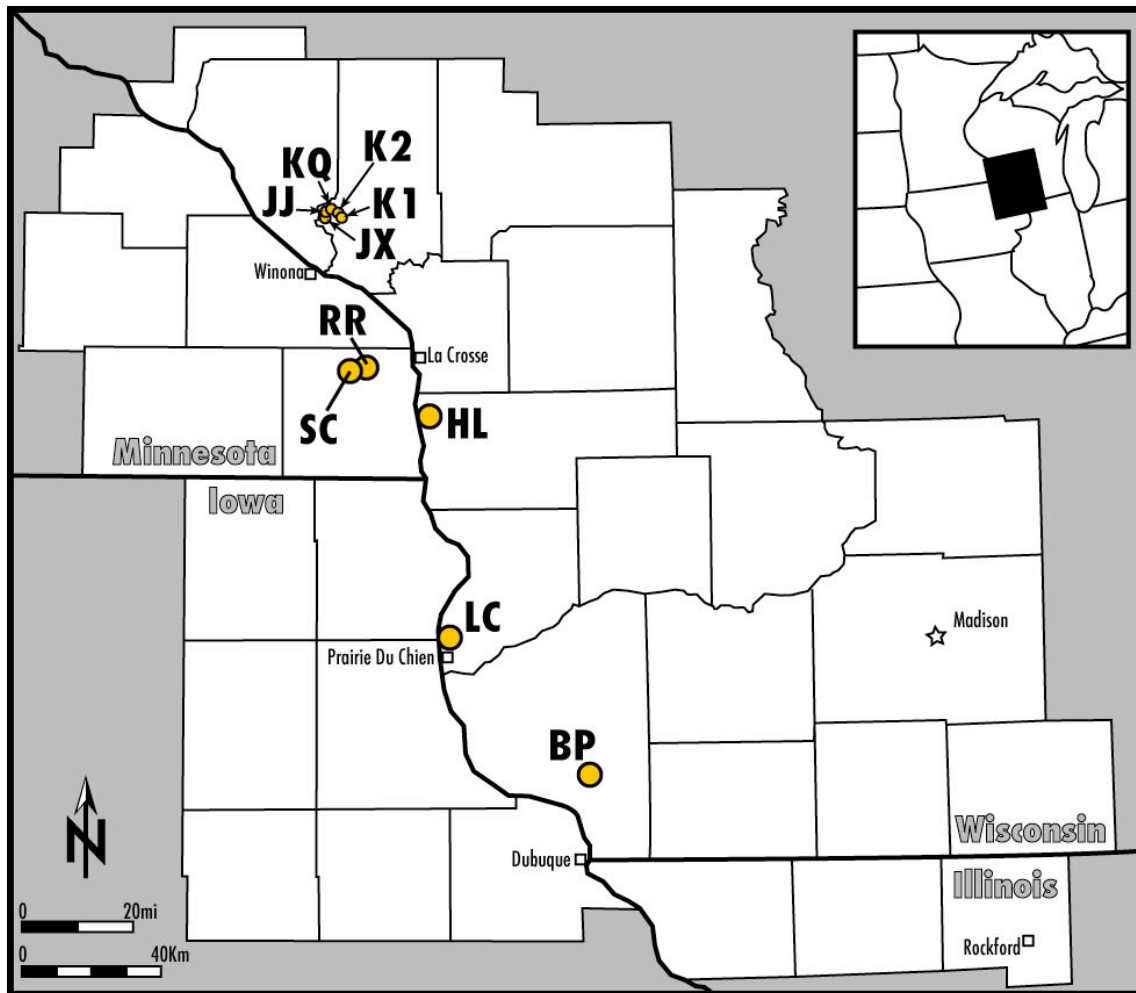


Figure 2.2 Locations of sites discussed in this chapter. KQ=Kulas Quarry, K1=Kulas-1, K2=Kulas-2, JJ=Hwy-JJ, RR=Root River, SC=Storer Creek, HL=Hideaway Lane, LC=Limer Coulee, BP=Big Platte.

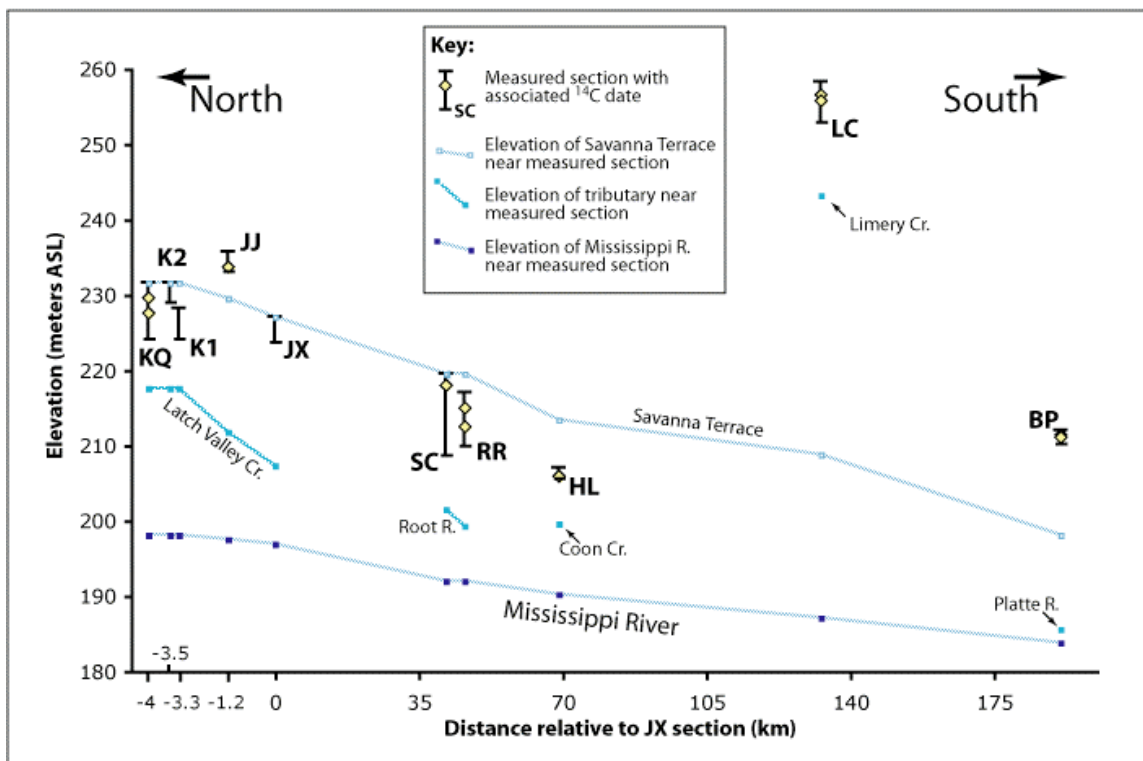


Figure 2.3. Locations of study sites relative to Savanna Terrace and modern stream surfaces. Note: horizontal distances between Latch Valley sections are exaggerated 10x for clarity. See Figures 2.1 and 2.2 for location information. The slope break of the Savanna Terrace at Hideaway Lane (HL) is likely exaggerated due to the proximity of the younger, intermediate Bagley Terrace complex near this location.

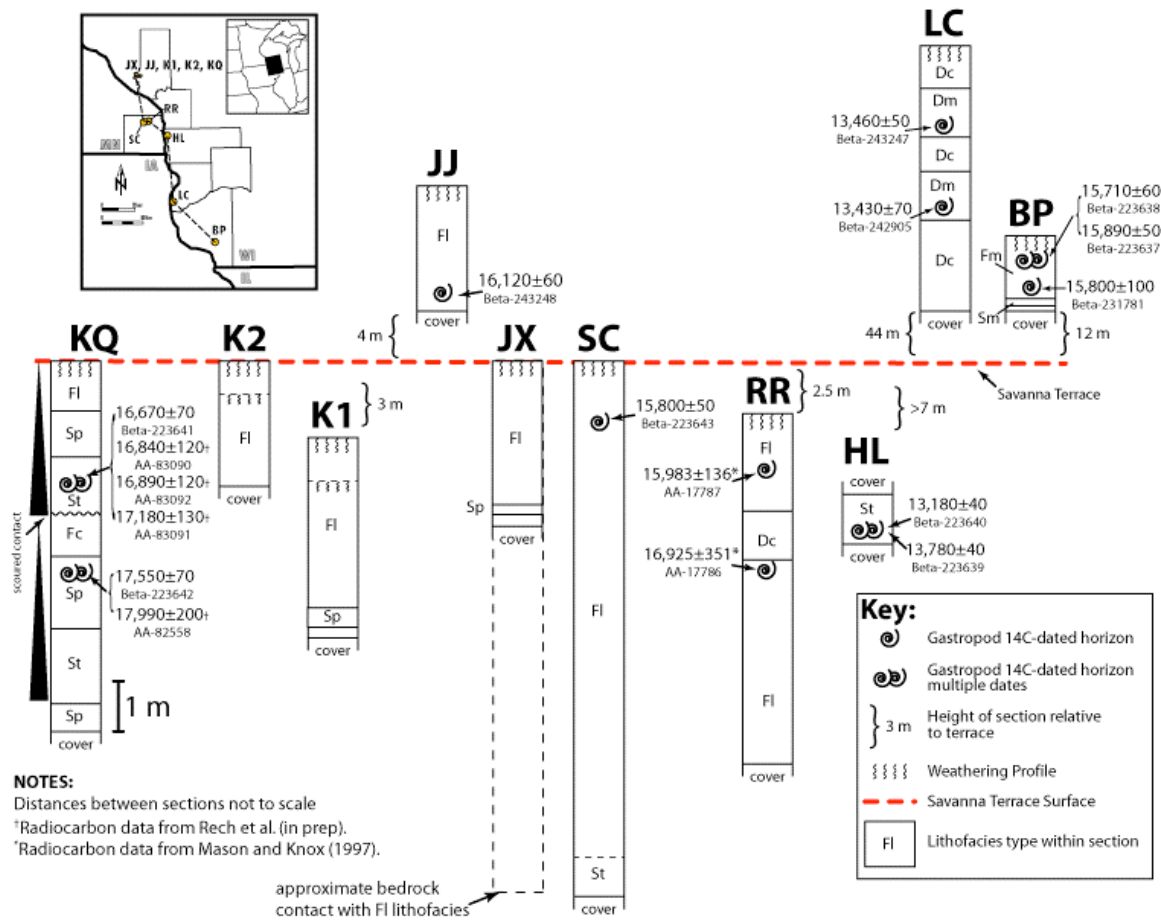


Figure 2.4. Stratigraphic sections described in text. KQ = Kulas Quarry, K2 = Kulas-2, K1 = Kulas-1, JJ = Hwy-JJ, SC = Storer Creek, RR = Root River ("Lehman" in Mason and Knox, 1997), HL = Hideaway Lane, LC = Limery Coulee, BP = Big Platte.

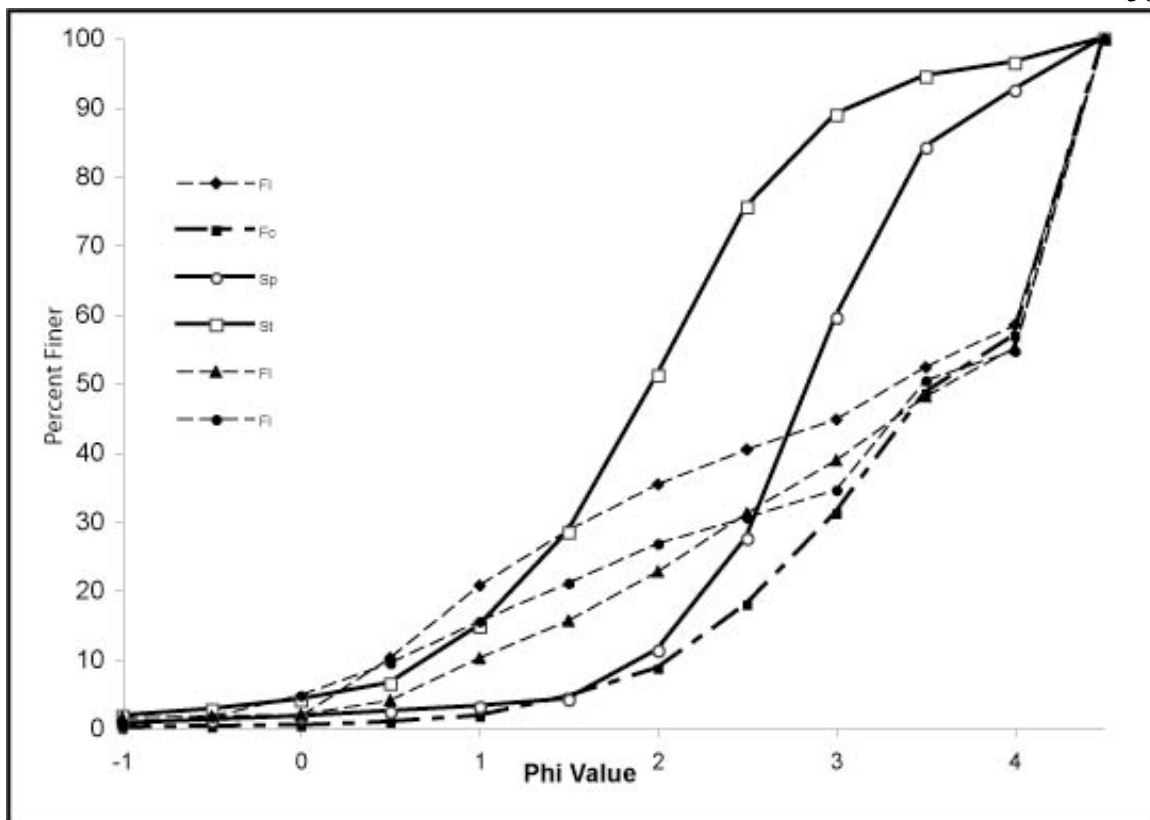


Figure 2.5. Cumulative grain size curves for selected lithofacies. Note lack of sand in fine-grained lithofacies, in particular, the convolute silt (Fc).

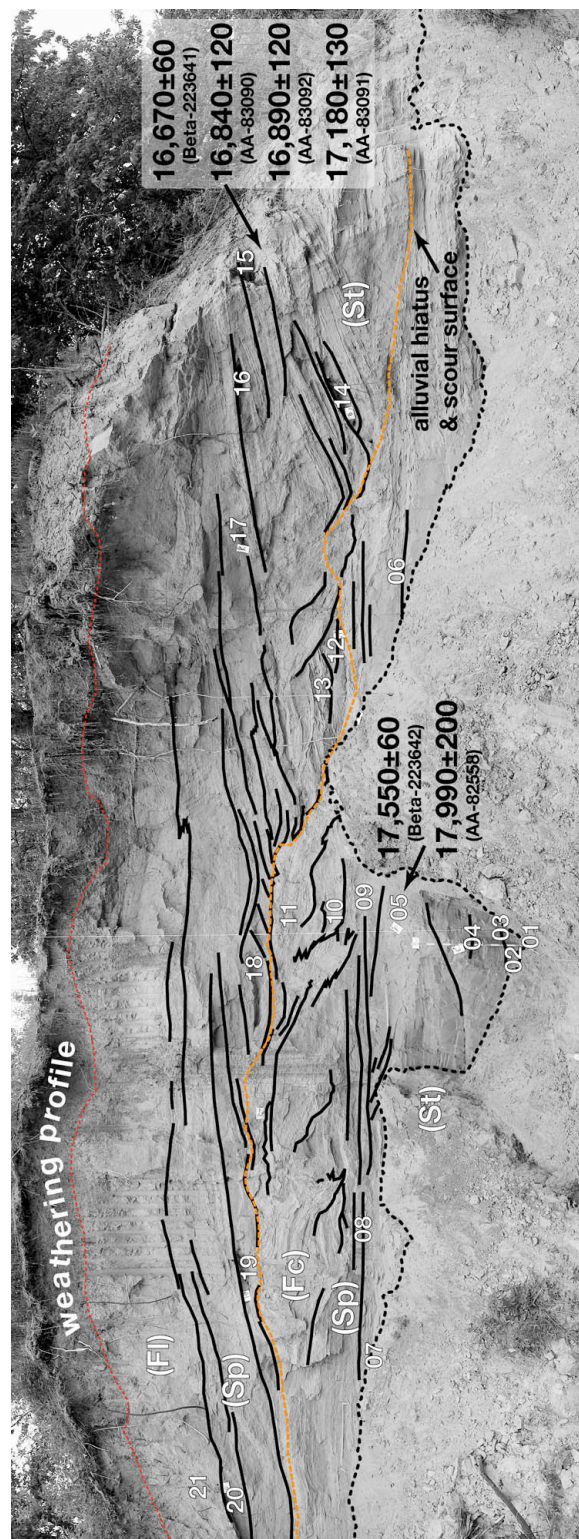


Figure 2.6A. Composite panoramic photograph of the Kulas Quarry exposure. View is to the Northwest. Jacobs staff in lower middle of picture is 1.5 m tall.

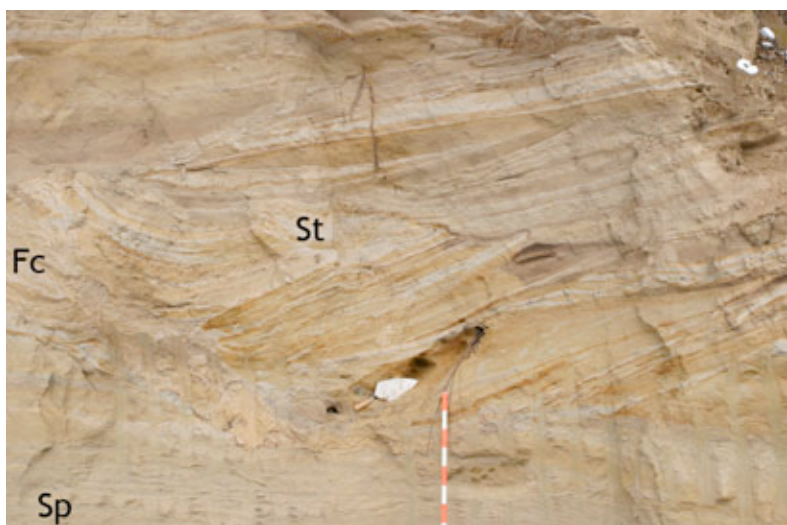


Figure 2.6B. Close view of characteristic lithofacies at Kulas Quarry. Color bands on Jacobs Staff are 10 cm wide.



Figure 2.6C. Close up photograph of Fc lithofacies at Kulas Quarry.



Figure 2.7A. Kulas-1 in outcrop. View is to the East.



Figure 2.7B. Closeup view of laminated silt at Kulas-1 showing root traces and deformed bedding (near base). Color bands on Jacobs Staff are 10 cm.



Figure 2.7C. Outcrop exposure of Kulas-2. Farm buildings behind exposure are built on top of the Savanna Terrace surface. View is to the North.



Figure 2.7D. Close up of F1 lithofacies at Kulas-2. Note dark clay-rich band near top of Jacobs staff. Marks on staff are 10 cm tall.



Figure 2.8. Outcrop photo of Hwy-JJ. Total exposure height is approximately 3 m. View is to the West.



Figure 2.9A. Outcrop exposure at JX. Note Jacobs Staff (1.5 m) in center. The top of the exposure is correlative with the Savanna Terrace surface. Note swallow nests within finer F1 and Fm lithofacies near the top of exposure. View is to the East.



Figure 2.9B. Close view of contact between tan-gray silt and Cambrian Wonewoc Formation. Note irregular, dark weathering surface at contact and incorporated bedrock fragments. Exposure lies approximately 100 m East and 5 m lower than base of JX outcrop. Shovel is approximately 0.8 m tall.



Figure 2.10. Composite panoramic photograph of Storer Creek. Total width of exposure is approximately 200 m. Top of exposure is correlative with Savanna Terrace, and lies approximately 9 m above roadway.



Figure 2.11. Root River exposure. Note Jacobs Staff (1.5 m) in center. This is equivalent to the Lehman site discussed by Mason (1995) and Mason and Knox (1997). The top of the exposure lies approximately 1.5 m below the Savanna Terrace Surface.



Figure 2.12A. Exposure at Hideaway Lane. Jacobs Staff is 1.5 m tall and oriented perpendicular to foreset surface.



Figure 2.12B. Closeup of foreset surfaces at Hideaway Lane. Note the white shell fragments. Circular burrow is modern insect hibernaculum – note box elder bugs at far right.



Figure 2.13. Exposure at Limery Coulee. Jacobs Staff (1.5 m) is to the left of the photograph center. Note bedrock exposure in the back right.



Figure 2.14. Exposure at Big Platte. Fossiliferous material is located along the left side of the exposure. Jacobs Staff (1.5 m) and person (R. Slaughter, kneeling) for scale.

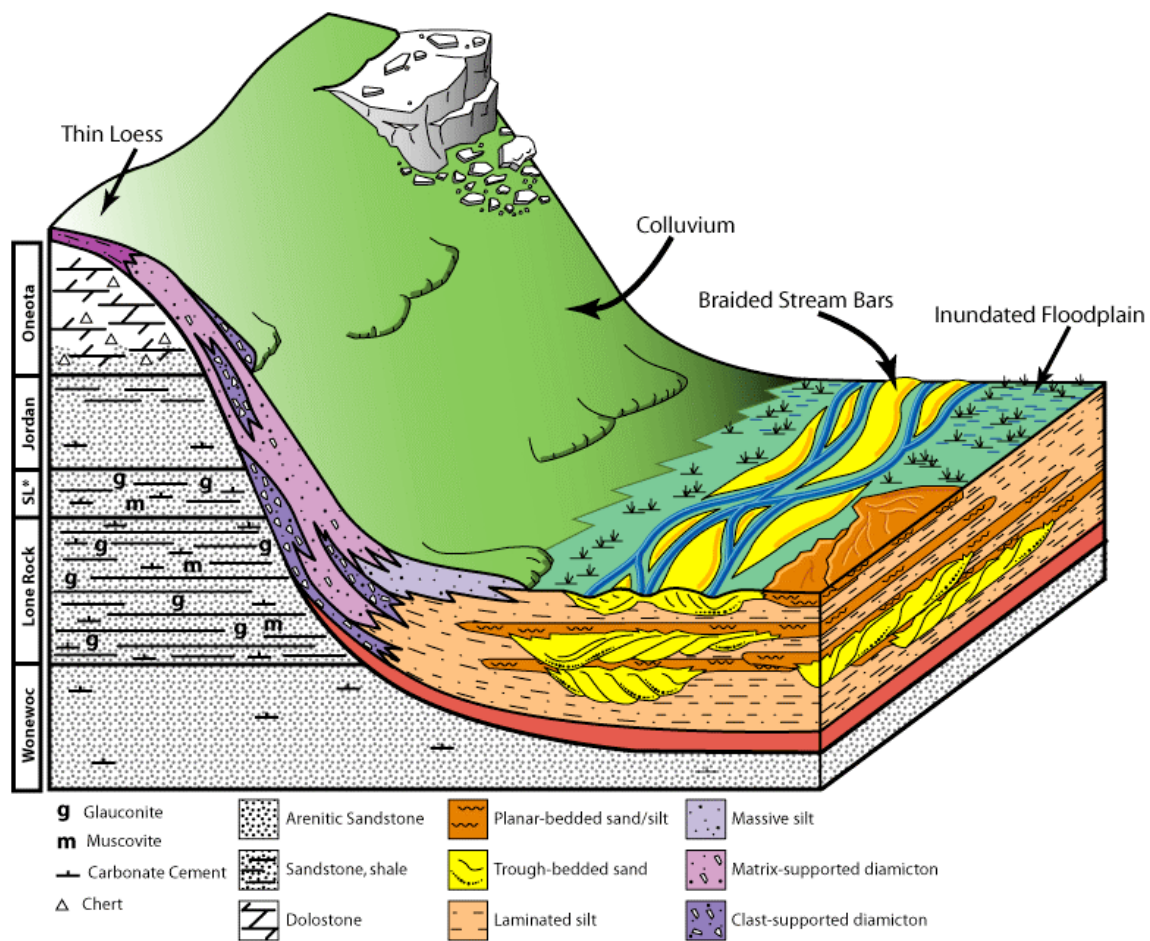


Figure 2.15. Generalized block diagram of a typical UMV cross-section ca. 17,000 cal. yr BP showing spatial relationships and sedimentary architecture with associated lithofacies. Note: backflooding and incision will be inset into these sediments.

Chapter 3

*An assessment of the paleoecological implications of terrestrial gastropods
from western Wisconsin using Amino Acid Racemization*

ABSTRACT

Many important questions in paleoecological studies rely upon the temporal fidelity of a fossil deposit. The amino acid composition of 236 terrestrial gastropod shells from two late Pleistocene fossil localities in western Wisconsin (Big Platte and Kulas Quarry) was measured using HPLC. Four amino acids (aspartic acid, glutamic acid, serine, and alanine) were analyzed for their total concentration and D/L values. ^{14}C dates from succineid shells at these sites indicated a full-glacial age for the assemblage (ca. 22,000 – 18,000 cal yr BP). Cordilleran-Boreal taxa (*Succinea*, *Catinella*, *Discus*, *Vertigo*, *Columella*, *Pupilla*, and *Vallonia*) had more weathered shells and D/L Asp values from 0.300 to 0.350, characteristic of late Pleistocene ages. The less weathered shells of rare Eastern Deciduous Forest taxa (*Helicodiscus*, *Hawaiiia*, *Glyphalina*, *Pupoides*) had D/L Asp values between 0.060 and 0.170, indicating that these shells were introduced into the assemblage after its deposition. The small variance in D/L Asp for succineid shells and the close agreement of multiple radiocarbon shell ages suggests time averaging within individual stratigraphic horizons was on the order of 100 years. Principal components analysis (PCA) of the AAR data showed that the D/L ratios of rapidly-racemizing amino acids (serine, aspartic acid) had strong, positive loadings on the first principle component (PC1), while the concentration of L-Ser had a strong, negative loading. PC1 accounted for 40% and 38% of the variance within the Big Platte and Kulas Quarry data respectively. This component is interpreted to represent a contamination gradient with high L-Serine loading negatively, and a D/L value gradient where higher D/L values load positively. PC2 correlated positively with Depth (distance below surface) and [Sum] (total amino acid concentration; pM/mg shell), whereas high D/L values of slower racemizing amino acids (glutamic acid, alanine) loaded negatively. PC2 accounted for 18% and 24% of the total variation within the data from Big Platte and Kulas Quarry respectively. The negative correlation between depth and D/L Glu and D/L Ala indicates that either L-Ala and L-Glu are preferentially removed (by leaching free amino acids) or D-Ala and D-Glu are introduced at the surface. D/L Asp – an indicator of age – did not correlate, or showed a slight negative correlation with Depth. Surface heating may partially explain stratigraphic aberrations in D/L Asp values. The anomaly in Glu and Ala may be a result of surface contamination from bacteria, as the peptidoglycan in the cell walls of many bacteria is enriched in D-Ala and D-Glu. This has not previously been observed in terrestrial gastropod AAR studies, but has significant implications for future gastropod-based amino acid geochronologic studies – especially where D/L Glu is used as an independent or longer interval (e.g. beyond radiocarbon utility) estimate. Data screening should include an analysis of excessive D-Ala, or bleaching gastropod shells to focus analyses upon intra-crystalline proteins.

3.1 INTRODUCTION

The age structure of a fossiliferous deposit is of fundamental importance to its paleoecologic interpretation. The scale of time represented by a deposit – both in terms of the accrued time to assemble the sediment and fossils as well as the time differential between individual shells – controls the types of questions that can be addressed (e.g. Kowaleski et al., 1998). Virtually all fossil accumulations are time-averaged to some extent; individual shells within a deposit may differ in age (i.e. time since death) by tens to tens of thousands of years or more (e.g. Kidwell and Flessa, 1995). Considerable attention has been paid to the age structures of marine shelly deposits (see Carroll et al., 2003 and references therein) and to a lesser extent lacustrine (e.g. Cohen, 1989) or terrestrial deposits (e.g. Goodfriend, 1989; Yanes et al., 2007).

Amino acid racemization (AAR) analyses have become an increasingly important tool for assessing the temporal fidelity of shelly deposits. This technique has several advantages over radiocarbon analyses; the process is quick, relatively inexpensive, and can be carried out on samples as small as a single foraminifer test or ostracod valve (e.g. Kaufman, 2000; Kaufman, 2006). Amino acid geochronology is a relative-dating method or, when coupled with numerical methods like radiocarbon, a calibrated-dating tool. It can therefore be used to address important paleoecological questions such as time averaging within fossil deposits (e.g. Carroll et al., 2003), paleotemperature estimates (e.g. Kaufman, 2003), and stratigraphic correlation (e.g. Miller and Hare, 1980; Miller et al., 1987).

In addition, many late Pleistocene terrestrial fossil assemblages include species whose modern ranges do not overlap (i.e. non-analog faunas; Graham and Meade, 1987).

The question of whether these non-analog faunas result from individual responses to past climate change by specific taxa, or post-mortem mixing of fossil remains is of fundamental importance (e.g. Stafford et al., 1997). The combined problems of time-averaging and non-analog faunas can lead to erroneous paleoclimatic interpretations. Previous studies have often focused on primary loess deposits, because it is assumed that their degree of temporal and spatial mixing has been negligible (e.g. La Rocque, 1970; Hubricht, 1985). Combined use of AAR and radiocarbon can improve our understanding of the temporal fidelity of fossil assemblages.

Amino acid analyses result in a large amount of raw data with many intercorrelated variables; reduction of the data is necessary to identify the most important influences. Sources of non-temporal variation within AAR data have the potential to strongly affect age-related inferences, but the underlying mechanisms and sources of error are not well understood (e.g. Kosnik and Kaufman, 2008). Modern contamination and diagenetic effects such as leaching of free amino acids are both major concerns with amino acid geochronology. Methods for identifying anomalous results have largely focused on univariate and bivariate statistical analyses (e.g. Kaufman, 2000; Laabs and Kaufman, 2003; Kaufman, 2006; Kosnik and Kaufman, 2008). However, removing anomalous or poorly fitted data increases the risk of rejecting material that may actually represent a fraction of the age-distribution of shells from a fossil deposit.

Late Pleistocene gastropod fossils from the Driftless Area of western Wisconsin represent an abundant, but underutilized, fossil proxy for paleoenvironmental interpretation. These are among the most northern late Pleistocene fossil assemblages in the Midwest (Kuchta et al., 2007b) and they have the potential to characterize local full-

glacial, ca. 24,000 - 18,000 cal. yr BP, conditions near the ice margin in Wisconsin (all dates are given in calibrated calendar years before present unless noted). However, the temporal resolution and fidelity of individual fossil horizons must be addressed before any detailed ecological inferences can be made. This study represents a new application of multivariate statistics (PCA) to study variation within terrestrial gastropod AAR data, and the first AAR study of fossil gastropods from Wisconsin.

The goal of this paper is to use amino acid racemization (AAR) techniques on shells from two radiocarbon-dated fossil localities in order to: 1) determine the relative age relationships of several non-analog species that co-occur within these fossil deposits, 2) describe the amount of time averaging in shells from a single taxon, and 3) identify factors that may affect the quality of the geochronologic signal obtained from AAR analysis (e.g. diagenesis, contamination, etc.) using uni- and multi-variate statistical analyses.

3.2 GEOLOGIC BACKGROUND

This study focuses on two sites in the Driftless Area of western Wisconsin: Big Platte and Kulas Quarry (Figure 3.1). Big Platte is a south-facing colluvial exposure in southwestern Grant County. Kulas Quarry is a large exposure of alluvium on the north side of the Latch Valley in Trempealeau County. These sites were discovered during surveys of fossiliferous outcrops throughout the region (see Chapter 2 of this thesis for a more detailed description). Late Pleistocene sediments throughout western Wisconsin commonly include terrestrial gastropods, which have heretofore gone unstudied. These sites have a similar species composition to other late Pleistocene biotic sites, such as

Elkader and Conklin Quarry in Iowa: all are dominated by gastropod species with modern Cordilleran-Boreal range distributions.

Thick colluvium mantles many of the hillslopes within the Driftless Area, and consists primarily of reworked loess and large clasts of local bedrock. These colluvial sediments grade laterally into alluvial sediments covering the valley floor (Knox, 1989; Mason, 1995). Several researchers have speculated that Driftless Area colluvial deposits resulted from late Pleistocene periglacial activity (ca. 25,000 to 16,000 cal. yr BP), and that these sediments were relatively stable during the Holocene (e.g. Knox, 1989; Mason and Knox, 1997). Alternatively, Black (1969) proposed that increased Holocene precipitation induced colluvial activity.

Late Wisconsinan alluvial sedimentation is characterized by valley aggradation in braided streams with a high sediment bedload (Knox, 1996). In river valleys not directly affected by glacial meltwater, much of this sediment consists of weathered bedrock and reworked silt and clay (Mason, 1994). This aggradational phase began by at least 25,000 cal. yr BP and continued until approximately 16,000 cal. yr BP (Flock, 1983; Knox, 1996). Alluvial deposits consist primarily of either vertically aggrading laminated silts and planar-bedded sands, or laterally accreting trough cross-bedded sands and gravels.

3.3 METHODS

3.3.1 Sample collection and processing.

Samples for AAR and faunal analysis were collected from Big Platte and Kulas Quarry at multiple stratigraphic horizons (Figure 3.2A, B). To minimize the effect of elevated surface temperatures on the rate of racemization, it is recommended that samples

come from at least 1 m depth (e.g. Goodfriend, 1992). At Big Platte, sample depths were constrained by the narrow distribution of the fossiliferous material and the need for stratigraphic control of each sampling horizon. The distribution of shells within the Big Platte exposure was limited: most shells were retrieved from the upper half of the exposure, whereas only a few shells were retrieved from the base. At Big Platte, a total of eight separate samples were collected at least 30 cm back from the scarp surface. Additional AAR samples were collected with a 60 cm soil auger attached to a cordless drill to retrieve material from further back without disturbing a barbed-wire fence post near the top of the exposure (Figure 3.3A). Based on the length of recently exposed roots and un-vegetated slump blocks below the scarp surface, approximately 50 cm of material had been removed due to mass wasting, likely within the past year. Thus, the minimum depth below the surface prior to collection was approximately 80-100 cm.

The original Kulas Quarry exposure was created when the landowner expanded a borrow pit in the spring of 2006. Based on the geometry of the cut and length of exposed tree roots, approximately 1-2 m of material had recently been removed prior to sample collection. I sampled multiple discrete fossiliferous beds along the exposure face (Figure 3.3B). To facilitate bulk collection of deeper material, the lowest two meters at Kulas Quarry were excavated with a bucket loader by the landowner (Figure 3.3C).

Samples were wet-sieved (smallest mesh = 0.425 mm) and allowed to air dry. Individual shells were picked from the matrix using flexible steel forceps to avoid contamination from modern amino acids (in fingerprints, saliva, etc.). Shells were identified to species (or subspecies) using Pilsbry (1948), Burch (1962), Barthel and Nekola (2000), and reference collections from the University of Iowa Museum of Natural

History. Succineid gastropods cannot be assigned to species without soft-tissue dissection (e.g. Pilsbry, 1948). Shells in my collections were assigned to either “*Succinea* cf. *gelida*” or “*Catinella* cf. *gelida*” based on the size and aspect ratio of the shell aperture; “*Succinea*” shells are generally taller than 1 cm and have an apertural Height:Width ratio greater than 2.0, while “*Catinella*” are much smaller (rarely > 0.5 cm) with an aperture H:W of less than 2.0 (Figure 3.4). Identifications were verified by Jeffery Nekola of the University of New Mexico. Specimens are catalogued and stored at the University of Wisconsin Geology Museum under the catalog number UW1987.

Gastropod taxa found within Big Platte sediments include taxa with Cordilleran-Boreal and Eastern Deciduous Forest ranges (*sensu* Wells and Stewart, 1987; Table 3.1; Figure 3.5A, 3.5B). In general, shells of the latter group were more transparent and less worn compared to the Boreal and Cordilleran taxa (Figure 3.4, 3.6). Succineids were chosen for the bulk of the AAR analyses because of their abundance and quality of preservation at both sites. Additional taxa were chosen for analysis because they either 1) represented the most abundant species at Big Platte, or 2) had shells that were much more “fresh” in appearance and whose ranges were very different from the majority of the species recovered (e.g. Cordilleran-Boreal vs. Eastern Deciduous Forest).

To minimize the effect of intrashell variability (e.g. Carroll, 2003), only the body whorls of *Discus* shells were analyzed; AAR results from other taxa represent whole shell analyses. Some samples of *Succinea* had surface discoloration. These shells were broken and only fragments clear of these black spots were analyzed.

Shells of Eastern Deciduous Forest species were in general much better preserved than those of Cordilleran-Boreal species (Table 3.1; Figure 3.4). Live terrestrial

gastropods often have a glossy and transparent or translucent shell, which becomes increasingly opaque and white with age (M. Kuchta, personal obs., 2007). To test the hypothesis that shell condition reflects age, the shells analyzed for amino acid racemization were graded on a qualitative scale from 1 to 5 based on their condition. This scale ranked the appearance of individual shells where 1 = fully transparent/translucent shell with glossy surface, 2 = partially opaque shell with minor surface wear, 3 = fully opaque shells with little or no surface wear, 4 = fully opaque shell material with dull surface texture, 5 = opaque and dull shell material with significant surface wear (Figure 3.6). These shell condition scores were then compared to the D/L ratios of aspartic and glutamic acids to determine the relationship between relative shell age and appearance. If shells that look younger are significantly different in age, there is justification to eliminate them from subsequent paleoecological reconstruction, and future studies can consider these taxa anomalous when found within fossil deposits.

3.3.2 AAR Concept

Fossil gastropods are well suited for AAR analysis (e.g. Oches and McCoy, 2001). Gastropods synthesize amino acids (such as Aspartic acid) in their L-form (levorotary) to make the proteinaceous matrix that supports their calcareous shells. At death these L-amino acids undergo a reversible inversion (racemization) to their chiral D-form (dextrorotary). This racemization reaches equilibrium when the ratio of D- to L-forms (D/L) of an amino acid equals 1.0. The rate of racemization is a function of temperature and time: D/L ratios will increase over time to the equilibrium point, and will do so more rapidly as ambient temperature increases (McCoy, 1987; Goodfriend, 1992).

Because two separate shells from within the same deposit have shared a similar post-depositional temperature history, the difference in their D/L values can be used to assess the relative age differences between them (e.g. McCoy, 1987; Yanes et al., 2007).

Different molluscan taxa may exhibit different rates of racemization; therefore, taxonomically restricted samples are preferred in order to reduce variation in the measured D/L ratios due to this “vital effect” (Oches et al., 1996; Roof, 1997).

Analyses were carried out at the Amino Acid Geochronology Lab at Northern Arizona University using Reverse-Phase, High-Performance Liquid Chromatography (HPLC) to measure the D/L ratios of several amino acids, including aspartic acid (Asp), glutamic acid (Glu), serine (Ser), and alanine (Ala). Asp and Glu likely include a small amount of asparagines and glutamine, respectively, as these can be converted to Asp and Glu during laboratory hydrolysis. Amino acid compositions reported here reflect the total hydrolysable amino acids (THAA) within the shell, which includes both inter- and intra-crystalline proteins. For detailed methods, see Kaufman and Manley (1988) and updates by Kaufman (2000, 2006).

I focused on Asp and Glu for geochronology because they are among the most clearly resolved with HPLC. Asp racemizes at a much faster rate than does Glu; it is least an order of magnitude faster than the commonly used alloisoleucine/isoleucene (A/I). Glu racemizes at a rate comparable to A/I, and provides a quasi-independent estimation of sample age (Kaufman, 2000; Hearty and Kaufman, 2009). The concentration of the labile amino acid Ser, when compared to concentrations of more stable amino acids, is often used as an indicator of modern contamination (Kaufman, 2000; Kosnik et al., 2008). The general expectation is that D/L values for Asp and Glu will increase over time

(~stratigraphic depth) and/or as increased temperatures accelerate racemization. At mid-latitudes, the effective age range for AAR techniques is typically 2 ma. A description of each variable presented in this study is presented in Table 3.2.

Variation in the diagenetic history of samples can influence measured D/L values. Leaching of free amino acids from the shell, usually enriched in D-amino acids, will yield younger-than-expected D/L ratios (e.g. Roof, 1997). Contamination by modern amino acids (often enriched in L-amino acids, especially L-Ser) will also yield lower D/L values (e.g. Kosnik and Kaufman, 2008). While contamination is generally thought to produce younger-than-expected D/L values, the peptidoglycan within bacterial cell walls is enriched in D-Ala and D-Glu, which may produce an excess of D-amino acids as a result of bacterial growth. Anomalies in the D-amino acid fractions of both Ala and Glu may point to bacterial contamination of the intra-shell amino acids (e.g. Blackwell et al., 2000; Nyberg et al., 2001).

3.3.3 Radiocarbon

I obtained radiocarbon dates from succineid gastropod shells. Succineid gastropods are abundant in many late Pleistocene deposits, and are often the only organic material available for radiocarbon dating (e.g. Mason and Knox, 1997; Pigati et al., 2004). There are two primary sources of error in radiocarbon dates obtained from gastropod shells. The first is recrystallization of aragonite to calcite, which can yield younger-than-actual ages. This error can generally be avoided by using shells without visibly recrystallized, “chalky” shell material and by pre-etching the sample in acid before analysis (Goodfriend and Stipp, 1983; Goodfriend and Hood, 1983). The second

problem is harder to detect and occurs when the snail ingests ^{14}C -depleted carbonate, which can yield anomalously old radiocarbon ages (Goodfriend and Hood, 1983; Goodfriend and Stipp, 1983, Pigati et al., 2004). Succineid gastropods do not appear to ingest old carbonates, even when in a ^{14}C -depleted carbonate environment. Other gastropods, however, can show significant variation in radiocarbon age because they often ingest these depleted carbonates (e.g. *Vallonia*; Pigati et al., 2004; Rech et al, in prep).

Radiocarbon ages were calibrated to calendar years using the “CalPal-2007^{online}” software (Danzeglocke et al., 2007). Additional statistical analyses of radiocarbon results were performed using the Calib 5.1beta program (Stuiver and Reimer, 1993).

3.3.4 Data Screening

Non-temporal sources of variation (e.g. contamination or leaching) can have a profound effect on AAR data. Understanding the source of this variation can identify outliers that are truly aberrant, as opposed to older, reworked shells. Identification of AAR outliers is carried out empirically, but no universal standard for recognizing and rejecting outliers exists. A set of screening criteria for one taxon may not be applicable to others. Kaufman (2003) rejected ostracod AAR data when L-Ser/L-Glu ratios exceeded 1.0, whereas Kaufman (2006) rejected foraminiferal AAR data when L-Ser/L-Asp ratios exceeded 0.8 (> 1.5 in degraded samples). Kosnik and Kaufman (2008) compare transformed marine mollusk AAR data to linear models and flag residuals greater than a specified cutoff value.

I followed the suggestions of Kaufman (2000), Kaufman (2006), and Kosnik et al. (2008) to systematically identify outliers in *Succinea*, *Catinella*, and *Helicodiscus* (see Appendix B for further discussion). The remaining taxa consisted of too few individuals to provide reliable outlier estimates. The outlier screens presented here are a modification of those described in the literature (e.g. Kaufman, 2006; Kosnik and Kaufman, 2008) and are based on empirical analysis of the Big Platte and Kulas Quarry data sets. To reduce the influence of screening on the inferred age-population of the shells, I only flagged samples whose residuals were more than three standard deviations outside the mean for a normal distribution. Samples that were flagged by more than one screening test were rejected.

Tests for outliers included the following: 1) the covariance of L-Ser/(L+D Asp) versus D/L Glu. Values of the labile L-Ser should be small; samples with abnormally high L-Ser may indicate modern contamination (e.g. Kaufman, 2000). 2) Covariance of L-Ser/(L+D Glu) with D/L Asp is a quasi-independent test compared to 1 (*sensu* Kosnik and Kaufman, 2008). 3) The concentration of [Asp] and [Glu] should covary as a function of time. Departures from this relationship may indicate aberrant behavior. Total concentration of amino acids ([Sum]) was calculated as the sum of the peak D+L areas within each sample, calibrated to an internal spike of the non-protein amino acid L-*h*Arg (Kaufman, 2000). 4) Finally, D/L Asp and D/L Glu should both increase over time (D/L Asp at a faster rate) and samples that do not display this well-documented covariance may indicate an alternate diagenetic pathway (e.g. Kaufman, 2003). 5) In addition to univariate tests, I used the “Outlier Analysis” option in PC-ORD 5.0 (McCune and Mefford, 2006) to analyze the entire data matrix for outliers within rows (samples). This

method creates a frequency distribution for the calculated average distances between all entities in the matrix and flags multivariate outliers from this distribution at user-defined cutoffs. I transformed the data matrix by subtracting the mean from each variable and dividing by its standard deviation. This transformed matrix represents the total variation within each column. The distances between individual samples were measured using the Euclidean distance measure. I flagged samples whose average distance was more than three standard deviations above the mean average distance for all samples.

3.3.5 Statistical analyses of succineid age-structure

Descriptive statistics and tests were performed in Minitab and PAST (Hammer et al., 2001). The significance of pair-wise ANOVA results was corrected for multiple comparisons using the conservative Bonferonni correction of $\alpha=0.05/n$ (where n =total number of within-test comparisons). To test for time-averaging using D/L Asp values as an indication of age, I compared the measured coefficient of variance (C.V. = standard deviation/mean*100%) for samples of succineid shells at Big Platte and Kulas Quarry to an expected range due to laboratory precision and inter-shell variation. Laboratory precision of D/L Asp measurements is typically $\leq 5\%$ (Kaufman, 2000). The inter-shell variability in D/L values is unknown for “live-collected,” congeneric shells.

Theoretically, the initial D/L value of live-collected shells should be zero, but a small amount of laboratory-induced racemization occurs during sample hydrolysis (Kaufman, 2000). Furthermore, there are few measurements of amino acids in shells known to have coexisted because remnant soft tissue, or chemical removal of this soft tissue, can significantly alter the D/L ratios of the shell. Hearty and Kaufman (2009) reported D/L

Asp values in shells from museum collections of the terrestrial gastropod *Cerion* from Jamaica that varied between 10 and 25%. These museum collections were acquired over several centuries; the snails analyzed were not alive at the same time. Walther (2004) reported D/L Asp values from three live-collected *Succinea* shells that varied by 18.5%. Terrestrial gastropod fossils in eolian sediments typically have within-horizon C.V.s for D/L Asp values between 10 and 15% (Walther, 2000; Oches et al., 2005; Ortiz et al., 2006). Previous authors have reported between 10% and 20% variation in D/L Asp values from assemblages considered representative of a “single-age” population (e.g. Murray-Wallace, 2000; Yanes et al., 2007). However, because previous studies examined shells not known to exist at exactly the same time and due to the problems associated with accurately measuring D/L Asp values from live shells, I conservatively estimate a truly live-collected population of shells should exhibit 5-10% variation in their measured D/L Asp values.

Principal components analysis (PCA) is an eigenvector-based method of data reduction. The goal of PCA is to reduce a large, multivariate dataset (such as that produced by AAR analysis) to a small number of synthetic variables (eigenvalues) that represent the principal components of the variation within the entire data (see also McCune and Grace, 2002). Previous applications of PCA to amino acid data include characterizing the degradation of organic material in marine sediments (Dauwe and Middleburg, 1998), estimating the influence of taphonomic factors such as shell breakage on the amino acid concentration in brachiopods (Carroll et al., 2003), and determining the amount of variance represented by the D/L values of various amino acids (Ortiz et al., 2006).

PCA is ideally suited to data with approximate linear relationships among variables. Many AAR variables, such as D/L Asp approximate a linear relationship with time over relatively narrow ranges (e.g. D/L Asp values between 0.300 and 0.400; Kaufman, 2000). Although PCA does not require independent variables, it does assume multivariate normality of the data, although this requirement is more relaxed for descriptive purposes (McCune and Grace, 2002). McCune and Grace (2002) suggest that when $|\text{skew}| < 1$, PCA performs quite well. However, because PCA seeks the strongest linear correlation among variables, it is highly sensitive to outliers. Therefore, PCA was run after data screening. It is possible to use this technique to identify outliers within the AAR dataset, although this method was not explored in detail for this study.

I used a correlation matrix for the PCA routine, which subtracts the mean from the actual value within each column and divides this by the standard deviation. The reduced data set displays the eigenvalues, or principal component (PC), responsible for the majority of the variation. The first PC represents the greatest variance within the dataset. The second PC accounts for the majority of the remaining variance, and so on. Because each PC is orthogonal to the rest, they are not correlated to one another. Only the first three principal components were calculated, and to determine which were important, I compared the eigenvalues of each PC to the value expected from a random “Broken-Stick” model (e.g. Jolliffe, 2002). If the calculated eigenvalue was greater than the random expectation, the PC was considered significant. *P*-values for each eigenvalue were calculated by the formula suggested by Peres-Neto (2005):

$$p=(n+1)/(N+1)$$

where n is the number of randomizations with an eigenvalue greater than observed, and N is the total number of randomizations ($N=999$).

The eigenvalues calculated by PCA can be shown graphically on an ordination diagram where the distance between individual samples (points) approximates their distance in multidimensional space (e.g. McCune and Grace, 2002). Samples that are similar to each other will plot closer together. Samples with values close to the average for all variables will plot near the origin, while outliers will plot much further away (Legendre and Legendre, 1998). The correlation between variables, represented by each eigenvector, is calculated in the cross-product matrix produced during construction of the PCA. Eigenvectors can be plotted on the ordination in a biplot, providing a visual representation of the relative strength of the loading and correlation of the variable to the ordination axes (Legendre and Legendre, 1998). I created a distance-based biplot in PC-ORD 5.0, which scales the eigenvector to its unit length. The length of the vector on the biplot represents its relative loading on a particular component (eigenvalue) and its direction represents its correlation to the eigenvalues (e.g. Legendre and Legendre, 1998; McCune and Grace, 2002). The angles between individual eigenvectors, however, are meaningless, because the ordination is “flattened” into just two dimensions (correlations between vectors are calculated in the cross-product matrix). An object (=sample unit) projected at a right angle to the vector approximates the object’s position along that vector.

3.4 RESULTS AND DISCUSSION

Results are presented in the following sequence: 1) first, a summary of the data with results of outlier detection and the samples rejected based on this analysis. Rejected samples are excluded from subsequent analyses. 2) Amino acid differences between taxa based on their range (Cordilleran-Boreal vs. Eastern Deciduous Forest) and shell condition. 3) Relative time averaging and age structure patterns within succineid shells at Big Platte and Kulas Quarry based on radiocarbon and D/L ratios. 4) PCA of Big Platte and Kulas Quarry succineids using the raw AAR data, supplemented by additional univariate analyses of the identified trends.

3.4.1 Data Summary

A total of 236 shells were analyzed for AAR (Appendix A). The shells came from 10 bulk sediment samples at Kulas Quarry (all *Catinella* cf. *gelida*.; n=57), and 179 shells from 8 bulk sediment samples at Big Platte: *Succinea* cf. *bakeri* (n=131), *Helicodiscus parallelus* (n=11), *Discus* sp. (n=7), *Vertigo modesta modesta* (n=6), *Columella columella alticola* (n=6), *Vallonia gracilicosta* (n=5), *Hawaiiia minuscula* (n=5), *Pupilla muscorum* (n=4), *Euconulus fulvus* (n=2), *Pupoides albilabris* (n=1), and *Glyphalinia indentata* (n=1). An AAR “sample” consisted of a single shell from one of these species, identified by a UAL lab number (Appendix A).

Several of these taxa have modern ranges that do not overlap (Figure 3.5A, 3.5B). For example, *Columella columella alticola* is associated with alpine tundra habitats with a Cordilleran-Boreal distribution centered over the Rocky Mountains, whereas *Helicodiscus parallelus* is generally associated with Eastern Deciduous Forests

(Hubricht, 1985). The Cordilleran-Boreal taxa are typically much more abundant compared to those from the Eastern Deciduous Forest (Table 3.1). *Helicodiscus parallelus*, however, is often more abundant in samples than the Cordilleran-Boreal species *Vertigo modesta parietalis* and deciduous forest species that prefer colder climates (i.e. *Euconulus fulvus*, *Disscus whitneyi*; Table 3.1). It is possible that these Eastern Deciduous Forest taxa were introduced after the Cordilleran-Boreal shells were deposited, but, in many cases, the occurrence of a few rare species provides greater insight into the environmental conditions than do the abundant ones (Miller and Bajc, 1987). Therefore, before any environmental reconstruction can be done, separating younger shells from older ones based on D/L AA data is vital.

Data screening of *Succinea*, *Catinella*, and *Helicodiscus* flagged a total of 18 outliers in at least one test. Only seven shells (4 *Succinea*, 2 *Catinella*, 1 *Helicodiscus*), about 3.5% of all analyzed, were flagged in two or more tests and rejected (Table 3.3; Figure 3.7). Three shells (UAL#s 6573J, 6846E, and 6566A) were flagged in a majority of tests, while the others were flagged by one or two tests. Samples that were flagged by one test often did not appear as unusual in another. For example, L-Ser/(D+L Asp) flagged five samples that were not flagged in the L-Ser/(D+L Glu) test. The multivariate distance test was the least conservative, flagging four samples (all of which were rejected), while the covariance of Asp to Glu was more conservative, and identified nine samples as outliers. Setting the cutoff for multivariate distance at two standard deviations resulted in flagging an additional four samples, one of which (UAL# 6849D) was flagged in only one other test and would have been rejected based on this lowered cutoff value (see Appendix B).

3.4.2 Amino acid differences between taxa

3.4.2.1 D/L differences by taxon range

The four amino acid D/L ratios measured for each taxon are summarized in Table 3.4, and Figure 3.7, 3.8A). In general, species whose range is currently in the Cordilleran-Boreal regions had significantly higher D/L values than those of Eastern Deciduous Forest species (one-way ANOVA, D/L Asp $p < 0.001$; Table 3.5A). The Cordilleran-Boreal taxa had D/L Asp ratios above 0.250, whereas Eastern Deciduous Forest species had D/L Asp ratios below 0.200 (Figure 3.7, 3.8A). The D/L ratios for the other three amino acids were also lower for Eastern species, and the differences in slow racemizing amino acids (Glu and Ala) were less than differences between fast racemizing amino acids (Asp and Ser; Figure 3.8A). Pairwise comparisons between taxa showed that D/L values for taxa from within a particular province (either Cordilleran-Boreal or Eastern Deciduous Forest) were similar to each other, but significantly different from those of the other province (Table 3.5A, 3.5B). This pattern was most pronounced in the rapidly racemizing amino acids (Asp and Ser). In addition, although there were smaller differences in the absolute values, slowly racemizing amino acids (Glu and Ala) showed the greatest statistical differences between Cordilleran-Boreal taxa. Eastern Deciduous Forest species were not significantly different from each other for any D/L value (Figure 3.8A, Table 3.5A, 3.5B).

3.4.2.2 D/L differences by shell condition

The shells of Eastern Deciduous Forest taxa were generally “fresher” in appearance compared to the Cordilleran-Boreal taxa. These condition scores correlated strongly with D/L ratios; slowly racemizing amino acids displayed stronger and more

significant correlations than did rapidly racemizing amino acids (Table 3.4). Shells with lower condition scores had smaller D/L values compared to shells with high condition scores (Figure 3.8B). D/L values were significantly different between the best-preserved shells (shell condition = 1 or 2) and more weathered shells (shell condition = 3 or 4) (Table 3.6A, 3.6B).

These results show that the well-preserved shells of Eastern Deciduous Forest taxa have significantly lower D/L values than do the lower-quality shells of Cordilleran-Boreal taxa. This suggests that some of the Eastern Deciduous Forest species (*Helicodiscus*, *Glyphalinia*, *Hawaiiia*, and *Pupoides*) were introduced much later, whereas deciduous forest species *Discus whitneyi* and *Euconulus fulvus* were contemporaneous with the Cordilleran-Boreal species. The colluvium was likely deposited during the late Pleistocene as a result of permafrost-induced solifluction (Mason and Knox, 1997), which would account for the abundance of Cordilleran-Boreal taxa with relatively high D/L values. Incorporation of the younger shells could have occurred during the Holocene, when these species adjusted their ranges as a response to climate changes (e.g. Miller and Bajc, 1987). *Glyphalinia*, *Hawaiiia*, and *Helicodiscus* have been reported burrowing into the soil several cm (Pilsbry, 1948; Sparks, 1964). Motter (1898) observed live *Helicodiscus parallelus* and *Hawaiiia miniscula* on exhumed human cadavers. The presence of live gastropods within these graves, all more than 1 m below the surface, indicates an exceptional burrowing capacity for these species. Future paleoecological interpretations of terrestrial gastropod assemblages will have to account for the possibility of introduced species with significantly different climatic preferences. The obvious difference in shell preservation, however, can provide an important first-order

estimate of specimen age. These results contrast with studies from marine shelly assemblages, where taphonomic condition did not correspond well to actual age (e.g. Carroll et al., 2003).

3.4.3 Time averaging estimation of succineid shell assemblages

3.4.3.1 Radiocarbon results

A total of nine radiocarbon dates were obtained from succineid shells for this study (Table 3.7). Three succineid shells from Big Platte yielded ages between $18,964 \pm 228$ and $19,075 \pm 215$ cal yr. BP. Two separate stratigraphic intervals were examined at Kulas Quarry. Samples from KQ05 (depth = 4.5 m) provided two dates at $20,961 \pm 314$ and $21,673 \pm 448$ cal yr BP, whereas samples from KQ15 (depth = 2.75 m) provided four dates between $19,929 \pm 295$ and $20,617 \pm 330$ cal yr BP. In general, radiocarbon results are consistent with stratigraphic position; shells from the same sample horizon yielded radiocarbon dates within a few hundred years or less of one another (Figure 3.2A, B). Reported age dates were significantly different between sites (X^2 , $T=667.9$, $df=8$, $p<0.001$; radiocarbon statistical tests performed with Calib 5.1 BETA software; Stuiver and Reimer, 1993). Samples from Big Platte were not significantly different from each other (X^2 , $T=4.2$, $df=2$, $p=0.069$). Dates from Kulas Quarry samples showed a greater range in reported values from within a selected horizon. The two dates from KQ05 were significantly different at $\alpha=0.05$, but not at $\alpha=0.01$ (X^2 , $T=4.31$, $df=1$, $p=0.038$), while the three dates from KQ15 reported by the Arizona lab were not significantly different (X^2 , $T=4.2$, $df=2$, $p=0.12$; Table 3.7).

3.4.3.2 D/L Asp variation in succineids

The mean D/L Asp values from Big Platte were significantly higher than those of Kulas Quarry (two-sample t-test; $t=2.747$, $p=0.024$; Table 3.4, however the variance for the two sites was similar (test of variance; $F=1.3098$, $df=1$, $p=0.264$). D/L Glu, however, was significantly different in both mean and variance ($F=2.236$, $df=1$, $p<0.001$; unequal variance t-test, $t=14.17$, $p<0.001$). Taken at face value, the D/L Asp values suggest that Big Platte is older than Kulas Quarry, and are at odds with the radiocarbon data that show Kulas Quarry is older than Big Platte. Radiocarbon age results for succineids from Big Platte and Kulas Quarry show that the within-horizon age differences between ^{14}C measurements was relatively small (ca. 10^2 years), and that Kulas Quarry is about 10^3 years older than Big Platte. However, the D/L Asp ratio is a function of both time *and* temperature. Most samples from Big Platte were obtained within 1 m of the surface, whereas Kulas Quarry samples were obtained from more than 2 m. Therefore, it is possible that the relatively high D/L Asp values at Big Platte resulted from elevated surface temperatures rather than greater elapsed time. Oches et al. (1996) noted similar “reversals” in amino acid racemization rates in shells obtained from loess from the Upper Mississippi Valley. In addition, groundwater-induced leaching of free amino acids (enriched in D-amino acids) would be more prevalent in the permeable sand at Kulas Quarry, yielding lower D/L values compared to the clay-rich silt at Big Platte.

The coefficients of variance in succineid shells for D/L Asp at Big Platte and Kulas Quarry were about 5% (Table 3.4), which can be attributed to analytical uncertainty. Other Cordilleran-Boreal taxa such as *Discus*, *Columella*, and *Vertigo* had similarly low variance in D/L Asp. The Eastern Deciduous Forest taxa (*Helicodiscus* and *Hawaiiia*) typically had more variability in the D/L Asp values. Some of this variability

can be attributed to sample size, but the large variability in D/L Asp values in *Helicodiscus* compared to those of most Cordilleran-Boreal taxa suggests a much larger range in relative age for *Helicodiscus* shells. The introduction of these younger shells likely occurred over a much longer time range compared to deposition of the initial assemblage. Previous authors have cautioned that alluvial deposits may contain assemblages that are inherently more mixed due to long-range transport and sediment reworking (e.g. La Rocque, 1970; Hubricht, 1985). The range in D/L Asp values from this study is generally less than that reported for stratigraphically restricted samples of late Pleistocene succineids from eolian deposits in North America and Europe (e.g. 12.5% in Oches et al., 2002; and 4-8% in Walther, 2004) and helicids from the Canary Islands (e.g. 3-12% in Ortiz et al., 2006). Thus, based on D/L Asp values, the scale of age mixing within Big Platte (colluvium) and Kulas Quarry (alluvium) appears to be similar to that other terrestrial deposits.

It is also interesting to note that the D/L Asp values for Big Platte and Kulas Quarry were approximately normally distributed (Shapiro-Wilk normality, $p > 0.5$) with relatively low skewness and kurtosis (Table 3.8). Yanes et al. (2007) reported a higher proportion of left-skewed, platykurtic (less peaked than normal) age distributions within stratigraphic samples of helicid gastropods in the Canary Islands than expected if their samples were drawn from a right-skewed population. Time-averaging studies from marine deposits often yielded right skewed, leptokurtic (more peaked than normal) age distributions (Flessa et al., 1993; Carroll et al., 2003; Kidwell et al., 2005). These authors attributed the right-skewed age distributions as a result of rapid burial with brief periods of exposure allowing an exponential decay of shelly material along the marine shelf. The

results from this study compare with Yanes et al. (2007) and suggest that terrestrial shelly deposits may be controlled by different factors.

3.4.4 Amino acid trends in PCA

The summary statistics for the AAR results from all succineid shells used in the PCA ordination indicate that many of the variables approximate a normal distribution ($|\text{skewness}| < 1$; Table 3.8). Some values displayed $|\text{skew}| > 1$; variables that are not normally distributed tend to influence the PCA results more strongly than normally-distributed variables (McCune and Grace, 2002). D/L Ala values were positively skewed for both Big Platte and Kulas Quarry, while L-Ser/(D+L Glu) and D/L Glu showed positive skewness for the Kulas Quarry samples. The eigenvalue and eigenvector results of the PCA for both sites are provided in Tables 3.9 and 3.10, respectively, and plotted as ordination diagrams in Figures 3.9 and 3.10. Only the first two principal components (PC) were considered significant, accounting for about 58% of the variance at Big Platte and 62% of the variance at Kulas Quarry (Table 3.9).

At Big Platte, the first principal component (PC1) is defined by D/L Asp (positive loading; +), D/L Glu (+), D/L Ser (+), L-Ser/D+L-Asp (negative loading; -), and L-Ser/D+L-Glu (-). The second principal component (PC2) is defined by Depth (+), [Sum] (+), D/L Asp (+), D/L Glu (-), and D/L Ala (-) (Table 3.10; Figure 3.9). The PCA results from Kulas Quarry exhibit a pattern of loadings similar to that for the Big Platte analysis on the first two PC's. (Table 3.10; Figure 3.10). PC1 for the Kulas Quarry data loaded most strongly with D/L Asp (+), D/L Ser (+), L-Ser/D+L Asp (-) and L-Ser/D+L Glu (-),

whereas PC2 loaded most strongly with Depth (+), [Sum] (+), D/L Glu (-), D/L Ala (-), and L-Ser/D+L Glu (-).

The cross-product matrix for Big Platte (Table 3.11) showed the strongest positive correlations for the total concentration of amino acids, [Sum] with D/L Asp; racemization of most amino acids, D/L values of Asp, Glu and Ser; and indicators of elevated L-Ser content (D+L-Asp and D+L Glu). The strongest negative correlations were observed for Depth with D/L Glu and D+L Glu, indicators of elevated L-Ser (L-Ser/D+L-Asp and L-Ser/D+L Glu) with D/L Ser; and D/L Glu versus D+L-Asp and D/L Ser.

The ordination scores for individual shells from Big Platte and Kulas Quarry show different distributions along the first two principal components. Shells in the Big Platte ordination plot on both principal components equally. Shells that were taken from shallow stratigraphic sediment samples are more widely dispersed and plot lower on the second component than samples from further below the surface (Figure 3.9). The Kulas Quarry ordination scores for shells from different stratigraphic horizons show more overlap along PC2 and more separation between horizons along PC1 (Figure 3.10). All the shells from stratigraphic horizon KQ18 and one shell from KQ17 plot much further away from the origin than most samples, which may indicate contamination (the shell from KQ17 was flagged as a single-test outlier, but not rejected during screening).

For both localities, PC1 may represent a contamination and higher D/L AA value gradient in that samples with high L-Ser content (a sign of modern contamination) plot further to the left of the origin, while samples with higher D/L Asp and D/L Glu or lower L-Ser (therefore higher D/L Ser) plot to the right. D/L Ala loads weakly on PC1 but in the same direction as the D/L values of other amino acids. At Big Platte, D/L Asp shows

a moderate positive loading on PC1, whereas it shows a weak negative loading on PC1 at Kulas Quarry (Table 3.10). PC2 may represent a gradient for depth, total concentration, and D-isomers of Ala and Glu, related to bacterial contamination. Deeper samples with a higher total amino acid content plot above the origin of both ordinations, while shells with higher D/L Ala and D/L Glu values plot lower.

While these variables load on similar components, they are not necessarily correlated with each other (Table 3.11). In other words, variables that contributed to the total variance did so independently; no single source of variation could be identified with the PCA. At Big Platte, shells from deeper stratigraphic samples (Depth) were negatively correlated with D/L Ala and D/L Glu, whereas Kulas Quarry shells displayed a negative correlation of Depth with D/L Ala, but not D/L Glu. Depth did not directly correlate with [Sum] in either ordination. D/L Glu showed a strong negative correlation with [Sum] at Kulas Quarry, but these variables were not correlated with each other at Big Platte. D/L Ala was weakly correlated with [Sum] in both ordinations.

It is interesting to note that variables expected to increase (Depth, D/L Asp, D/L Glu) or decrease ([Sum]) with time often show either no correlation or are opposite to the expected trend (Table 3.11). Alternate diagenetic pathways than time such as contamination appear to be responsible for the observed results. D/L Asp and D/L Glu are positively correlated in both ordinations, but Depth is negatively correlated with D/L Glu in shells from Big Platte. In addition, [Sum] shows a strong positive correlation with D/L Asp. Typically, high D/L values indicate older, more racemic mixtures, but will also increase if these amino acids had experienced higher temperatures. If surface heating was responsible for this pattern, the D/L values for the less stable amino acids Asp and Ser

should show a strong negative correlation with Depth. There is a small positive correlation between D/L Asp and Depth at Big Platte, but no correlation at Kulas Quarry (Table 3.11). Therefore, surface heating cannot account for the alteration of D/L Asp values at Big Platte. However, several stratigraphic samples from Kulas Quarry were retrieved from similar depths below the surface (Figure 3.2B), which may account for the lack of a relationship between Depth and D/L Asp at this location.

A connection between amino acid concentration, [Sum], and D/L Asp or Depth (~relative age) may exist. As the protein matrix within the shell breaks down, the resulting free amino acids (typically enriched in D-amino acids) are often more susceptible to leaching. Excessively leached shells may produce anomalously younger D/L results (e.g. Roof, 1997; Penkman et al., 2008). [Sum] displayed little correlation with most variables, but a strong positive correlation with D/L Asp at Big Platte, and a strong negative correlation with D/L Glu at Kulas Quarry (Table 3.11). Leaching may account for the observed behavior of D/L Glu at Kulas Quarry, but does not appear to correspond to the trends observed at Big Platte.

Summary statistics of both the Big Platte and Kulas Quarry data revealed that D/L Ala and D/L Glu were the most skewed variables. This departure from a normal distribution is probably contributing to the loading on PC2 (Table 3.8; Figure 3.9, 3.10). In addition, several of the outliers flagged during screening but retained for the PCA, lie further out along PC1 or PC2. Several of these outliers have particularly high D-Glu and D-Ala values, perhaps due to bacterial contamination. Previous authors have attributed anomalous D/L values in the diagenesis of recent mammal bones (Blackwell et al., 2000), marine sediment (Keil et al., 2000; Pedersen et al., 2001; Grutters et al., 2002), and

scleractinian corals (Nyberg et al., 2001) to bacterial growth. Child et al. (1993) isolated several strains of soil and fecal bacteria that produced collagenase between 10° and 12°C, suggesting some microorganisms have the potential to alter collagen D/L values.

Furthermore, the peptidoglycan within the cell walls of bacteria is enriched in D-Glu and D-Ala (Friedman, 1999), and can also contain D-Asp and D-Ser (Pedersen et al., 2002).

Contamination (as L-amino acids on PC1, or D-amino acids on PC2) appears to have a strong relationship to the variance of the data. Because they load on different PCs, modern contamination (high L-Ser/(D+L AA)) appears to be independent of where in the section a sample was retrieved (Depth; Figures 3.9, 3.10). However, the negative correlations of Depth with D/L Glu and D/L Ala at Big Platte, and Depth with D/L-Ala at Kulas Quarry suggests shallow stratigraphic samples are more likely to be enriched in D-Glu and D-Ala (Table 3.12). Given the locations of Big Platte and Kulas Quarry near agricultural activity, especially livestock and manure, surficial bacterial contamination is a plausible explanation for much of the observed variation in the D/L values. Kaufman (2000, unpublished data) noted elevated D/L values of Ala and Ser, decreased amino acid concentrations, and visual evidence of microbial attack upon gastropod shells subjected to extensive bacterial activity. Child et al. (1993) noted the presence of bacterial enzymes that could preferentially alter specific amino acids in bone collagen. Therefore, sample collection and processing that attempt to minimize bacterial contamination may not be feasible: bacterial contamination may only be detected with anomalous data.

The Big Platte *Succinea* AAR data reveals that some shells have D-Ala values that do not appear to covary with other peak-measured amino acids (such as L-Ala, as shown in Figure 3.11). Decomposition of Ser to Ala may account for some of the higher

D-Ala values, however, the lack of covariance with any L- or D-amino acid suggests this could be from D-Ala that is added from an external source. A logarithmic transformation of the D/L Ala values would reduce the skewness of this variable, however, transformation of D/L Glu would preclude its chronologic utility.

3.5 CONCLUSIONS

3.5.1 Summary

This study demonstrates the potential applications as well as the potential difficulties of applying AAR techniques to fossil gastropods from the study area. A summary of the findings:

1). The gastropod fossils from the Big Platte locality include both Eastern Deciduous Forest and Cordilleran-Boreal taxa, which appear to comprise a non-analog fauna. However, analysis of D/L Asp values from individual shells indicates several Eastern Deciduous Forest taxa (*Helicodiscus*, *Glyphalinia*, *Pupoides*, *Hawaiiia*) are much younger and may have burrowed into the soil, becoming incorporated with the assemblage after deposition. The non-analog component of the Big Platte fauna is partially a result of post-depositional processes, and not attributable to climatic influences.

2). Radiocarbon and D/L Asp results from succineids show minor age differences between shells. Radiocarbon dates on individual shells suggests the degree of age mixing within a stratigraphic horizon may be only a few hundred years; D/L Asp values for succineid shells were well within the range of analytical uncertainty. While younger shells were occasionally introduced after deposition, the shells of Cordilleran-Boreal taxa

show relatively little time averaging. The rare Eastern Deciduous Forest taxa (*Euconulus fulvus*, *Discus whitneyi*) that were identified as late Pleistocene in age are generally widespread and common throughout their range today (Leonard, 1952). This suggests that the late Pleistocene climate may have been similar to those areas where they are rare today; climate reconstructions should not be based on the entire range of these widespread taxa.

3). Principal Component Analysis (PCA) of the amino acid data loaded most strongly on the first component (PC1) with L-Ser (negative) and D/L AA values (positive), perhaps as a result of modern contamination with L-amino acids. The second component (PC2) loaded most strongly with Depth and [Sum] (positive) and D-Ala, D-Glu (negative), which might indicate bacterial decomposition of shell protein and introduction of D-amino acids. Using multivariate statistical techniques, it is possible to observe the net effects of alteration on the entire data set; these anomalies may be overlooked by univariate analysis and screening methods.

Conventional AAR studies measure the total hydrolysable amino acids within gastropod shells, which may be susceptible to contamination (as suggested in this study). Alternatively, intra-crystalline shell proteins appear to behave as a closed system and may be preferable for high-resolution AAR studies (e.g. Penkman et al, 2008) especially from sites at high risk for significant contamination. In addition, data screening can be complex and rejection criteria will vary depending upon the research question of interest. Data that appear “normal” in one variable may be aberrant in another. For example, shells that displayed a relatively normal distribution of D/L Asp values sometimes contained aberrant values for other amino acids (such as D/L Glu or D/L Ala). Whether these

aberrant amino acids affect other values is not known at this time. Data screening for AAR is unique to each situation and a universal set of cutoff points has not been determined (e.g. Kosnik and Kaufman, 2008). Based on these results, additional screening methods to identify aberrant D-Glu and D-Ala values may reveal potentially contaminated samples.

3.5.2 Taxonomic AAR trends

The gastropod assemblage recovered at Big Platte contained several non-analog species whose modern ranges include both Cordilleran-Boreal and Eastern Deciduous Forest distributions. Eastern Deciduous Forest species are unique in that they have climate preferences incompatible with the inferred conditions found during the late Pleistocene and their shells appeared considerably newer (Figure 3.8B). The D/L ratios of these shells confirmed that the Eastern Deciduous Forest taxa were considerably younger, having been incorporated into the assemblage after deposition. *Euconulus fulvus* and *Vallonia gracilicosta*, however, are also relatively temperate species. Based on the similarity of the D/L values, these taxa appeared to be contemporaneous with the remaining late Pleistocene gastropod fauna at Big Platte. The presence of these temperate species in the Upper Mississippi Valley at the same time as colder, Cordilleran-Boreal species supports the interpretation by Baker et al. (1986) and Woodman et al. (1996) that conditions were colder, but more equable – with less extremes in summer and winter temperatures – than today.

There were significant differences in the amino acid data of the gastropods from this study. If the influence of microbial activity is relatively small, the variation of amino

acids in succineid shells may be due to taxonomic differences, which would support the conclusions of others (e.g. Oches et al., 1996) that individual genera can yield significantly different D/L values. However, succineids pose a taxonomic problem, due to the morphological similarities of their shells. It is difficult to identify succineids to genus, let alone species, based on shell characters. The large differences observed between *Succinea* and *Catinella* from this study have implications for future paleotemperature gradient studies (e.g. Oches et al., 1996) that compare D/L values in different succineid taxa.

3.5.3 Time averaging of succineids

Based on the radiocarbon and AAR results, it appears that individual horizons at Big Platte and Kulas Quarry are not time-averaged on a scale detectable with AAR. In contrast, radiocarbon results do suggest that the age difference between shells *within* a sample horizon is small, perhaps less than 100 years for Big Platte (Table 3.7). The multiple dates from each stratigraphic horizon at Kulas Quarry are within ca. 700 years of each other. Ages between the KQ-15 and KQ-05 horizons at Kulas Quarry indicate these samples are separated by at least 1,000 years, yet the differences in their D/L Asp values are quite small, perhaps as a partial result of surface heating, which could have increased the D/L Asp values at Big Platte and the stratigraphic samples from Kulas Quarry at similar depths. Interestingly, D/L Asp and D/L Glu ratios from Big Platte are higher than those at Kulas Quarry, even though the latter is over 1,000 years older. The significant difference in the mean D/L Asp values may be a result of differential heating, leaching, and/or contamination. However, the variance of D/L Asp values at Kulas Quarry is not

significantly different from the D/L Asp variance at Big Platt and suggests the overall variance in each deposit may represent similar magnitudes of time averaging, or diagenetic alteration.

Previous AAR studies of shelly faunas from marine settings showed significantly right-skewed, leptokurtic distributions of estimated age values, which have been interpreted as a result of time averaging and an exponential loss of older specimens (Flessa et al., 1993; Kowaleski et al., 1998; Carroll et al., 2003; Kidwell et al., 2005). Terrestrial shell assemblages may be subject to different taphonomic mechanisms compared to marine ones; the duration of sediment deposition and possibilities for shell reworking may be reduced (e.g. Yanes et al., 2007), however, the data presented here do not point to any particular taphonomic bias. The range of D/L Asp ratios observed at Big Platte (colluvium) and Kulas Quarry (alluvium) are similar to the ranges reported from loess (e.g. Oches et al., 2002). In addition, the radiocarbon results from this study indicate similar ages between shells. Much concern has been raised regarding the temporal fidelity of gastropod fossils within alluvial deposits due to uncertainties in the reworking and mixing of shells during sediment transport and deposition (e.g. LaRocque, 1970; Hubricht, 1985). These results suggest that alluvial deposition is not an *a priori* reason to ignore the shells contained within these deposits.

3.5.4 Trends from Principal Component Analysis

The results of this study demonstrate the utility of PCA for analyzing AAR data. Previous studies have mentioned the redundancy and covariance of D/L values for multiple amino acids as a method of error checking and independent chronometers (e.g.

Kaufman, 2003). Ordinations of shells from both Big Platte and Kulas Quarry showed the same general patterns in the loadings on each principal component (Table 3.10; Figures 3.9, 3.10). I interpret PC1 to represent a gradient of L-Ser (negative correlation; modern contamination) and higher D/L AA values (positive). PC2 likely represents a gradient of Depth and [Sum] (positive correlation) and bacterial contamination with D-Glu and D-Ala (negative). This may be a result of bacterial attack on the shells, which would account for higher D-Ala and D-Glu and breaking down shell proteins (lower total AA concentration) near the surface.

While a positive correlation among D/L values is expected as a result of increased racemization with time and diagenesis, several of these results appear to be contradictory. If surface heating was responsible for the higher D/L Asp values at Big Platte, there should be a *negative* correlation between D/L Asp and Depth, since deeper samples would be insulated and therefore less racemic. If the increase of D/L Asp with Depth shown in Figure 3.9 was a result of leaching near the surface (thereby preferentially removing free, D-Asp), D/L values for one or more of the other amino acids (particularly labile Ser) should show a similar trend, and [Sum] would be expected to decrease as these amino acids are removed from samples close to the surface. Finally, D/L ratios of the slow racemizing amino acids Glu and Ala decrease with Depth (Table 3.11; Figures 3.9, 3.10). While leaching of amino acids can account for the increase in total concentration with Depth, this leaching would preferentially remove free amino acids, which are generally enriched in their D- forms. Surface heating may account for the correlation of D/L Asp with Depth at Big Platte given the proximity of these samples to the surface. In contrast, D/L Asp shows almost no correlation with Depth at Kulas Quarry, which may

be partly a function of the increased depth (>2 m) at this site from which stratigraphic samples were taken.

The strong negative correlation between Depth and D/L Glu and D/L Ala suggests a relative decrease in the proportion of their L-amino acids. Because D/L Asp is either positively or un-correlated with Depth and D/L Ser shows no correlation, heating and leaching alone are insufficient to explain this pattern. Near-surface bacterial contamination of Big Platte and Kulas Quarry samples with D-amino acids (particularly D-Ala and D-Glu) would account for this trend. Bacterial enrichment in D-amino acids would be more prevalent near the surface, and it would explain why samples were flagged as outliers in some tests, but not in others. Addition of D-Glu or D-Ala would skew only the results of those tests that look for variation in the relative proportions of specific D-amino acids.

The implications of bacterial contamination are unknown. This pattern has not been previously observed in gastropod shells, although it has been noted in terrestrial mammal bones and marine corals (Blackwell, et al., 2000; Nyberg et al., 2001). Regardless, bacterial alteration of the D/L Glu ratio independently of D/L Asp reduces the utility of these variables as independent tests of age (e.g. Kaufman, 2000). The potential for bacterial contamination to affect future AAR analyses seems high, given the proximity of many fossil localities in the Upper Mississippi Valley to agricultural centers. By comparison, the lack of correlation between L-Serine and Depth suggests that this contamination occurs during or after sample collection (since all samples are collected and processed using the same methods regardless of depth). Reduction of this source of contamination may be as simple as wearing latex gloves during sample collection and

processing. While transformation of the data can reduce the influence of these processes, using D/L Glu as a chronometer will require refined data screening techniques.

The results presented here suggest potential avenues of future work. The lack of correlation between D/L Asp and either radiocarbon or stratigraphic results prevented making a calibrated AAR time/temperature from this data. Given the demonstrated influence of contamination on these results, analysis of intercrystalline proteins may provide more robust results for geochronological estimates (e.g. Penkman et al., 2008). In order to assess the influence of microbial activity, it would be informative (although non-trivial) to culture bacteria from individual shells and examine the shell surface with an SEM to look for microbial traces. Data screening methods should include testing for aberrant values for D-Glu and D-Ala, (e.g. Figure 3.11) which are present in high quantities within bacterial peptidoglycan. Although shell condition has been shown not to be an indicator of age in marine shelf deposits (e.g. Carroll et al., 2003), clear, glossy shells in Quaternary terrestrial sediments may indicate younger shells (e.g. Plug, 1990) have been incorporated into the assemblage.

The non-temporal influences on the AAR data suggest additional screening will be necessary if this method is to be applied to other fossiliferous deposits in Wisconsin. Moscow Fissure (Foley, 1984) contained numerous boreal and deciduous forest vertebrate taxa. A one-kilogram bulk sample of snake vertebrae from this site yielded a full-glacial age for the site (ca. 21,000 cal yr BP). The few gastropods described were all Eastern Deciduous Forest species. AAR analysis of the gastropods from this site may shed light on this fauna. In addition, if shelly material can be retrieved from pre Late

Wisconsin sediments, the methods described here may provide useful to constrain the timing of these earlier events.

3.6 ACKNOWLEDGEMENTS

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Table 3.1. Brief description of the distribution and habitat affinity for taxa discussed in text. Big Platte Fauna (shell counts) provided to illustrate relative abundance of individual species. See range maps in Figure 3.5A and 3.5B.

Taxon	Province	Ecology	Big Platte Fauna
<i>Columella columella alticola</i>	C-B	Very cold, moist, willow scrub, high elevations often above 2000m elevation.	357
<i>Pupilla muscorum</i>	C-B	Dry, open arctic, catholic spp.	96
<i>Vertigo modesta modesta</i>	C-B	Willow-birch thickets, cold, moist	561
<i>Discus shimeki</i>	C	Cold, montane forest above 2000m elevation	498
<i>Discus whitneyi</i>	W	Cold, moist to dry, open to forest habitats; warmer habitats than <i>D. shimeki</i> .	4
<i>Vallonia gracilicosta</i>	C-B	Dry, open environments.	28
<i>Euconulus fulvus</i>	C-B (EDF)	Widespread, moist to dry environments, most common in northern regions.	8
<i>Catinella</i> cf. <i>gelida</i>	MW	Common late Pleistocene fossil throughout Midwest, relict in UMW (Frest, 1987).	131
<i>Succinea</i> cf. <i>bakeri</i>	MW	Common in fossil assemblages from Nebraska to Illinois, thought to be extinct.	1848
<i>Helicodiscus parallelus</i>	EDF	Prefers humid woodlands, range extends from Newfoundland west to the plains border.	24
<i>Hawaiiia miniscula</i>	W (EDF)	Widespread from Alaska to Newfoundland and south to Mexico. Typically found in more forested habitats.	13
<i>Pupoides albilabris</i>	EDF	Found under leaf litter in moist woodlands to dry, open grasslands.	4
<i>Glyphalinia indentata</i>	EDF	Common in woodlands, occasionally found in more open areas.	3

Notes: C-B = Cordilleran-Boreal distribution, C = Cordilleran, W = widespread, EDF = Eastern Deciduous Forest, MW = Midwest Biome (Frest and Fay, 1980). Big Platte Fauna obtained from 72.6 kg of sediment, $N=3575$ shells, note relative paucity of some EDF fauna (e.g. *Glyphalinia*) but not *Helicodiscus*. Shells analyzed for AAR include 55 shells of *Catinella* cf. *gelida* from Kulas Quarry.

Table 3.2. Description of AAR variables used in this study and their abbreviations.

Variable	Description
D/L Asp	Ratio of D- to L-Aspartic Acid. Racemizes quickly, one of most commonly used aminochronologic measures with HPLC (e.g. Kaufman, 2000).
D/L Glu	Ratio of D- to L-Glutamic Acid. Racemizes more slowly than Asp. Together with Asp are abundant in mollusk shell protein and among most precisely resolved AA's.
D/L Ser	Ratio of D- to L-Serine. Racemizes quickly; very labile with complicated racimization and decomposition kinetics. Excessive L-Ser indicative of modern contamination.
D/L Ala	Ratio of D- to L-Alanine (Ala). A slow racemizer, it is also a byproduct of Ser decomposition (e.g. Collins and Riley, 2000).
L-Ser/(D+L Asp)	Ratio of L-Serine to total Aspartic Acid. High L-Ser values indicate contamination by modern AA's (e.g. Kosnik and Kaufman, 2008).
L-Ser/(D+L Glu)	Ratio of L-Serine to total Glutamic Acid. When plotted against D/L Asp, serves as a quasi-independent test of contamination with L-Ser/(D+L Asp) vs. D/L Glu.
[Asp]	Concentration of Aspartic Acid (pM per Mg shell), calibrated to internal spike of L-hArg during analysis by HPLC (Kaufman and Manley, 1998).
[Glu]	Concentration of Glutamic Acid, should covary with [Asp] (e.g. Kosnik and Kaufman, 2008).
[Ser]	Concentration of Serine. Very unstable AA, present in shelly material at low concentrations, high [Ser] values often indicate contamination (e.g. Kaufman, 2006).
[Ala]	Concentration of Alanine.
[Sum]	Total concentration of Asp+Glu+Ser+Ala (pM per Mg shell). In general, concentration should decrease with time as organic material degrades and is lost from shell.

Note: L-Ser and "D+L AA" values determined from peak areas measured by HPLC, while concentrations were calibrated to the internal spike of synthetic L-hArg.

Table 3.3. Outliers flagged during screening. Note that samples that flagged in more than one test were rejected.

UAL#	Samp. Loc.	Taxon	Screening Criterion:					#
			D+L Asp	D+L Glu	D/L-Glu, D/L-Asp	[Asp], [Glu]	MV	
6573J	BP-C1a	<i>Succinea</i>		X	X	X	X	4
6303A	BP-C1a	<i>Succinea</i>				X		1
6303B	BP-C1a	<i>Succinea</i>				X		1
6572A	BP-C1b	<i>Succinea</i>				X		1
6572N	BP-C1b	<i>Succinea</i>	X					1
6572R	BP-C1b	<i>Succinea</i>	X		X			2
6329E	BP-C1c	<i>Succinea</i>	X					1
6570B	BP-C1d	<i>Succinea</i>				X	X	2
6330D	BP-C2a	<i>Succinea</i>	X	X				2
6574C	BP-C2a	<i>Succinea</i>		X				1
6574F	BP-C2a	<i>Succinea</i>				X		1
6331A	BP-C3a	<i>Succinea</i>	X					1
6331C	BP-C3a	<i>Succinea</i>	X					1
6846E	KQ-09	<i>Catinella</i>	X	X	X	X	X	5
6849D	KQ-15	<i>Catinella</i>				X		1
6850C	KQ-17	<i>Catinella</i>	X	X				2
6850F	KQ-17	<i>Catinella</i>			X			1
6566A	BP-C1a	<i>Helicodiscus</i>	X	X	X	X	X	4

Notes: **X** indicates sample was flagged as a 3 σ outlier; **D+L Asp** = covariances of L-Ser/(D+L Asp) vs. D/L Glu; **D+L Glu** = covar of L-Ser/(D+L Glu) vs. D/L Asp; **MV** = multivariate euclidean distance; **#** = total number of shells flagged by screening criterion; rejected outliers (7 shells) in boldface type.

Table 3.4. AAR summary data for all taxa. *Catinella* shells are from Kulas Quarry, while the remaining shells are from the Big Platte Fauna.

TAXON	n	D/L Asp			D/L Glu			D/L Ser			D/L Ala			S.C.
		mean	$\pm 1\sigma$	CV	mean	$\pm 1\sigma$	CV	mean	$\pm 1\sigma$	CV	mean	$\pm 1\sigma$	CV	
<i>Succinea</i>	127	0.333	0.019	5.60	0.099	0.007	6.73	0.541	0.055	10.18	0.190	0.034	17.89	3
<i>Catinella</i>	55	0.327	0.016	4.98	0.078	0.010	12.74	0.496	0.060	12.13	0.136	0.015	11.03	3
<i>Discus</i>	7	0.331	0.026	7.92	0.088	0.008	9.16	0.479	0.044	9.19	0.193	0.021	10.88	3.17
<i>Vertigo</i>	6	0.336	0.013	3.82	0.111	0.003	2.64	0.510	0.047	9.29	0.284	0.013	4.58	3
<i>Columella</i>	6	0.296	0.020	6.74	0.121	0.019	15.54	0.437	0.062	14.07	0.282	0.023	8.16	3.17
<i>Vallonia</i>	5	0.283	0.054	19.16	0.074	0.019	25.27	0.365	0.129	35.37	0.141	0.018	12.77	3.6
<i>Pupilla</i>	4	0.333	0.009	2.72	0.124	0.019	15.62	0.507	0.043	8.47	0.330	0.051	15.45	3.5
<i>Euconulus</i>	2	0.322	0.006	1.98	0.109	0.005	4.56	0.520	0.003	0.54	0.221	0.001	0.45	3
<i>Helicodiscus</i>	10	0.141	0.037	26.38	0.046	0.013	28.67	0.168	0.050	29.64	0.069	0.019	27.54	2.1
<i>Hawaii</i>	5	0.111	0.046	41.01	0.046	0.011	23.64	0.128	0.055	42.87	0.061	0.019	31.15	2
<i>Pupoides</i>	1	0.081	NA	NA	0.032	NA	NA	0.118	NA	NA	0.032	NA	NA	1
<i>Glyphalinia</i>	1	0.139	NA	NA	0.040	NA	NA	0.166	NA	NA	0.050	NA	NA	1
Spearman-Rho		0.575			0.712			0.500			0.754			
P-value		0.050			0.009			0.000			0.005			

Notes: n=total number of shells analyzed (whole shell analyzed, except for *Discus*); CV=coefficient of variance = (SD/mean)*100; S.C. = shell "taphonomic score." Spearman-Rho correlation coefficient calculated by shell condition versus D/L of each amino acid (Wessa.net CITE).

Table 3.5. Pairwise ANOVA results for D/L values by taxon. Comparisons for each amino acid are grouped in the upper right, or lower left.

A: Tukey's pairwise comparisons, **p-val** by taxon. D/L Asp (upper right) and D/L Glu (lower left)

	<i>Succinea</i>	<i>Catinella</i>	<i>Discus</i>	<i>Vertigo</i>	<i>Columella</i>	<i>Vallonia</i>	<i>Pupilla</i>	<i>Euconulus</i>	<i>Helicodiscus</i>	<i>Hawaiiia</i>	<i>Pup/Gly</i>
<i>Succinea</i>		1.000	1.000	1.000	0.096	0.011	1.000	0.906	<0.001	<0.001	<0.001
<i>Catinella</i>	0.008		1.000	1.000	0.305	0.057	1.000	0.994	<0.001	<0.001	<0.001
<i>Discus</i>	0.711	0.753		1.000	0.164	0.023	1.000	0.963	<0.001	<0.001	<0.001
<i>Vertigo</i>	0.434	<0.001	0.001		0.060	0.006	1.000	0.832	<0.001	<0.001	<0.001
<i>Columella</i>	0.002	<0.001	<0.001	0.790		1.000	0.118	0.935	<0.001	<0.001	<0.001
<i>Vallonia</i>	0.001	1.000	0.324	<0.001	<0.001		0.015	0.556	<0.001	<0.001	<0.001
<i>Pupilla</i>	<0.001	<0.001	<0.001	0.414	1.000	<0.001		0.932	<0.001	<0.001	<0.001
<i>Euconulus</i>	0.774	<0.001	0.009	1.000	0.456	<0.001	0.153		<0.001	<0.001	<0.001
<i>Helicodiscus</i>	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001			0.519	0.456
<i>Hawaiiia</i>	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	1.000		1.000
<i>Pup/Gly</i>	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.793	0.814	

1-Way ANOVA, unequal var: D/L Asp (F=31.4, df=12.07, p<0.001); D/L Glu (F=62.5, df=11.83, p<0.001)

B: Tukey's pairwise comparisons, **p-val** by taxon. D/L Ser (upper right) and D/L Ala (lower left)

	<i>Succinea</i>	<i>Catinella</i>	<i>Discus</i>	<i>Vertigo</i>	<i>Columella</i>	<i>Vallonia</i>	<i>Pupilla</i>	<i>Euconulus</i>	<i>Helicodiscus</i>	<i>Hawaiiia</i>	<i>Pup/Gly</i>
<i>Succinea</i>		0.981	0.840	0.999	0.151	<0.001	0.998	1.000	<0.001	<0.001	<0.001
<i>Catinella</i>	0.110		1.000	1.000	0.884	0.017	1.000	1.000	<0.001	<0.001	<0.001
<i>Discus</i>	1.000	0.077		0.999	0.989	0.077	1.000	0.990	<0.001	<0.001	<0.001
<i>Vertigo</i>	<0.001	<0.001	<0.001		0.663	0.004	1.000	1.000	<0.001	<0.001	<0.001
<i>Columella</i>	<0.001	<0.001	<0.001	1.000		0.685	0.730	0.472	<0.001	<0.001	<0.001
<i>Vallonia</i>	0.207	1.000	0.153	<0.001	<0.001		0.006	0.001	<0.001	<0.001	<0.001
<i>Pupilla</i>	<0.001	<0.001	<0.001	0.295	0.240	<0.001		1.000	<0.001	<0.001	<0.001
<i>Euconulus</i>	0.865	<0.001	0.916	0.023	0.033	0.001	<0.001		<0.001	<0.001	<0.001
<i>Helicodiscus</i>	<0.001	0.012	<0.001	<0.001	<0.001	0.004	<0.001	<0.001		0.992	1.000
<i>Hawaiiia</i>	<0.001	0.002	<0.001	<0.001	<0.001	0.001	<0.001	<0.001	1.000		1.000
<i>Pup/Gly</i>	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.910	0.993	

1-Way ANOVA, unequal var: D/L Ser (F=75.1, df=15.6, p<0.001); D/L Ala (F=242.5, df=15.8, p<0.001)

Notes: Pup/Gly=Pupoides/Glyphalinia; Bonferroni transformation of $\alpha_{(0.05/46)}=0.00109$

Table 3.6. Pairwise ANOVA for shell condition.

A: Tukey's pairwise ***p-val*** by shell condition D/L Asp (upper right); D/L Glu (lower left).

	SC=4	SC=3	SC=2	SC=1
SC=4	1	0.822	<0.001	<0.001
SC=3	0.911	1	<0.001	<0.001
SC=2	<0.001	<0.001	1	0.611
SC=1	<0.001	<0.001	0.617	1

1-way ANOVA, unequal var: D/L Asp (F=89.8, df=3.96, p<0.001); D/L Glu (F=94.9, df=4.33, p<0.001)

B: Tukey's pairwise ***p-val*** by shell condition D/L Ser (upper right); D/L Ala (lower left).

	SC=4	SC=3	SC=2	SC=1
SC=4	1	0.076	<0.001	<0.001
SC=3	0.357	1	<0.001	<0.001
SC=2	<0.001	0.001	1	0.992
SC=1	<0.001	<0.001	0.814	1

1-way ANOVA, unequal var: D/L Ser (F=192, df=4.18, p<0.001); D/L Ala (F=123, df=4.68, p<0.001)

Table 3.7. Radiocarbon results from Kulas Quarry and Big Platte.

Sample Loc	Lab#	¹⁴C Age	Cal Age	Depth (m)	<i>p-val</i>
KQ-15	Beta-223641	16,670±60	19,929±295	2.75	
KQ-15 ^a	AA-83090	16,840±120	20,059±296	2.75	T=12.61,
KQ-15 ^a	AA-83091	17,180±130	20,617±330	2.75	<i>0.0056^b</i>
KQ-15 ^a	AA-83092	16,890±120	20,122±288	2.75	
KQ-05	Beta-223642	17,550±70	20,961±314	4.5	T=4.31,
KQ-05**	AA-82558	17,990±200	21,673±448	4.5	<i>0.038</i>
BP-C1a	Beta-223638	15,710±60	18,964±228	0.15-0.45	
BP-C1a	Beta-223637	15,890±50	19,075±215	0.15-0.45	T=4.2,
BP-C1b	Beta-231781	15,800±100	19,021±229	0.7	<i>0.069</i>
					Tot: T=107, <i>p</i> <<0.0001

Notes: **Depth (m)** indicates below top of section, all dates obtained via AMS ¹⁴C analysis of gastropod shell carbonate. ^aAdditional Kulas Quarry dates analyzed by Rech et al. (in prep). **Cal Age** = Calibrated age (cal yr. BP). **T**-statistic based on chi-square distribution of similarity in radiocarbon ages. ^aProbability of same age for KQ-15 improves to *p*=0.122 if Beta 14C sample omitted.

Table 3.8. Descriptive statistics for variables used in PCA. Variables represent AAR results for all succineid shells from Big Platte (*Succinea* cf. *bakeri*) and Kulas Quarry (*Catinella* cf. *gelida*). Results in bold to highlight non-normal data distributions. Refer to Table 3.4 for other summary statistics.

Variable	Big Platte (n=127)		Kulas Quarry (n=55)	
	skew	kurt	skew	kurt
Depth	0.86	-0.02	0.45	-0.79
[Sum]	0.82	3.45	-0.40	0.46
D/L Asp	0.03	-0.04	0.18	-0.47
D/L Glu	0.11	0.05	2.26	8.20
D/L Ser	-0.84	0.82	-0.35	1.33
D/L Ala	2.26	6.34	1.26	2.45
L-Ser/(D+L Asp)	0.74	0.41	0.91	0.30
L-Ser/(D+L Glu)	1.00	0.94	1.03	2.07

Notes: Skewness/Kurtosis values calculated for screened data from succineid shell AAR analyses. Kulas Quarry (*Catinella*) and Big Platte (*Succinea*). Values > 1 in bold to highlight non-normal variables. For data mean & variance, see Table 3.4.

Table 3.9. Eigenvalues from PCA of Big Platte and Kulas Quarry Data.

P.C.	Big Platte			Kulas Quarry		
	E.V.	%Var	B.S.	E.V.	%Var	B.S.
1	3.218	40.2	2.718	3.011	37.6	2.718
		<i>40.2</i>	<i>p=0.001</i>		<i>37.6</i>	<i>p=0.001</i>
2	1.449	18.1	1.718	1.947	24.3	1.718
		<i>58.3</i>	<i>p=0.001</i>		<i>61.9</i>	<i>p=0.001</i>
3	1.078	13.5	1.218	1.22	15.3	1.218
		<i>71.8</i>	<i>p=0.879</i>		<i>77.2</i>	<i>p=0.286</i>

Notes: **P.C.**=Principal Component; **Eigenval.** = eigenvalue of P.C.; **%Var** = proportion of variance explained by component (cumulative in italics); **B.S.** = "Broken Stick," expected eigenval. from random model - if E.V.>B.S., component can be considered "important" (e.g. Jackson, 1993); **p-value** calculated $(n+1)/(N+1)$, where n is no. of randomizations with an E.V. for that axis \geq observed and N is the total no. ($N=999$) of randomizations (Peres-Nato et al., 2005).

Table 3.10. Eigenvectors for variables along the first three PCs. Only the first two PCs are considered significant. Note also that “D+L-Asp” is an abbreviation for L-Ser/(D+L Asp) and “D+L-Glu” is an abbreviation for L-Ser/(D+L Glu).

Var	Big Platte			Kulas Quarry		
	1st PC	2nd PC	3rd PC	1st PC	2nd PC	3rd PC
Depth	-0.09	0.67	-0.32	0.12	0.32	0.68
[Sum]	0.25	0.42	0.41	-0.01	0.42	-0.60
D/L-Asp	0.34	0.33	0.35	0.42	-0.11	-0.17
D/L-Glu	0.33	-0.37	0.41	0.25	-0.55	0.20
D/L-Ser	0.48	0.00	-0.29	0.48	0.12	-0.24
D/L-Ala	0.17	-0.31	-0.44	0.23	-0.52	-0.20
D+L-Asp	-0.50	0.11	-0.01	-0.50	-0.14	-0.09
D+L-Glu	-0.44	-0.15	0.40	-0.45	-0.33	-0.11

Note: Eigenvectors (loading) for variables on first three principal components (PCs) at Big Platte and Kulas Quarry. Higher values (+ or -) indicate stronger loading = greater contribution of that variable to the variance along a particular PC. Values $|EV| \geq 0.30$ are in bold.

Table 3.11. Cross-product matrix for variables from PCA.

Big Platte	Variable	Depth	[Sum]	D/L-Asp	D/L-Glu	D/L-Ser	D/L-Ala	D+L-Asp	D+L-Glu	Kulas Quarry
	Depth	1.00	-0.08	0.03	0.06	0.01	-0.28	-0.27	-0.38	
	[Sum]	0.09	1.00	0.01	-0.48	0.14	0.18	0.01	-0.15	
	D/L-Asp	0.13	0.46	1.00	0.33	0.56	0.36	-0.51	-0.35	
	D/L-Glu	-0.37	0.10	0.32	1.00	0.18	0.63	-0.22	-0.04	
	D/L-Ser	0.00	0.16	0.40	0.45	1.00	0.20	-0.67	-0.69	
	D/L-Ala	-0.15	-0.03	0.05	0.11	0.23	1.00	-0.20	0.00	
	D+L-Asp	0.26	-0.35	-0.44	-0.52	-0.69	-0.28	1.00	0.75	
	D+L-Glu	-0.46	-0.28	-0.03	-0.16	-0.80	-0.16	0.68	1.00	

Notes: numbers indicate correlation coefficients between variables (BP shown lower left, KQ in upper right), higher values (+ or -) indicate stronger correlation. Correlation of a variable and itself is = 1.00. Values of $|\text{coeff}| \geq 0.30$ in bold.

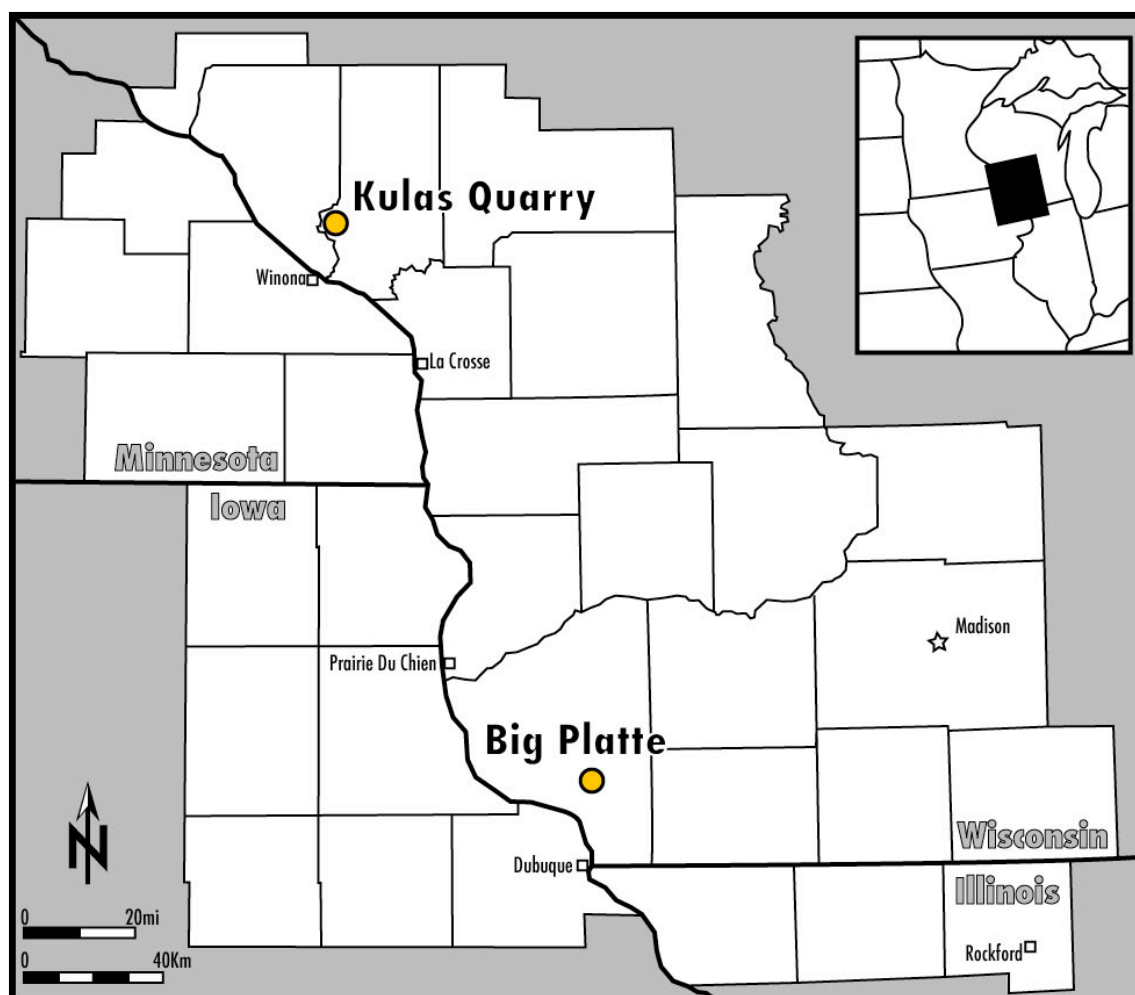


Figure 3.1. Locations of the sites discussed in this chapter.

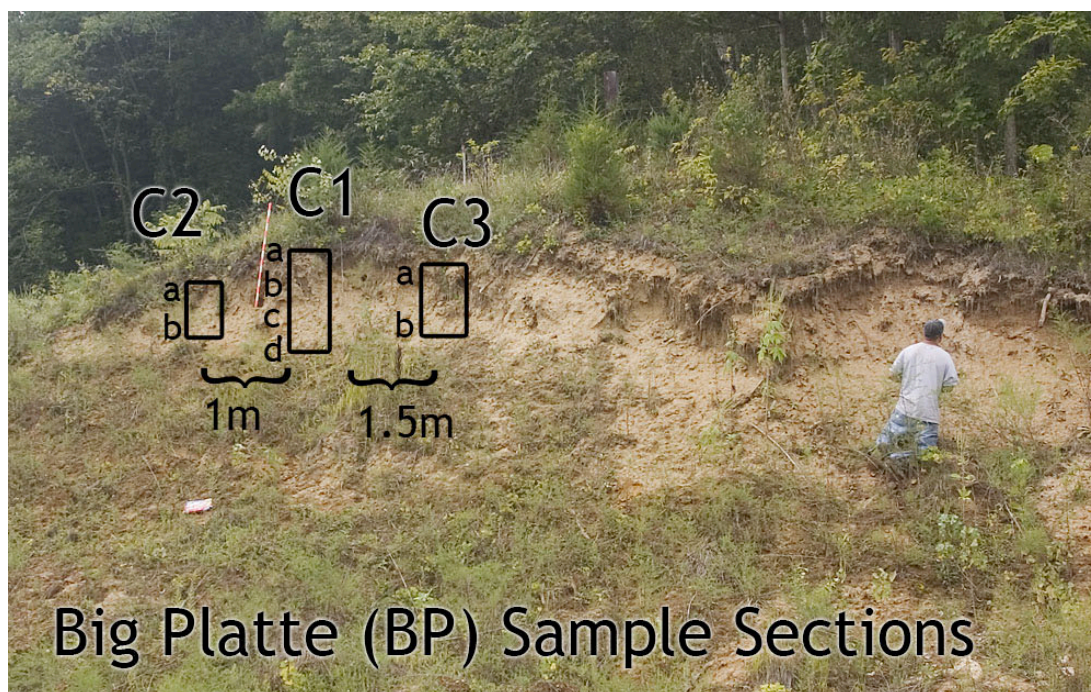


Figure 3.2A Big Platte exposure with locations of samples. Radiocarbon dates obtained from section C1 (See Table 3.8).

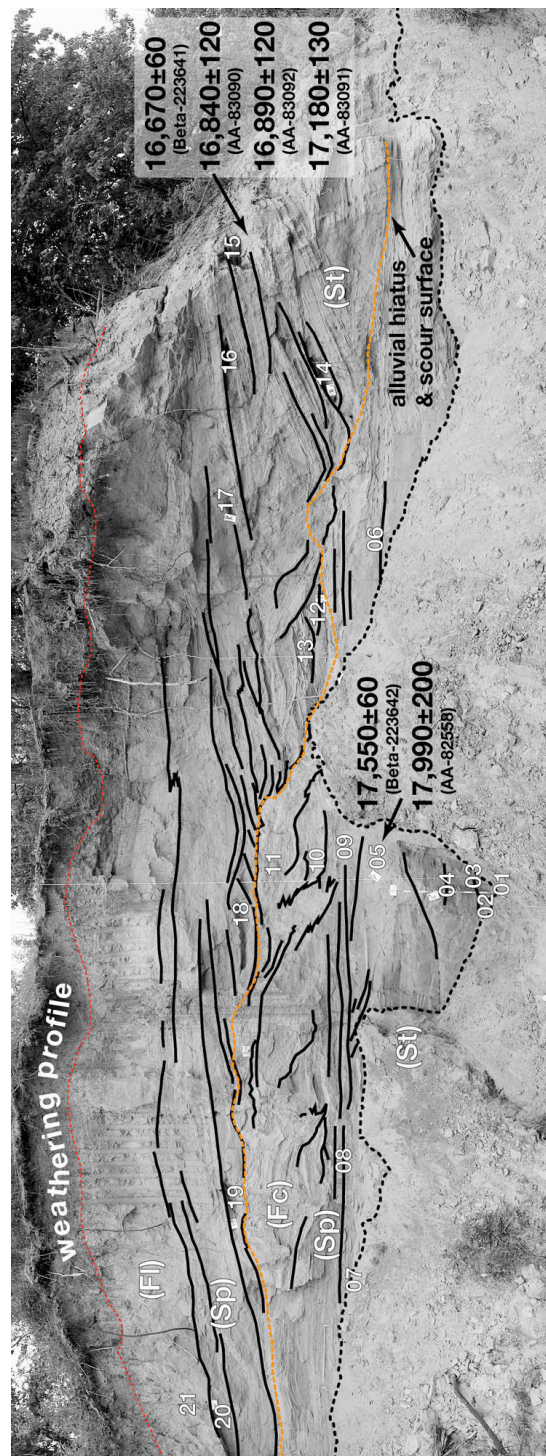


Figure 3.2B. Location of samples from Kulas Quarry. AAR samples obtained from 03, 05, 06, 09, 10, 12, 15, 17, 18, and 20.



Figure 3.3A. Auger sampling at Big Platte.



Figure 3.3B. Selective sampling at Kulas Quarry. Note large cross beds.



Figure 3.3C. Landowner using front-end loader to remove the lower 2 m of cover at Kulas Quarry.

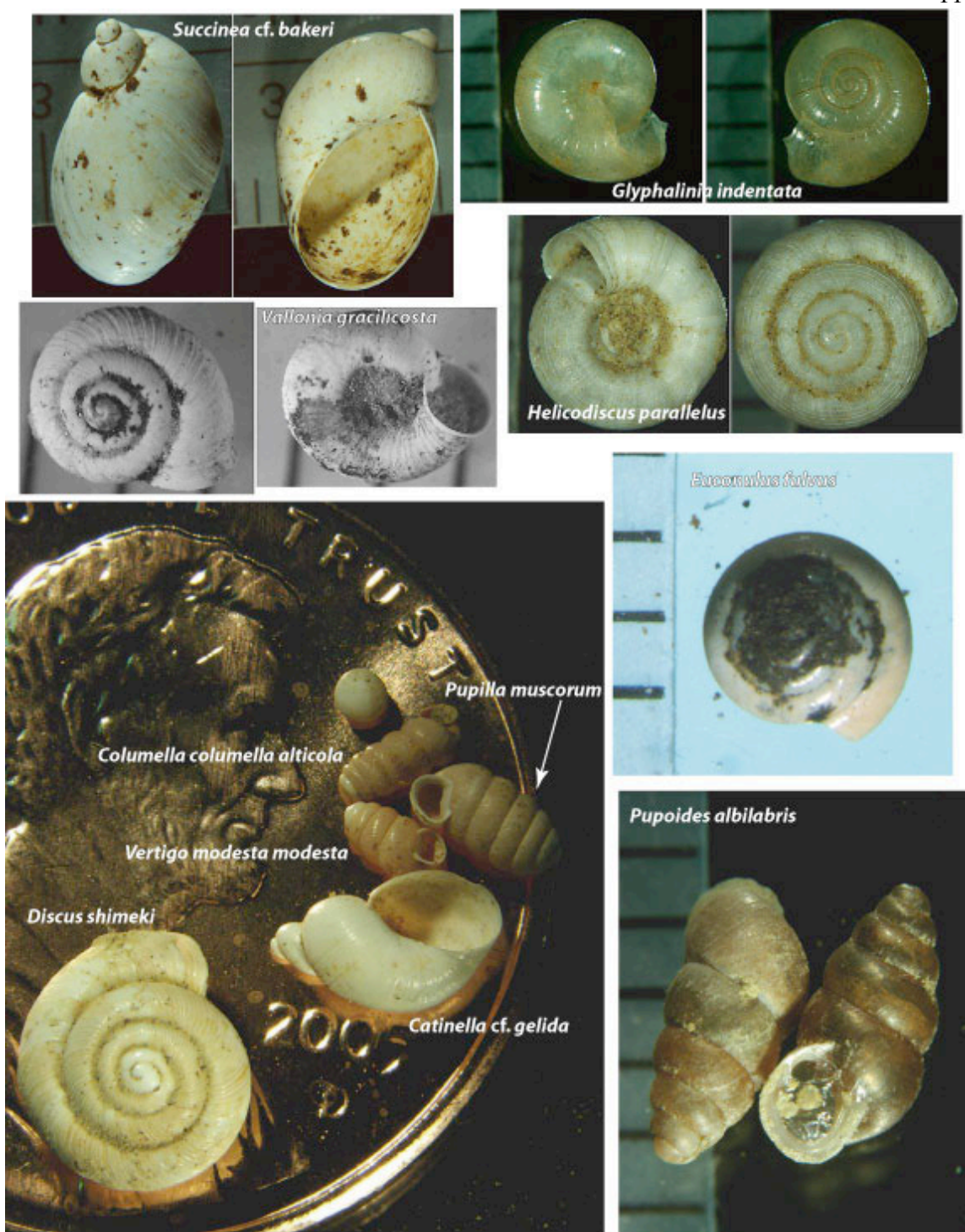


Figure 3.4. Representative photographs of snail taxa analyzed with AAR. Note difference in appearance between Cordilleran-Boreal and Eastern Deciduous Forest Taxa (Table 3.1).

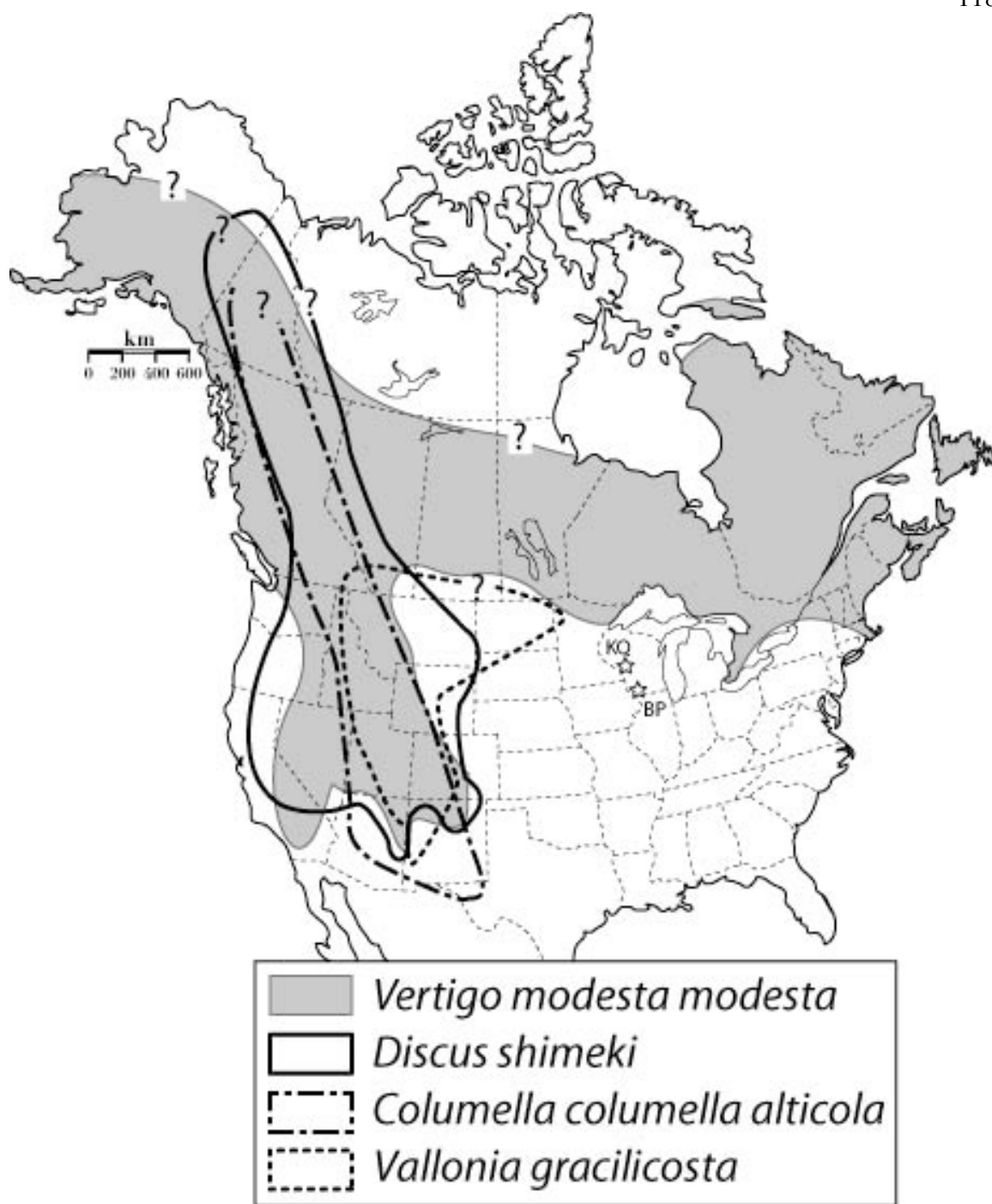


Figure 3.5A. Cordilleran-Boreal gastropod distributions. KQ = Kulas Quarry, BP = Big Platte.

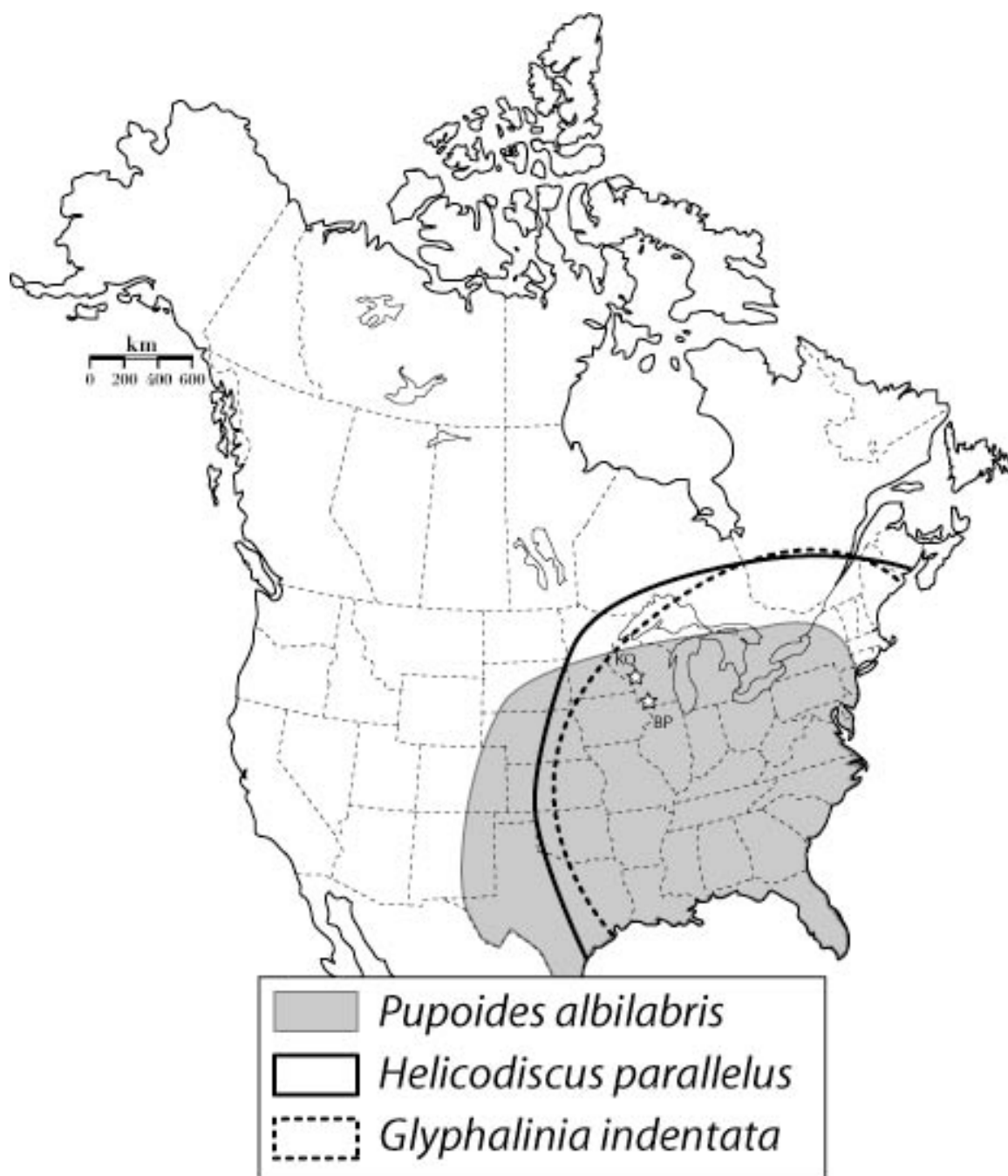


Figure 3.5B. Approximate distributions of selected Eastern Deciduous Forest taxa (data from Hubricht, 1985).

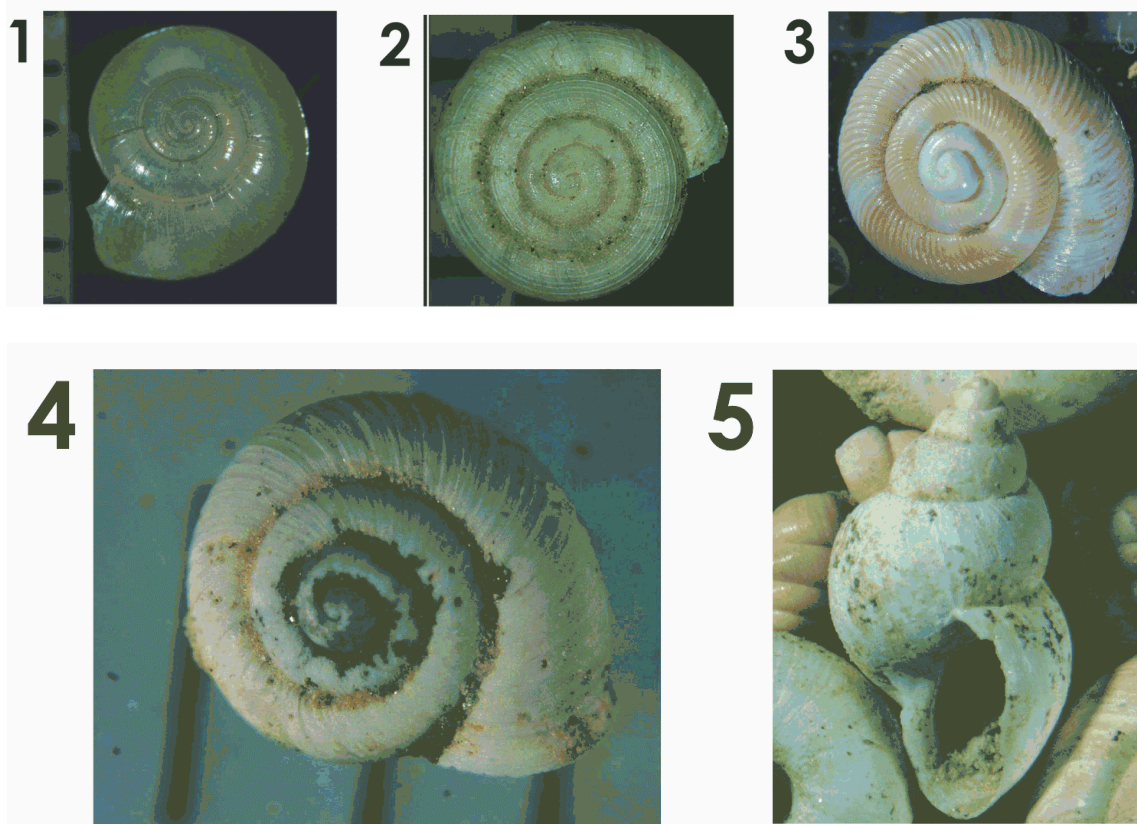


Figure 3.6. Qualitative scale used to score the condition of gastropod shells. 1: *Glyphalinia indentata*, 2: *Helicodiscus parallelus*, 3: *Discus shimeki*, 4: *Vallonia gracilicosta*, 5: *Fossaria* sp.. Note: “5” represents a freshwater gastropod not found at Big Platte.

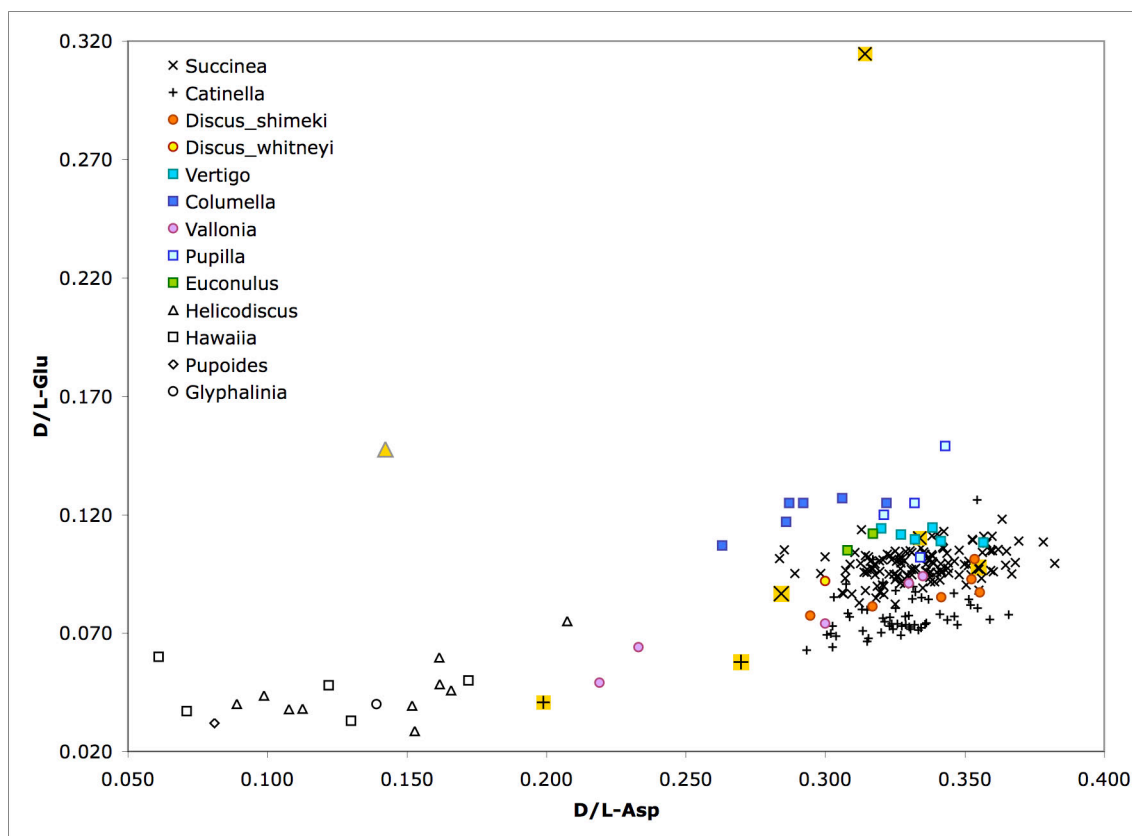


Figure 3.7. D/L Asp and D/L Glu values for all shells. Outliers rejected by data screening are larger and highlighted in yellow. “Younger” Eastern Deciduous Forest Species are represented by open symbols.

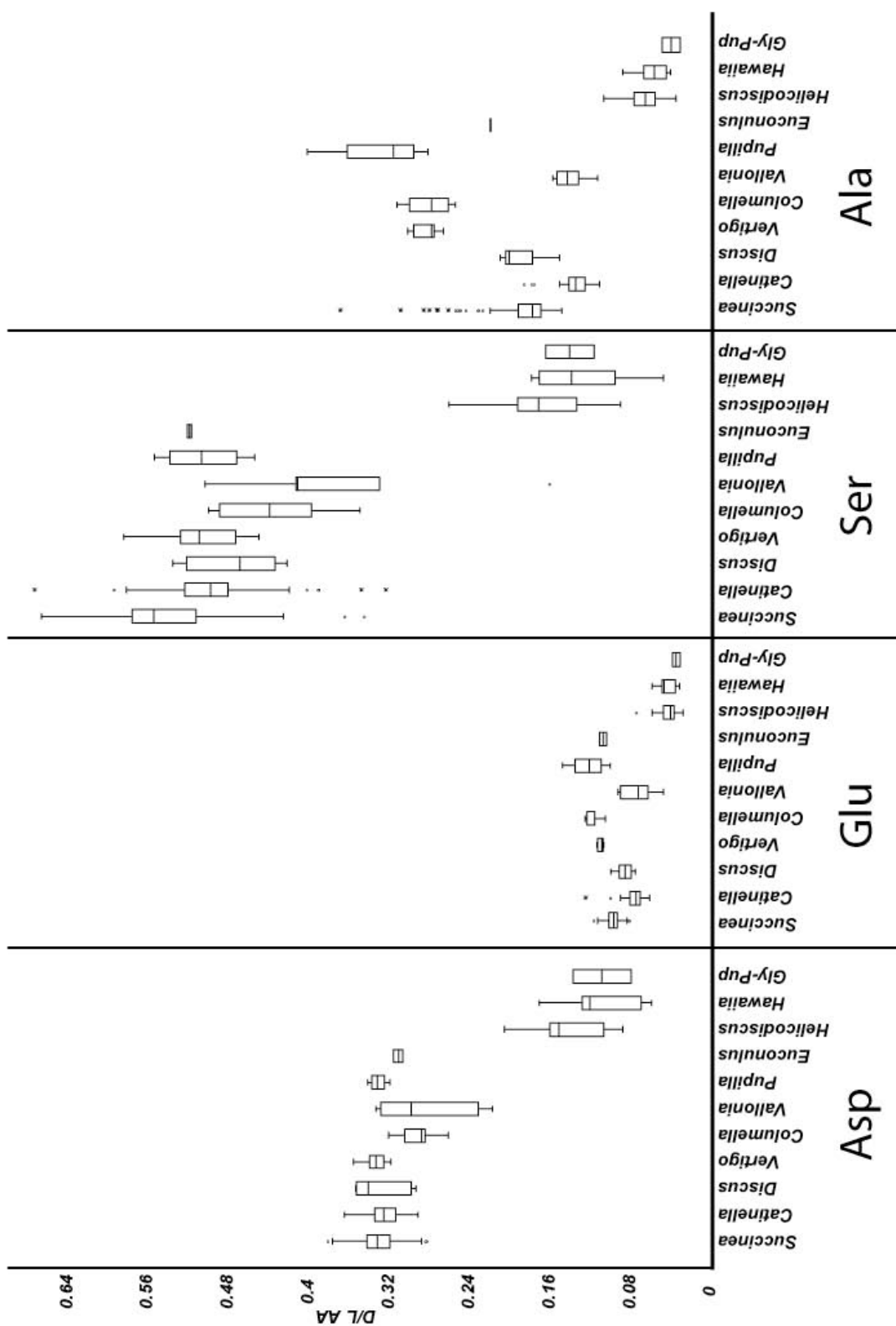


Figure 3.8A. D/L values by taxon. Note: “Gly-Pup” represents combined individual scores from *Glyphalinia* and *Pupoides* shells.

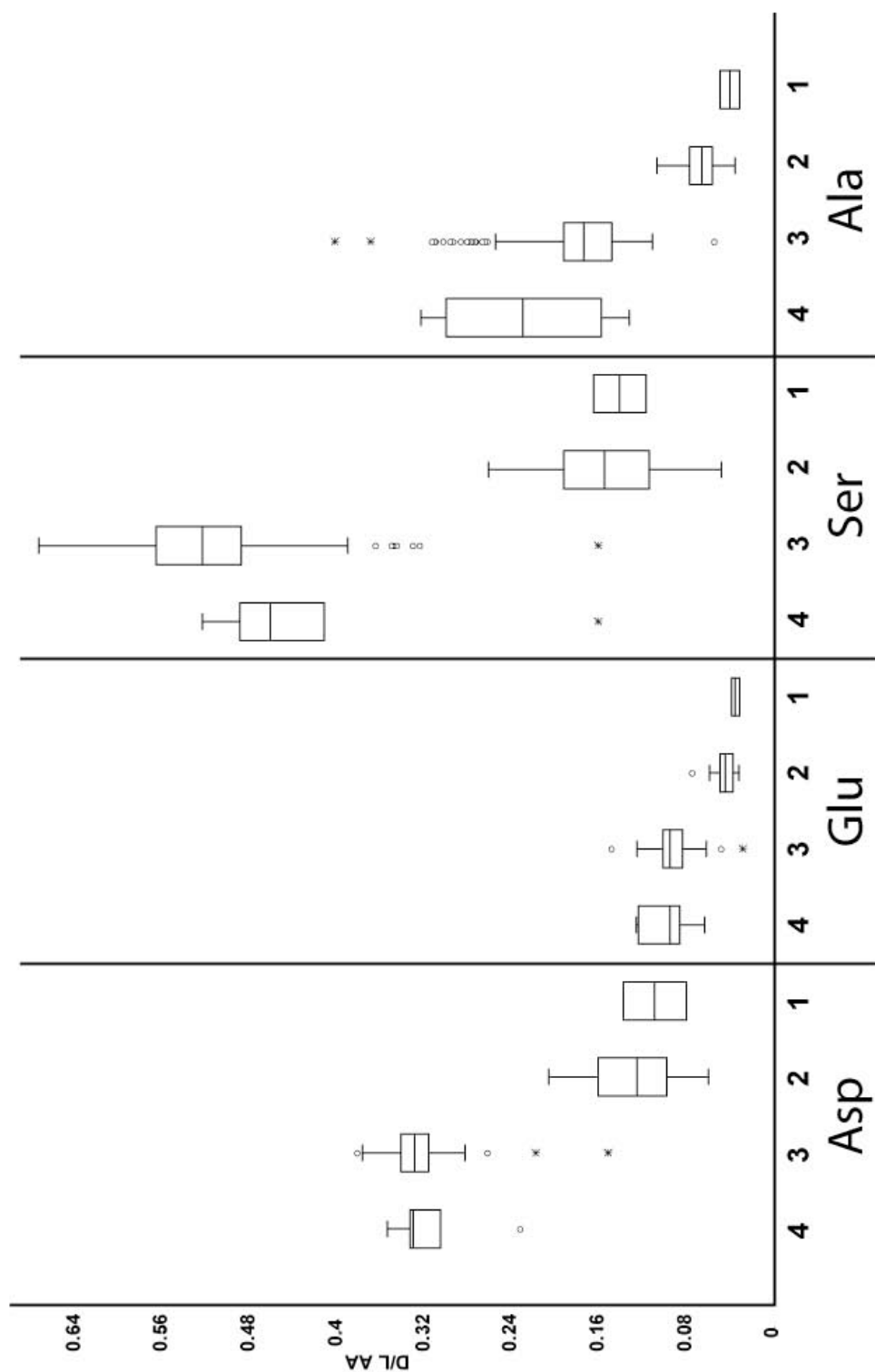


Figure 3.8B. D/L values by shell condition (See Figure 3.6). Note shells with lower condition scores (1 and 2) have lower D/L values for all amino acids compared to shells with higher scores (3 and 4).

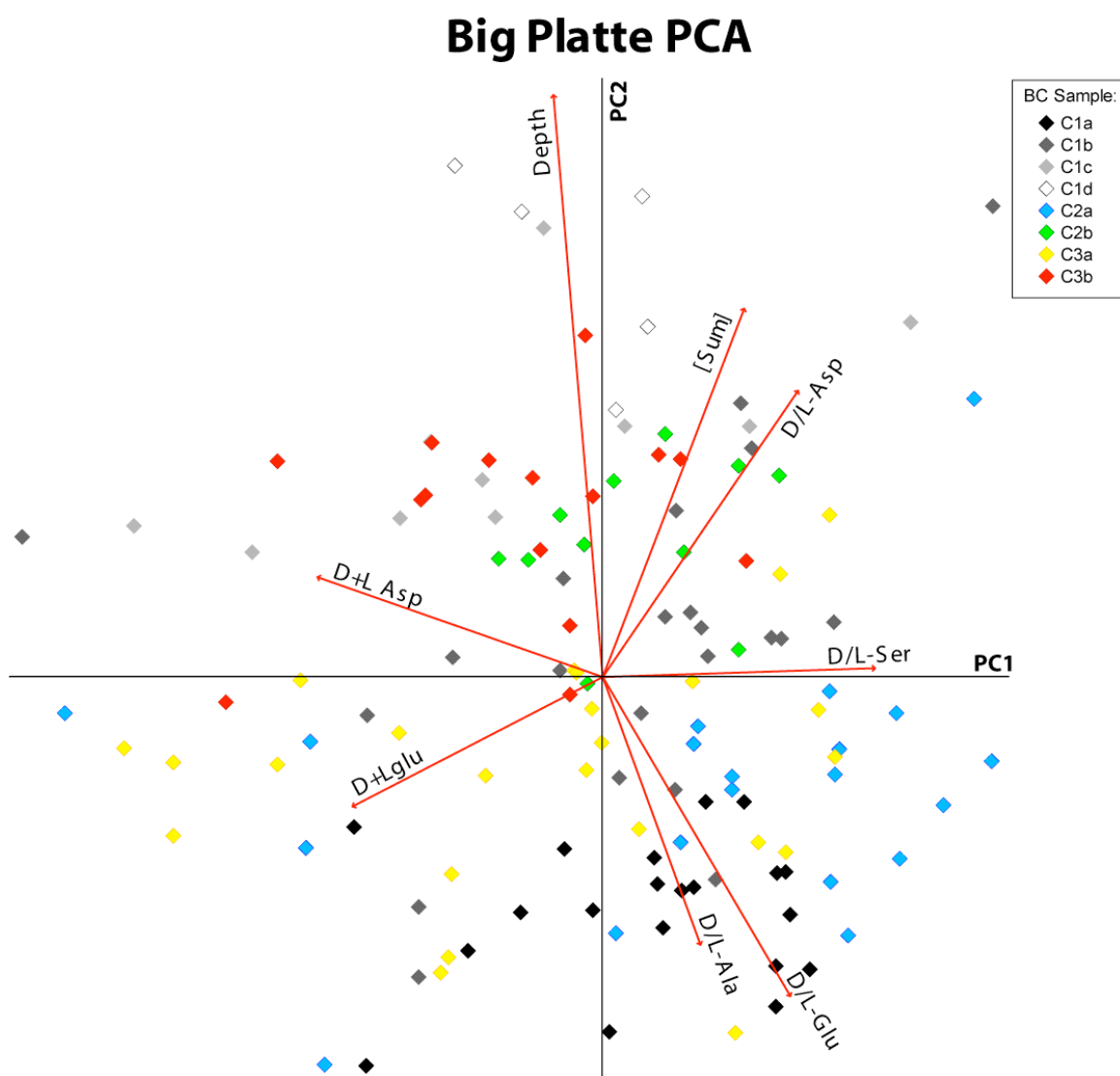


Figure 3.9. Big Platte PCA ordination diagram. Red vectors represent scaled plots of each variable with the length and direction corresponding to the contribution of that variable to each component. Note widely dispersed values for samples from higher in section (C1a, C2a, C3a), which plot lower along PC2 (higher D/L Ala and D/L Glu values).

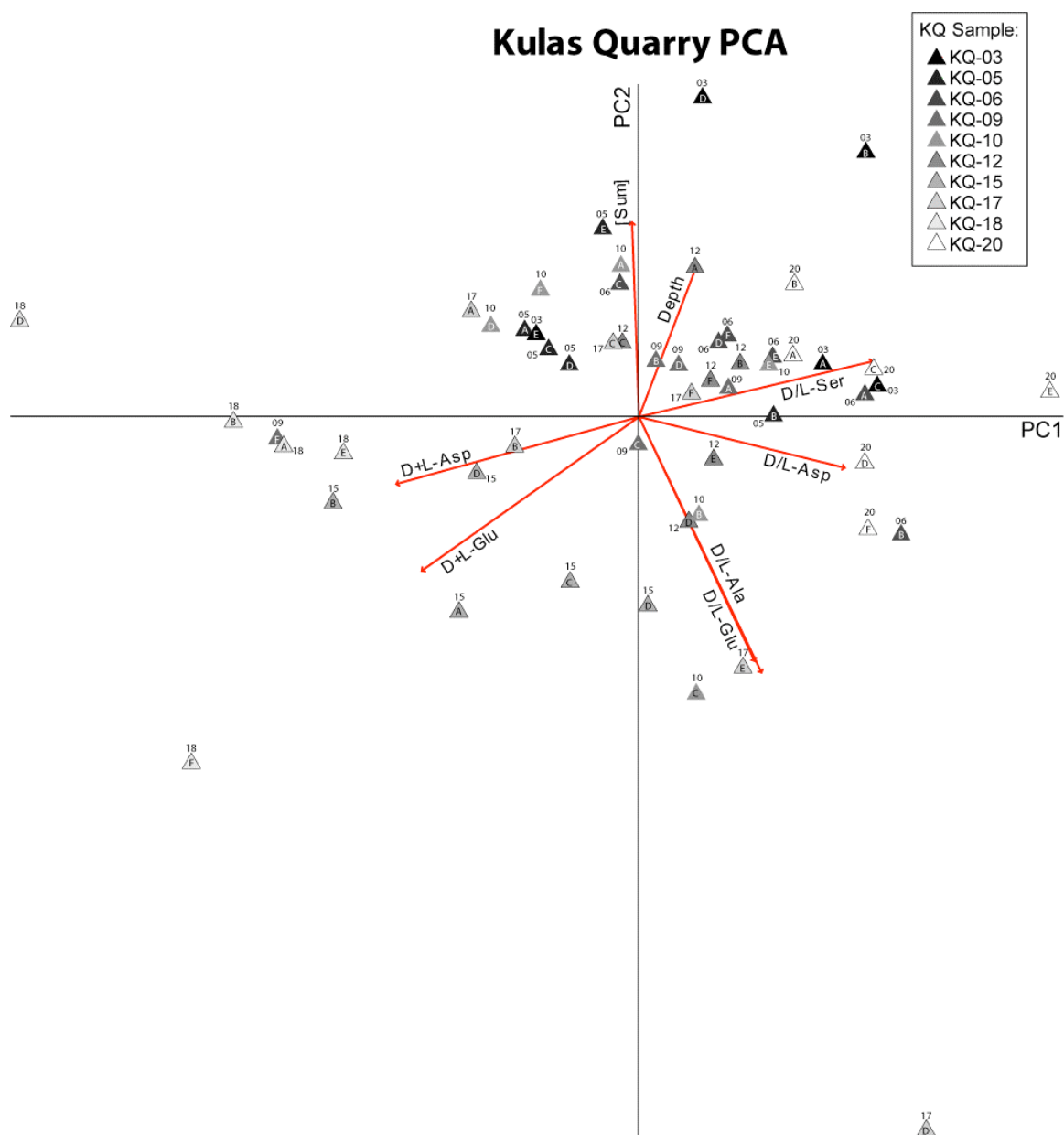


Figure 3.10. Kulas Quarry PCA ordination. Note outliers at left and lower right. Each triangle represents individual shell scores. Letters within triangle correspond to lab# suffix in Appendix A.

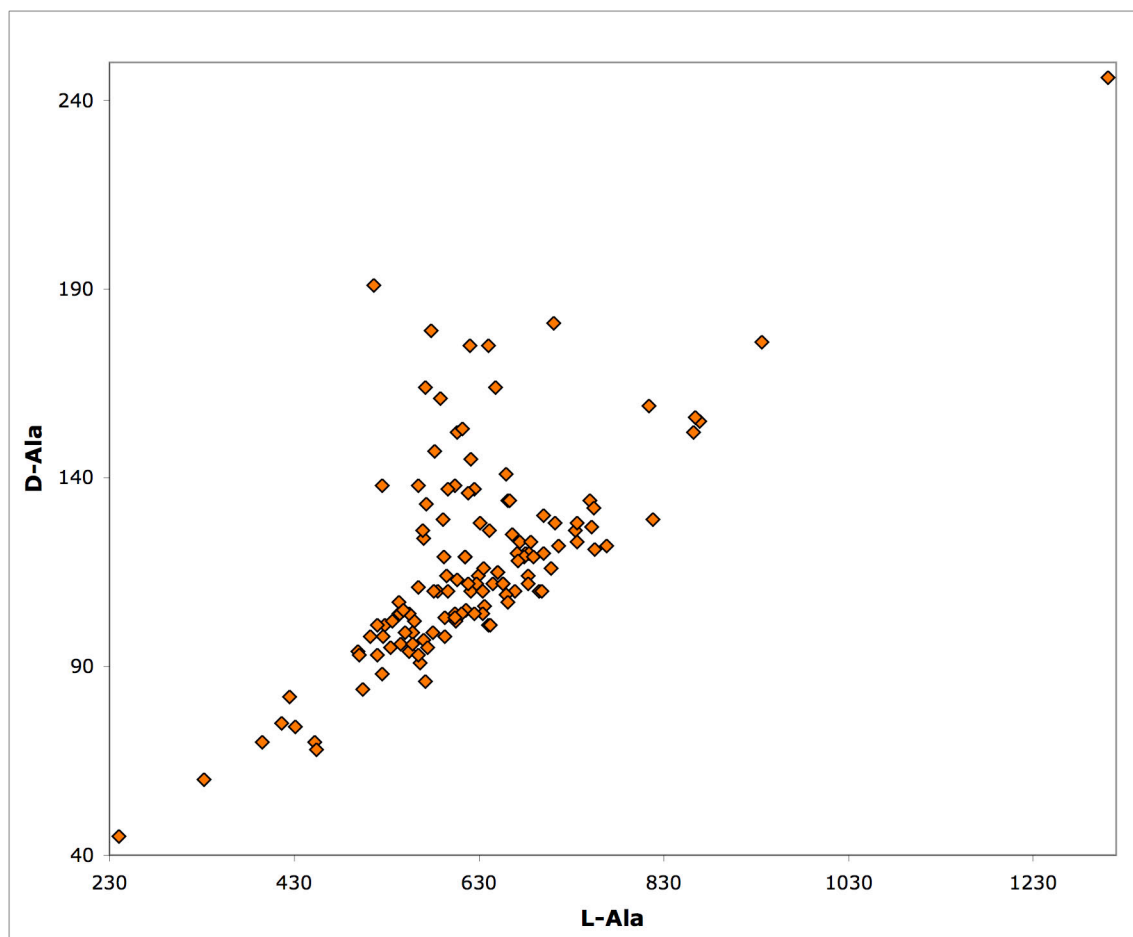


Figure 3.11. Scatterplot of Big Platte *Succinea* AAR data (measured HPLC peak area of L- and D-Ala) showing general linear relationship between D- and L-Ala. The covariance anomaly is represented by higher peak areas of D-Ala relative to L-Ala; although none of these data would appear as a univariate outlier of D-Ala or L-Ala.

Chapter 4

Paleoenvironmental significance of a full-glacial biota from the Latch

Valley, Trempealeau County, Wisconsin

ABSTRACT

Gastropods are valuable, yet underutilized fossil proxies in the Driftless Area of the Upper Mississippi Valley (UMV) region. Colluvial and alluvial sediments from two sites (Hwy-JJ and Kulas Quarry) within the Latch Valley, Trempealeau Co., Wisconsin, contain abundant terrestrial gastropod fossils and vertebrate remains. Identifiable dental elements from small rodents include those of *Dicrostonyx* sp. a tundra-dwelling lemming. The gastropod fauna is complex, and includes taxa with modern boreal-cordilleran affinities such as *Discus shimaki*, *Columella columella alticola*, and *Vertigo modesta*, which are not found in the region today. Other gastropods include species that prefer open, xeric habitats, and those that inhabit deciduous forests such as *Hendersonia occulta*. *H. occulta* is a locally endangered snail that inhabits the UMV today. Succineid gastropod shells yielded radiocarbon ages between 16,100 and 18,000 RCYBP and indicate the fauna is full-glacial in age. The differences in species richness observed between sites and samples can be largely attributed to the total number of shells within each sample. Samples with high numbers of shells per kilogram of matrix were the richest, while samples with few shells yielded few species. The rank order of abundance was nearly identical for all samples; the primary differences were between upland and floodplain samples, the former yielded a greater abundance of *Pupilla muscorum*, while the latter contained a larger number of rare species. This similarity in gastropod composition suggests a community that was largely unchanged throughout this time interval. The gastropod fauna from the Latch Valley is the northernmost full-glacial fauna in the UMV, located less than 100 km from the terminal moraine of the Chippewa Lobe of the Laurentide Ice Sheet. The age range of this deposit appears to coincide with a minor retreat of the Chippewa Lobe between the Stanley and Late Chippewa advances. These results generally agree with the ecological interpretations from other regional fossil localities of a tundra-like environment, however the presence of *H. occulta* at this site suggests the presence of minor amounts of deciduous vegetation, perhaps within topographically controlled microhabitats. It is likely that the Driftless Area of the UMV served as an important refuge for temperate species during the full-glacial period, much as it serves as an important refuge for northern species today.

4.1 INTRODUCTION

Reconstructing full-glacial (ca. 24,000 to 18,000 cal yr BP) environments near the Laurentide Ice Sheet is challenging. There are no surviving mid-latitude continental glaciers to serve as analogs, and much of the proxy evidence is ambiguous or contradictory. Geomorphic features indicate widespread permafrost, while fossil proxies consist of both tundra and boreal-hardwood forest taxa. The late Pleistocene sediments exposed within the Latch Valley, Trempealeau County, Wisconsin (Figure 4.1) contain abundant terrestrial gastropod remains. These fossils represent an unprecedented opportunity to examine full-glacial biotic communities preserved less than 100 km from the Chippewa Moraine, a major terminal moraine in north-central Wisconsin.

Gastropod fossils are valuable paleoecological proxies, particularly in the Driftless Area of the Upper Mississippi Valley (UMV). Their shells survive in a wide range of sediments that do not easily preserve other fossils such as pollen. Their shells can be radiocarbon dated, which provides an age of the fauna itself, not the surrounding sediment. Their limited range of movement makes them valuable indicators of local climate (e.g. Simmons, 1996; Rossignol et al., 2004). In addition, the small tributary drainage basins in the Driftless Area reduce the likelihood of long-distance transport of remains. Thus, uncertainties regarding provenance or differential destruction of gastropod remains as a result of sediment transport are unlikely complicating factors for these fossils (e.g. La Rocque, 1970; Miller and Bajc, 1990; Goodfriend, 1992).

The goal of this study is to use terrestrial gastropod fossils from two sites, Hwy-JJ and Kulas Quarry, within the Latch Valley to characterize the local full-glacial paleoenvironment. These gastropod assemblages contain an abundant and relatively

diverse fauna that provides valuable information regarding environmental conditions.

The differences and similarities between samples from these two sites in terms of their depositional setting and preserved shells will provide a context from which to draw environmental interpretations. Fossiliferous sediments within the Latch Valley offer a glimpse of an extreme landscape: the northernmost full-glacial fossil locality in the Midwest, less than 100 km from the maximum extent of the Laurentide Ice Sheet (Kuchta et al., 2007b).

4.2 BACKGROUND

4.2.1 Study Location

The Latch Valley basin in southwestern Trempealeau County, Wisconsin, contains a small, unnamed tributary creek of the Trempealeau River (Figure 4.2). This ca. 10 km² basin is located 10 km north of the Mississippi River in the Driftless Area of western Wisconsin (Mickelson et al., 1983; Syverson and Colgan, 2004). The basin's topography is similar to that of the Driftless Area in general, with deep, steeply sloping river valleys incised into Paleozoic bedrock.

Kulas Quarry and Hwy-JJ represent two distinct depositional environments. Hwy-JJ (Figure 4.3) is a 3m tall exposure of colluvial silt along the lower footslopes of the Latch Valley. The exposure at Hwy-JJ lies several meters above the top of Kulas Quarry; the concave-up surface can be traced downslope to the late Pleistocene terrace surface forming the top of the Kulas Quarry exposure. Kulas Quarry is a 21-meter wide, 7-meter tall exposure of alluvial valley fill (Figure 4.4).

4.2.2 Regional Geology

The Driftless Area is so named, because it lacks evidence of glacial modification; it likely remained ice-free throughout most or all of the Pleistocene (Chamberlin and Salisbury, 1885; Syverson and Colgan, 2004). The presence of heavily weathered tills to the North in Dunn and Pepin Counties suggests part of this region may have been covered during much earlier Pleistocene glacial advances (Syverson and Colgan, 2004). However, ice did not extend into Trempealeau County during the last full glacial period (ca. 24,000-18,000 cal yr BP; Figure 4.1).

The last advance of the Chippewa Lobe of the Laurentide Ice Sheet is generally poorly constrained, but is marked by several terminal moraines. The Stanley moraine is the oldest, and represents the southernmost extent of the Chippewa Lobe into Chippewa County (Syverson, 2007). To the west, geomorphic features from the Late Chippewa Phase obscure it. Syverson (2007) suggested that the Stanley moraine was formed approximately 24,000 cal yr BP, whereas the Late Chippewa Phase occurred between 18,000 and 15,000 cal yr BP.

The unconsolidated late Pleistocene sediments that overlie the bedrock within the Latch Valley Creek basin are similar to others found elsewhere in the Driftless Area. Throughout the region, loess creates a thin mantle on the gently sloping ridgetops, while the steep hillslopes are often covered with colluvium that grades into alluvial valley fill. These processes appear to have been much more active during the last glacial maximum (Mason and Knox, 1997).

Thick colluvium covers many of the steep valley sides throughout the Driftless Area, indicating active mass wasting along slopes. Based on radiocarbon and

stratigraphic analysis, colluvial deposition was most active from 25,000 to 14,000 cal. yr BP as a result of climatically induced mass wasting, probably dominated by solifluction (Mason, 1995; Mason and Knox, 1997). This colluvium consists of reworked eolian silt and clay and often contains large clasts of weathered bedrock. Along the lower footslopes in the Driftless Area, colluvial deposits often interfinger with alluvial sediments within the river valleys (Mason, 1995; Mason and Knox, 1997; Bettis et al., 2008).

Alluvial aggradation within the Upper Mississippi Valley began by 25,000 cal. yr BP and ended before 13,000 cal. yr BP (Flock, 1983; Knox, 1996). Much of the alluvial sediment is thought to be glaciofluvially derived (Flock, 1983; Knox, 1996). However, in river valleys not directly affected by glacial melt water, much of the valley fill consists of weathered bedrock and reworked silt and clay (Mason, 1995; see also Chapter 2).

Along the Upper Mississippi River Valley, the highest terrace surface not covered by loess is referred to as the Savanna Terrace (Flock, 1983; Knox, 1996). Terraces in tributaries of the Mississippi River are generally correlative with this surface (Mason, 1994; Knox, 1996). At the confluence of the Trempealeau and Mississippi Rivers, the Savanna Terrace is approximately 720 feet above sea level, whereas the highest terrace surface present in the Latch Valley is approximately 740 feet above sea level. Remnant terraces can be traced from the Latch Valley along the Trempealeau River downstream to the Savanna Terrace. Therefore, I consider the high terrace surface in the Latch Valley Creek basin as part of the Savanna Terrace.

Gently south-southwest dipping Cambrian and Ordovician bedrock underlies the entire basin (Runkel, 1994). The Cambrian section consists of orange, coarse sandstone

arenite of the upper Wonewoc Formation (Ironton Member), exposed along the mouth of the Latch Valley (Figure 4.2). At the mouth of the Latch Valley, the late Pleistocene sediments directly overlie the Wonewoc Formation and contain abundant weathered bedrock clasts. The Wonewoc is overlain by silty, glauconitic sandstone and shale of the Tunnel City (=Lone Rock) Formation; a large, ten-meter exposure lies approximately 800 m southeast of the field area, along Kulas Road. The remaining Cambrian section (Trempealeau Group) lies covered. At the head of the valley, however, Ordovician dolomite of the Oneota Formation (Prairie du Chein Group) crops out as a resistant bluff former.

4.2.3 Paleoenvironmental Background

Geomorphic evidence for the full-glacial climate in the Driftless Area includes periglacial features such as ice-wedge casts and patterned ground (Clayton et al., 2001). Permafrost development requires a mean annual temperature of several degrees below freezing and is generally associated with the absence of covered, forest habitats (Washburn, 1980; Pewe, 1983). Cryoturbated soils, talus slopes, rock glaciers, and colluvial stratigraphy show the influence of permafrost on the southwestern Wisconsin landscape from about 30,000 until about 16,000 cal yr BP (Mason and Knox, 1997; Clayton et al., 2001).

The porous, calcareous sediments within the Driftless Area often lack organic material such as pollen and plant macrofossils; although they can be preserved where the water table was high enough to prevent their degradation (e.g. Birks, 1976). Other important regional fossil localities include Conklin Quarry (Baker et al., 1986) and

Elkader (Woodman et al., 1996) in Iowa, and Jore-1 in Minnesota (Baker et al., 1999; Figure 4.1). These sites contain remains of tundra and subalpine vegetation such as *Dryas integrifolia* and *Salix* sp. (Baker et al., 1986; Baker et al., 1999). Elkader and Conklin Quarry contained a diverse assemblage of rodents, beetles, and gastropods with Cordilleran and Boreal/Arctic distributions (Baker et al., 1986; Woodman et al., 1996).

4.3 METHODS

4.3.1 Field Methods

The locations discussed in this chapter were discovered during a field survey in 2006. Sites were located by driving systematically along highways while looking for exposures of late Pleistocene sediments that contained abundant gastropod fossils. I selected the Latch Valley Creek basin for more detailed analysis because of the close association of different sedimentary facies, size of exposures, and abundance of gastropod fossils.

At each site, I described a generalized stratigraphic column to illustrate the vertical relationships between associated sedimentary facies. In addition, I took photographs to show the horizontal facies relationships and associations of prominent sedimentary structures. Some photographs were assembled into composite photographs using the “photomerge” function in Adobe Photoshop ®.

I followed facies designations as discussed by Miall (1977). These designations have been utilized for much older lithofacies, but can also be applied to Quaternary sediments (e.g. Mason, 1995). My strategy was to differentiate between sand-dominated and silt-dominated sediments, as these were relatively easy to distinguish in the field.

Sample locations and important sedimentological relationships are noted on the site photographs. Samples were limited to 30-cm intervals of individual facies and consisted of at least one 4-Liter plastic bag worth of material. I focused my sampling effort upon horizons that contained abundant gastropod fossils.

4.3.2 Radiocarbon Analysis

I obtained radiocarbon dates from succineid gastropod shells. Two samples were analyzed by Beta Analytic, Inc (BETA) and an additional five samples were analyzed at Arizona AMS lab (AA; Rech et al., in prep). Succineid gastropods are abundant in many late Pleistocene deposits, and are often the only organic material available for radiocarbon dating (Pigati et al., 2004). There are two primary sources of error in radiocarbon dates obtained from gastropod shells. The first is recrystallization of aragonite to calcite, which can yield younger-than-actual ages. This error can be avoided by using shells without visibly recrystallized, “chalky” shell material and by pre-etching the sample in acid before analysis (Goodfriend and Stipp, 1983; Goodfriend and Hood, 1983). The second problem is harder to detect and occurs when the snail ingests ^{14}C -depleted carbonate, which can yield anomalously old radiocarbon ages (Goodfriend and Hood, 1983; Goodfriend and Stipp, 1983, Pigati et al., 2004). Succineid gastropods do not appear to ingest these “old” carbonates (Pigati et al., 2004; J. Rech and J. Nekola personal communication, 2007). Radiocarbon ages were converted to calendar years using the “CalPal” online calibration software (Danzeglocke et al., 2009).

4.3.3 Lab Methods

I followed the standard processing and shell extraction methods described by La Rocque (1970), Frest and Dickson (1986), and Nekola (2004). Each sample was dried and weighed, then soaked in water and washed through a standard series of ATSM sieves (smallest mesh = 0.425mm) and then all identifiable shells and fragments were picked from the remaining residuum. Shells were identified to species (or subspecies) using Pilsbry (1948), Burch (1962), Barthel and Nekola (2000), and reference collections from the University of Iowa Natural History Museum. Jeffrey Nekola of the University of New Mexico verified specimen identification, and nomenclature follows Hubricht (1985) with additions by Nekola (2004). Richard Slaughter (UW Geology Museum) identified the rodent material. All specimens are catalogued and repositied at the University of Wisconsin Geology Museum under the catalog number UW1987.

The total number of individuals reported from a sample is the sum of whole shells and the most abundant portion of broken fragments, which represents a minimum number of individuals (MNI). Succineid shells smaller than 2 mm and juvenile shells and fragments lacking diagnostic characters were not counted. Rather than using a mathematical transformation, I determined that establishing a cutoff point of 1000 individuals for any species within a sample provided a reasonable compromise between determining the relative species' frequency and problems associated with over-counting juveniles and broken shells.

4.3.4 Statistical Methods

To evaluate whether or not samples from Kulas Quarry and Hwy-JJ represent distinct groups, I performed Multi-Response Permutation Procedure (MRPP) tests using

the PC-ORD 5.0 software package (McCune and Mefford, 2006). MRPP is a non-parametric procedure that tests the null-hypothesis that no difference exists between two or more groups of sample units. MRPP has distinct advantages over other multivariate methods such as Hotelling's T^2 and Discriminant Analysis in that it does not require assumptions of the data such as multivariate normality or homogeneity of variance (Mielke et al., 1981; McCune and Grace, 2002). This test is commonly used in ecological analyses and has tremendous potential in geological investigations (e.g. Orlowski et al., 1993; Bonuso and Bottjer, 2006).

MRPP compares the observed, average within-group distances of a data set (observed delta) to an expected value, the average distances for all possible partitions of the data set (expected delta). For example, if two a-priori groups within a data set are very different, the average of the within-group dissimilarities will be less than the average of the dissimilarities between randomly assigned groups of the entire data set (Mielke et al., 1981; McCune and Grace, 2002). The reported p-value represents the proportion of the expected-delta that is less than the observed-delta. In addition, MRPP reports a "chance-corrected agreement statistic" A [$A=1-(\text{obs-delta}/\text{exp-delta})$], which describes within-group homogeneity compared to the random expectation (McCune and Grace, 2002). If all items are identical within groups, the observed minus expected delta is zero, and $A=1$. If homogeneity within groups equals the expectation by chance, $A=0$. If within-group agreement is less than that expected by chance, $A<0$. For ecological data sets, values of A are often less than 0.1 (McCune and Grace, 2002).

I performed seven MRPPs using the Euclidean distance measure on the Latch Valley terrestrial gastropod data. Because species frequency can be autocorrelative (an

increase in one species' frequency necessitates the decrease in another) and is likely dependent on depositional factors (e.g. hydrodynamic sorting), I performed MRPP on the presence/absence data matrix. To meet the assumptions of independence, only samples obtained from discrete stratigraphic horizons containing at least five taxa were included. In addition, one species, *Discus whitneyi*, was represented by a single shell (out of nearly 10,000 counted) and was omitted from the analysis to avoid over-estimating the differences between samples.

The first set of comparisons tested for difference in species frequency in samples from separate facies (tabular, trough cross-bedded sands, and silt). The second test looked for differences between different stratigraphic age groups (lower Kulas, upper Kulas, Hwy-JJ). I also performed a test on the samples grouped by site (Kulas Quarry, Hwy-JJ).

4.4 RESULTS AND DISCUSSION

4.4.1 Data Summary

The data consist of a total of 29 samples, 21 from Kulas Quarry and 8 from Hwy-JJ, which yielded a total of 9,682 individuals from 10 terrestrial gastropod taxa with largely Cordilleran-Boreal habitat preferences (Tables 4.1, 4.2). Kulas Quarry samples were collected from planar-bedded sands (Sp; n=8), trough cross-bedded sands (St; n=11) and laminated/convolute silt (Fl, Fc; n=2). All 8 Hwy-JJ samples were laminated, colluvial silt. Three samples from Hwy-JJ (JJ06, 07, 08) were bulk samples not confined to one horizon.

Radiocarbon results obtained from these sites are in stratigraphic order, and multiple dates from individual horizons generally overlapped within one-sigma. These

radiocarbon results indicate that both Kulas Quarry and Hwy-JJ are “full-glacial” in age, but younger than the Jore-1 or Elkader faunas (Table 4.3; Figures 4.3, 4.4).

4.4.2 Site and sample group comparison

Richness correlated strongly with the total Shells/kg matrix for all samples (Spearman $\rho=0.838$, $p<<0.001$; Figure 4.5). Sample size (Sample Weight) also correlated with both Richness ($\rho=0.575$, $p=0.001$; Figure 4.6A) and Shells/kg matrix ($\rho=0.433$, $p=0.0199$; Figure 4.6B). However, this correlation was likely due to sampling bias: samples from horizons without visible shells were collected to obtain more complete coverage, but were generally smaller than samples from the most fossiliferous horizons. Excluding samples with five or fewer shells reduced the correlation of sample size to Richness and Shells/kg ($\rho=0.412$, $p=0.033$; $\rho=0.232$, $p=0.25$ respectively).

Colluvial silt samples from Hwy-JJ showed the little variation in gastropod richness and abundance with stratigraphic position (Figure 4.7A). At Kulas Quarry, both richness and abundance generally increased with stratigraphic position (=relative age; Figure 4.7B). The increase in richness at Kulas Quarry was likely due to changes in sedimentation rather than temporal variation. Trough cross-bedded facies were generally the richest in terms of gastropod species diversity and yielded the most abundant collections (Shells/kg of matrix). Richness and abundance within samples of tabular cross-bedded sands were the most variable, containing as few as two and as many as nine species, while the silt samples from Kulas Quarry contained only one species (*Catinella* cf. *gelida*).

The six most abundant species (*Catinella* cf. *gelida*, *Columella columella alticola*, *Discus shimeki*, *Vertigo modesta modesta*, and *Vertigo oughtoni*) were found at both sites (Table 4.1; Figure 4.8). Shells of *Catinella* cf. *gelida* were most abundant, and accounted for more than 56% of all shells counted. *Columella alticola*, *Vertigo modesta modesta*, *Discus shimeki*, slug plates, and *Pupilla muscorum* accounted for another 41%. *Pupilla muscorum* accounted for nearly 18% of the total shells in samples from Hwy-JJ, but only 3% at Kulas Quarry. *Vertigo oughtoni* was present, but rare, in most samples from Kulas Quarry, but it was found in only two samples from Hwy-JJ. Samples from Kulas Quarry included rare shells from species such as *Hendersonia occulta*, *Vertigo modesta parietalis* and *Discus whitneyi*; these taxa were not found in samples from Hwy-JJ (Table 4.1). In addition, aquatic taxa *Fossaria* sp. and *Helisoma* sp. were found in the upper beds at Kulas Quarry, but not in lower Kulas Quarry or any Hwy-JJ samples.

The rank abundance of taxa from Hwy-JJ was very similar to all sample groups from Kulas Quarry (Figure 4.8). The rank correlation of samples from Hwy-JJ was strongest with the pooled Kulas Quarry, Kulas Quarry upper bed, and Kulas Quarry “St” facies sample groups, but slightly lower for samples from the Kulas Quarry lower bed and Kulas Quarry “Sp” facies groups. The rank abundance of taxa within Kulas Quarry sub-groups were almost identical, with only small differences in the frequencies of individual taxa, including the presence of a single shell of *Discus whitneyi* (Figure 4.8).

Vertebrate remains consisted of heavily degraded, disarticulated mammalian dental and postcranial elements and occasional fish scales (Table 4.4). The most common identifiable elements were molars of *Dicrostonyx* sp. (collared lemming), a tundra-

obligate rodent. Molars from *Microtus* sp. that resembled both *M. miurus* and *M.*

xanthognathus were found, but these were too degraded to confidently assign to species.

In general, the fauna from these sites are characteristic of tundra and boreal forest habitats. The small rodents and the terrestrial gastropods no longer inhabit the UMV; they have Cordilleran-Boreal and Tundra modern distributions (Table 4.2; Figure 4.9A, 4.9B). *Dicrostonyx* sp. is found exclusively on the North American tundra, while the gastropods are more complex, with Cordilleran-Boreal and Eastern Deciduous Forest taxa. The low abundance of aquatic gastropods suggests a significant terrestrial sediment input. The fish scales and aquatic gastropods that were found, however, do suggest the presence of small pools and running water during warmer seasons. The aquatic gastropods may have been preferentially removed, swept away by channel streams.

Catinella cf. *gelida* and *H. occulta* both occur as relict populations in the Paleozoic Plateau region of the UMV, although Nekola (pers. comm. 2007) reported that the shell morphology of tundra populations of *Oxyloma groenlandica* is identical to that of fossil *C. gelida* and previous identifications of *C. gelida* in the Midwest (e.g. Frest, 1984; Baker et al., 1986) may be incorrect. However, accurate identification of succineids requires examination of soft tissues (i.e. genitalia). For consistency, I have chosen to follow the identification of earlier studies (e.g. Woodman et al., 1996) for this taxon, based on the overall size and aperture of the shell.

The recognition of *H. occulta* at Kulas Quarry is noteworthy because it was previously reported absent (Kuchta et al., 2007a). However, additional sampling and subsequent analysis of small fragments revealed its presence throughout the Kulas Quarry section. The co-occurrence of these taxa appears to constitute a non-analog fauna

(e.g. Graham and Mead, 1987), as they do not inhabit the same geographic ranges today (Figure 4.9A). Although not as diverse, the Latch Valley fauna is similar to that reported from Elkader in Iowa, which was interpreted as a sub-arctic climate with topographically controlled microhabitats that supported isolated patches of deciduous forest vegetation (Woodman et al., 1996). This deciduous vegetation was probably not very large; Baker et al. (1999) reported birch and willow macrofossils from a full-glacial site in southeastern Minnesota, both of these trees have cold-adapted dwarf forms. Alternately, fragments of *H. occulta* may be reworked from older sediments, suggesting that this species had been extirpated during the last full-glacial period and has since re-established its range. Because of the poor preservation and its occurrence throughout the Kulas Quarry section (to a depth of more than 5 m), it is unlikely that these shells burrowed into the deposit after deposition.

4.4.3 MRPP

MRPP results indicate that the distances between sample groups were greatest between Kulas Quarry samples and those from Hwy-JJ (Table 4.5). The distances between samples from Hwy-JJ and *a priori* sample groups from Kulas Quarry (all, upper/lower beds, St/Sp facies) were significant at $\alpha=0.05$. Distances between Kulas Quarry sample groups (Sp vs. St facies and lower vs. upper bed) were not significant at $\alpha=0.10$. In addition, the within-group heterogeneity for Kulas Quarry samples grouped by facies was greater than the random expectation ($A = -0.0101$; Table 4.5).

MRPP appears to be a useful tool in comparing fossil assemblages, especially as many paleoecological data sets do not meet assumptions of parametric tests. In this

analysis, the measured distances between groups based on presence-absence were significant when comparing alluvial samples from Kulas Quarry to the colluvial silt samples from Hwy-JJ, but the samples from within Kulas Quarry were not significantly different, regardless of the grouping criterion (Table 4.5). The difference between Kulas Quarry and Hwy-JJ may be due to the presence of rare taxa in Kulas Quarry samples compared to those from Hwy-JJ. Presence absence data tend to increase the influence of rare species and de-emphasize the effect of common species compared to frequency-based measures (e.g. Hill, 1973). Thus, the rare species present in most samples from Kulas Quarry (but absent at Hwy-JJ) were much more likely to affect the multivariate distances between the two sites than changes in the abundance of species between sites. For example, *Hendersonia occulta* represented less than 1% of the total shells counted and was not found at Hwy-JJ, but was present as at least one individual in most samples from Kulas Quarry. *Pupilla muscorum*, however, is much more abundant in samples from Hwy-JJ, but it is present at both sites (Table 4.1; Figure 4.8).

4.5 CONCLUSIONS

In general, the Latch Valley fauna suggests the presence of a tundra and boreal forest habitat in west-central Wisconsin between 21,700 and 19,200 cal yr BP. The terrestrial gastropod fauna from these study sites is somewhat less rich than other full-glacial gastropod sites, but still contains species with wide-ranging habitat preferences from open, xeric to shaded, mesic environments – including species that appear to feed exclusively on deciduous leaf litter (e.g. *Hendersonia occulta*; van der Schalie, 1939). These findings agree with the interpretations by other such as Baker et al. (1986) and

Woodman et al. (1996) who interpreted a dominantly tundra-forest habitat with topographically controlled microhabitats that supported the presence of deciduous vegetation in northeast Iowa during the last full-glacial period.

While samples from Kulas Quarry were different compared to samples from Hwy-JJ, there did not appear to be any monotonic change in the composition of the gastropod fauna within the Latch Valley. Differences in the observed species composition within samples appear to be a result of sample size, and depositional environment (e.g. large samples vs. small, colluvial hillslopes vs. trough cross-bedded facies). The similarity of all sample groups within Kulas Quarry suggests little or no change in the gastropod community at the time of deposition. In addition, there may have been some difference in the gastropod species assemblage located along hillslopes as compared to the floodplain. The high abundance of *Pupilla muscorum* in samples from Hwy-JJ suggests upslope conditions may have been drier and more open compared to lower elevations. It is possible that the large-scale climatic changes following the last glacial maximum did not result in observable changes to the full-glacial gastropod species assemblage until after 19,000 cal yr BP. Compared to the Elkader gastropod fauna, the Latch Valley fauna is about 2,000 years younger, but less diverse (Table 4.1; Woodman et al., 1996). It is possible that the fauna described here is also transitional, with gastropods migrating into a previously inhospitable periglacial climate.

Vertigo oughtoni is often described as a tundra-obligate species and can be found in muskeg and open, mesic bogs in Nunavut, northern Ontario, Manitoba, Newfoundland, and Baffin Island in Canada (Pilsbry, 1948; Oughton, 1948; Johnson, 1965; Waldén, 1966; Figure 4.9A). As a late Pleistocene fossil, it is often found at sites close to the ice

margin (Frest and Dickson, 1986). In eastern Iowa, it is present at both Conklin Quarry and Elkader (Baker et al., 1986; Woodman et al., 1996). It is also a common fossil from full-glacial sites in southwestern Ohio, along sites near the limit of late Wisconsin ice (LaRocque and Forsythe, 1967; Dell, 1991). While the presence of *V. oughtoni* is considered to indicate tundra, the presence of boreal forest gastropods in greater numbers within the same deposits implies a more complex correlation between a gastropod's modern and fossil ranges. Given the constricted, full-glacial climatic gradient that was present in the Upper Mississippi Valley (e.g. Schwert et al., 1997), competitive exclusion or other intraspecific interactions may have forced snails to occupy different habitats during the late Pleistocene.

Fragmentary remains of *Hendersonia occulta* were recorded from the majority of the samples collected from Kulas Quarry. This species is considered endangered within the state of Wisconsin today. It is found in the UMRV region, the Niagaran Escarpment of eastern Wisconsin and Michigan's Upper Peninsula, and the west central Appalachians (Van Der Schalie, 1939; Hubricht, 1985). *Hendersonia occulta* is a calciphile that requires moist, well-shaded habitats with sufficient leaf litter (Van Der Schalie, 1939; Pilsbry, 1948; Nekola, 2003). As a Pleistocene fossil, *H. occulta* occurs from western as Nebraska through eastern Ohio and southward along the Lower Mississippi River Valley to the Gulf of Mexico (Leonard, 1952; Hubricht, 1985).

Together, Kulas Quarry and Hwy-JJ represent the northernmost full-glacial fauna in the Midwest. The gastropod fauna (in particular, *Hendersonia occulta* and *Discus whitneyi*) suggests the presence of, at minimum, isolated deciduous vegetation in the northern Driftless Area soon after the last Glacial Maximum. Several species such as

Discus shimeki, *Columella columella alticola*, and *Vertigo modesta modesta* have mixed habitat preferences and are often found living within the leaf litter along forest edges (Pilsbry, 1948; Leonard, 1952). In eastern Iowa, Baker et al. (1986) and Woodman et al. (1996) interpreted the abundance of these taxa as indicative of coniferous-hardwood vegetation in the region during the full-glacial period.

The consistency of the gastropod fauna suggests the gastropod community was relatively stable and that a non-analog, mollusk fauna was established before 21,700 cal yr BP and remained unchanged through 19,200 cal yr BP. The dates reported for the Latch Valley fauna fit between the estimated dates for the glacial advances during the Stanley and Late Chippewa phases. It may be that the deposition at Kulas Quarry is connected to these glacial phases. However, a more detailed chronology would be needed. Alternately, the apparent stability of the gastropod fossil assemblage may indicate that the conditions necessary for the last advance of the Chippewa Lobe did not significantly impact the gastropod community. In addition, the remains of *Hendersonia occulta* at Kulas Quarry indicate that this species has been in the Driftless Area since the full-glacial period. Alternately, this species inhabited the region during the relatively warmer pre-glacial environment, and re-established itself in the UMV after the full-glacial period. It is interesting to note that living records of this species do not exist for Trempealeau County. This report expands the known Pleistocene range for this state-endangered species, and has implications for future conservation efforts.

Collectively, the gastropods preserved within the Latch Valley suggest cold tundra and tundra-forest environments similar to the tundra-forest boundary in Canada today characterized western Wisconsin at the end of the full-glacial period. The

deciduous forest elements were likely small, scrub-like plants similar to those found in subalpine Krummholz today (e.g. Baker et al., 1986). The presence of temperate species in close proximity to the glacial margin during the end of the full-glacial period suggests the Driftless Area served as a refuge for temperate species then, much as it currently harbors many northern species today.

4.6 ACKNOWLEDGEMENTS

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Table 4.1. Frequency and occurrence of gastropods within samples from Kulas Quarry and Hwy-JJ.

Kulas Quarry

Facies	Sample	Sample Wt (g)	Fossaria sp.	Helisoma sp.	Catinella cf. gelida	Columella columella alticola	Pupilla muscorum	Vertigo modesta modesta	Vertigo modesta parietalis	Vertigo alpestris ougtoni	Discus whitneyi	Discus shimeki	Hendersonia occulta	slug plates	Total Shells ^b	Richness	Shells/kg ^b	Stratigraphic Rank	
Fl	KQ21	2731.5				100.0										1	1	0.37	21
Sp	KQ20	3564.7	+	+		56.5	14.2	3.3	11.1	0.2	2.9		11.0	0.7	0.1	1771	9	520.94	20
St	KQ19	4582.2	+			59.1	11.5	1.9	15.2	0.3	8.3		2.9	0.5	0.3	374	9	82.71	19
St	KQ18	4646.5	+			72.4	4.8	0.3	11.8	0.3	0.8		4.0	16.3	0.5	526	9	117.08	18
St	KQ17	9039.4	+	+		65.3	5.8	0.6	7.1		1.9		4.5	14.3	0.2	467	8	52.77	17
St	KQ16	5031.1				75.1	5.2	0.3	9.0		0.6		2.9	6.4	0.6	346	8	68.77	16
St	KQ15	8623.1	+			50.5	18.6	3.7	12.0	0.2	1.7	0.03	10.9	2.2	0.1	3959	10	472.92	15
St	KQ14	5124.3	+			50.1	14.1	4.1	7.6		3.0		13.8	7.3		369	7	74.35	14
St	KQ13	4216.4	+			73.4	5.2	1.6	7.1		2.0		9.1	1.6		252	7	60.24	13
St	KQ12	4902.1				62.6	3.0		12.1		3.0		13.1	3.0	3.0	99	7	20.20	12
Fc	KQ11	1800				100.0										5	1	2.78	11
St	KQ10	5382.6	+			67.3	5.0		3.0				8.9	12.9	3.0	101	6	19.14	10
St	KQ09	4739.6				54.4	13.9	3.9	12.6		2.6		9.4	2.9	0.3	309	8	65.20	9
St	KQ08	4501.1				64.7	12.1	2.4	6.8		3.4		5.8	4.3	0.5	207	8	45.99	8
Sp	KQ07	4250.1				50.0	14.3	8.2	10.2	1.0	3.1		8.2	4.1	1.0	98	9	23.06	7
Sp	KQ06	4567.9				62.3	6.6	2.8	7.5		1.9		15.1	1.9	1.9	106	8	23.21	6
Sp	KQ05	4000				38.5	19.2	7.7	3.8		3.8		26.9			26	6	6.50	5
Sp	KQ04	3728.2				64.3	14.3						7.1	14.3		14	4	3.76	4
Sp	KQ03	8457.3				57.8	8.9	8.9	13.3				4.4	2.2	4.4	45	7	5.32	3
Sp	KQ02	2260							25.0					75.0		4	2	1.77	2
Sp	KQ01	1730				61.5		30.8	7.7							13	3	7.51	1
Hwy-JJ																			
Fl	JJ05	3870 ^a				54.1	9.9	4.5	10.8		13.5		1.8	5.4		111	7	28.68	5
Fl	JJ04	4126.7				66.7	2.7	2.7	21.3				4.0	2.7		75	6	18.17	4
Fl	JJ03	3200.1				54.3	4.3	35.7	1.4				4.3			70	5	21.87	3
Fl	JJ02	4170.9				78.6	2.4	4.8	11.9					2.4		42	5	10.07	2
Fl	JJ01	2653.1				38.1	7.1	28.6	4.8				14.3	7.1		42	6	15.83	1
Fl	JJ06	5700 ^a				44.4	5.6	22.2	9.3		13.0		1.9	3.7		54	7	9.47	bulk
Fl	JJ07	4683.4				34.7	16.9	28.0	7.6				5.1	7.6		118	6	25.20	bulk
Fl	JJ08	5015.1				48.7	3.8	16.7	9.0				10.3	11.5		78	6	15.55	bulk

Notes: ^aSample weight estimated by sample volume; "Total Shells" does not include aquatic taxa, however "Shells/kg" does, "Stratigraphic Rank" represents relative position where 1= stratigraphically oldest. Results for Eastern Deciduous Forest-type taxa are shaded.

Table 4.2. Radiocarbon results from Latch Valley exposures (locations indicated in Figures 4.3 and 4.3).

Site	Lab#	^{14}C Age	Cal Age	Depth (m)
Kulas Quarry	Beta-223641	16,670 \pm 60	19,929 \pm 295	2.75
Kulas Quarry**	AA-83090	16,840 \pm 120	20,059 \pm 296	2.75
Kulas Quarry**	AA-83091	17,180 \pm 130	20,617 \pm 330	2.75
Kulas Quarry**	AA-83092	16,890 \pm 120	20,122 \pm 288	2.75
Kulas Quarry	Beta-223642	17,550 \pm 70	20,961 \pm 314	4.5
Kulas Quarry**	AA-82558	17,990 \pm 200	21,673 \pm 448	4.5
Hwy-JJ	Beta-243248	16,120 \pm 60	19,236 \pm 236	2

Notes: "**Depth (m)**" indicates depth below top of section where ^{14}C date obtained; all dates obtained via AMS ^{14}C analysis of gastropod shell carbonate unless noted; site locations shown in Figure 1; radiocarbon calibration via calpal online (Danzeglocke et al. 2007); **dates from Rech et al. (in prep).

Table 4.3. Generalized ecological preferences for common taxa from Latch Valley fauna. Data from Pilsbry (1948), Leonard (1952), and J. Nekola (pers. comm. 2007).

Taxon	Province	Ecology
<i>Columella columella alticola</i>	C-B	Very cold, moist, willow scrub, high elevations often above 2000m elevation.
<i>Pupilla muscorum</i>	C-B	Dry, open cold, catholic sp.
<i>Vertigo modesta modesta</i>	C-B	Willow-birch thickets, cold, moist
<i>Discus shimeki</i>	C	Cold, montane forest above 2000m elevation
<i>Discus whitneyi</i>	W (EDF)	Cold, moist to dry, open to forest habitats; warmer habitats than <i>D. shimeki</i> .
<i>Catinella cf. gelida</i>	MW	Common late Pleistocene fossil throughout Midwest, relict in UMW (Frest, 1987).
<i>Hendersonia occulta</i>	EDF (MW)	Paleozoic Plateau, Niagaran Escarpment, Valley and Ridge Appalachians, limestone cliffs, talus, deciduous forest. Generally associated with areas subject to seasonal flooding (Leonard, 1952).
<i>Vertigo alpestris oughtoni</i>	N	Moist tundra

Notes: C-B = Cordilleran-Boreal distribution, C = Cordilleran, W = widespread, EDF = Eastern Deciduous Forest, MW = Midwest Biome (Frest and Fay, 1980).

Table 4.4. Vertebrate remains found within Kulas Quarry samples. MNI = Minimum Number of Individuals.

Sample	Fish Scales	Mammal	Identified Elements	MNI
KQ20	x	indet. fragments		
KQ19	x	indet. fragments		
KQ18	x	indet. fragments		
KQ17	x	<i>Dicrostonyx</i> sp.	M1/M2*, Lm2	1
KQ16	x	<i>Dicrostonyx</i> sp.	Lm2	1
		indet. rodent incisor	R upper	
KQ15	x	<i>Dicrostonyx</i> sp.	Rm1, 2 Lm1, Lm2, M1/M2*	2
		indet. Sciurid (aff. <i>Tamias striatus</i>)	cheek tooth root*	1
		indet. rodent incisors	R upper, L upper, L lower	
KQ14	x	<i>Microtus</i> sp.	Lm2	1
		indet. rodent incisor	R lower	
KQ13	x	indet. fragments		
KQ09	x	<i>Dicrostonyx</i> sp.	Lm1	1
KQ08	x	<i>Microtus</i> sp.	LM2, Lm2, 2 RM1	2
KQ07	x	indet. fragments		
KQ06	x	<i>Dicrostonyx</i> sp.	RM1, Lm1*	1
		<i>Microtus</i> sp.	RM1, LM2, Lm2	1
KQ05	x	indet. fragments		
KQ03	x			

*=tooth fragment, R=right, L=left, M=upper, m=lower

Table 4.5. MRPP results for *a priori* sample group comparisons. P values significant at $\alpha=0.05$ are in bold.

Group Comparisons	T	A	<i>p-value</i>
KQ _{all} vs. JJ	-4.715	0.1114	0.0017
KQ _u vs KQ _l	-1.117	0.0331	0.1274
KQ _l vs JJ	-2.627	0.0796	0.0223
KQ _u vs JJ	-5.325	0.2574	0.0009
KQ _t vs KQ _p	0.342	-0.0101	0.5506
KQ _p vs JJ	-2.301	0.0798	0.0306
KQ _t vs JJ	-5.366	0.2116	0.0005

Notes: A = average between-group differences, A=0 when all items identical within groups, A<0 if measured within-group distance greater than that expected by chance.

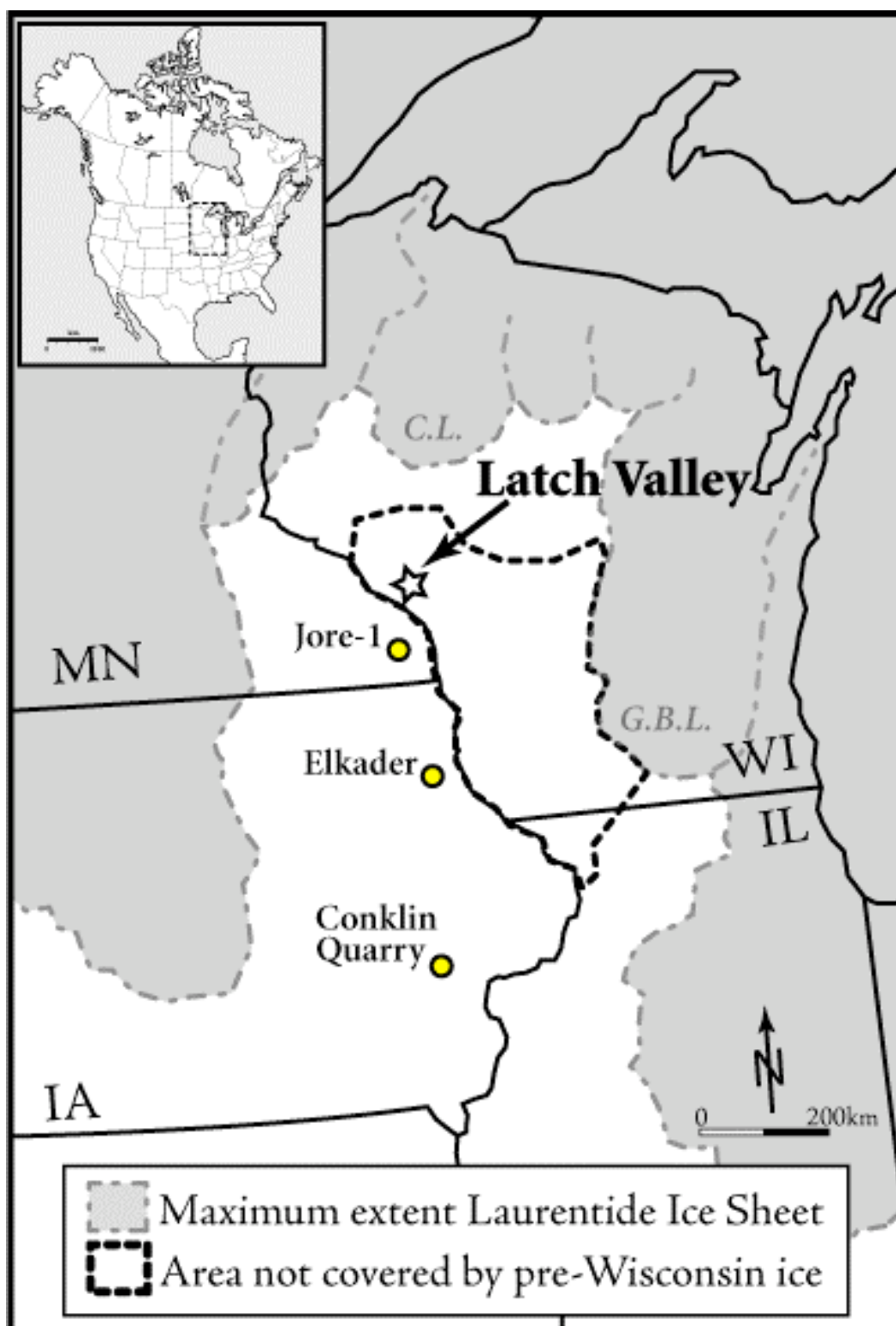


Figure 4.1. Map of study area and locations discussed in text. C.L. = Chippewa Lobe, G.B.L. = Green Bay Lobe. Ice extent based on Mickelson et al. (1984) and Syverson and Colgan (2004).

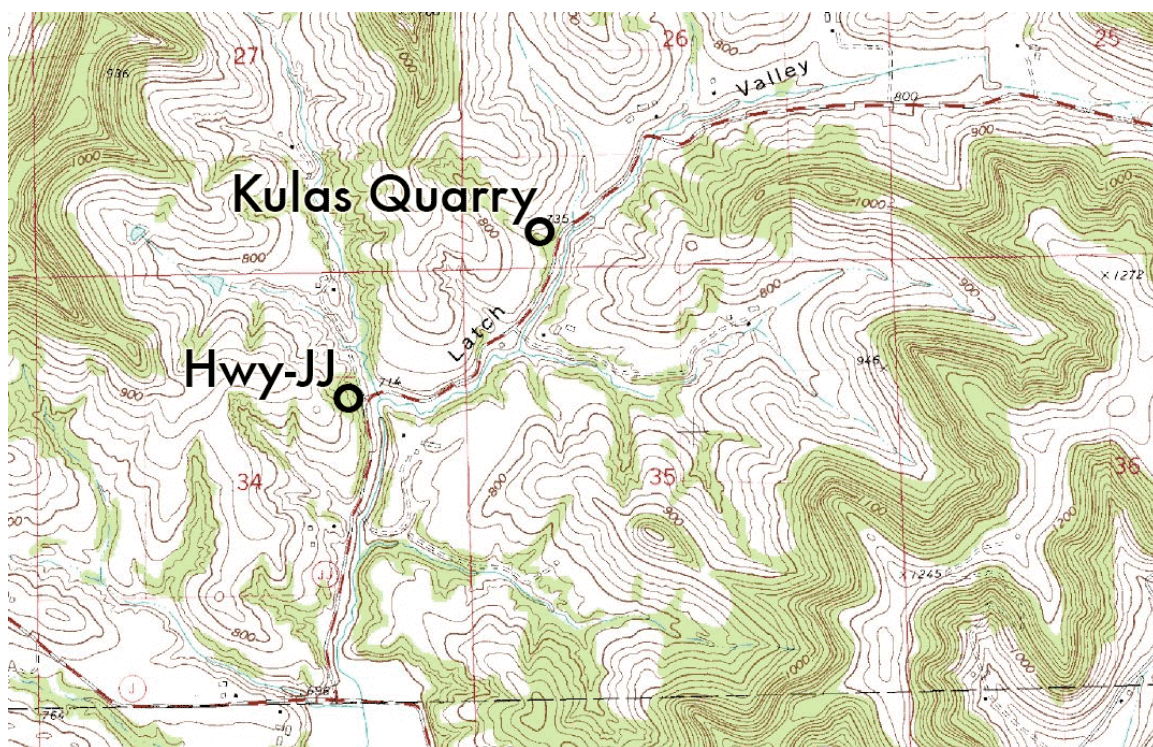


Figure 4.2. USGS topographic map of Latch Valley. Scale is approximately 1:25,000.



Figure 4.3. Hwy-JJ outcrop with gastropod shell radiocarbon date (BETA-243248) from material about 2 m below top of exposure.

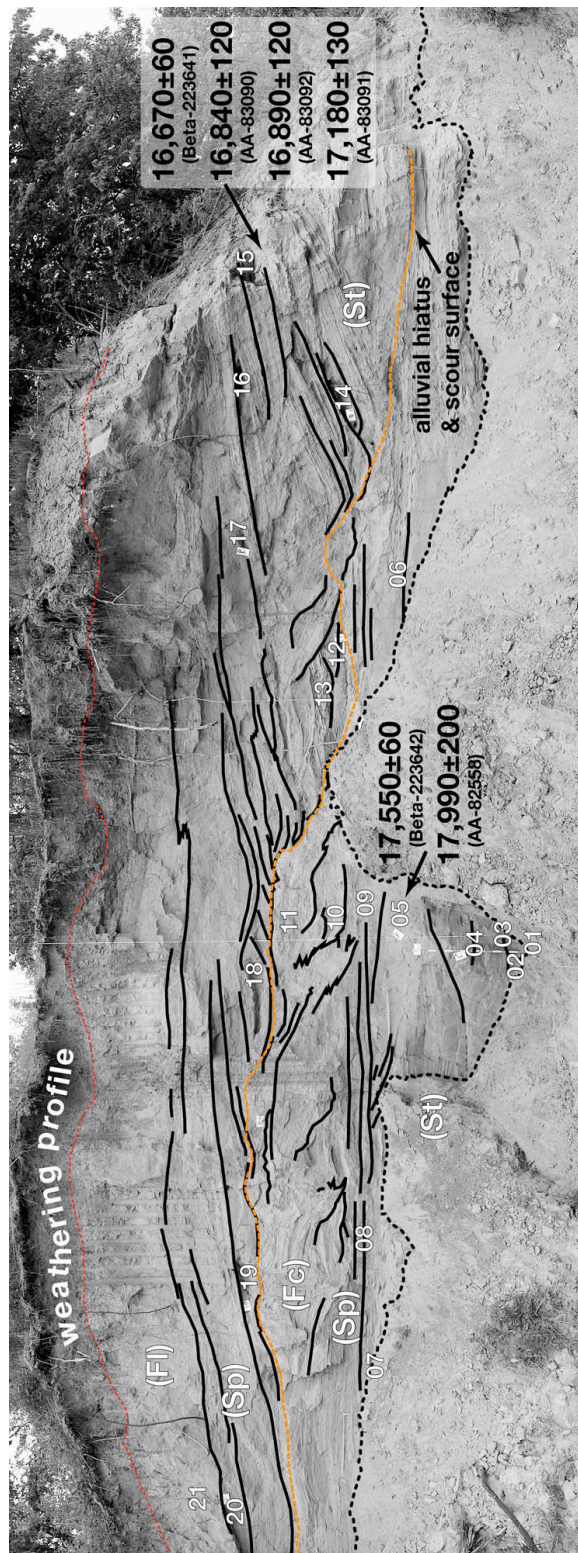


Figure 4.4. Kulas Quarry exposure showing stratigraphic relationships of samples and radiocarbon age results.

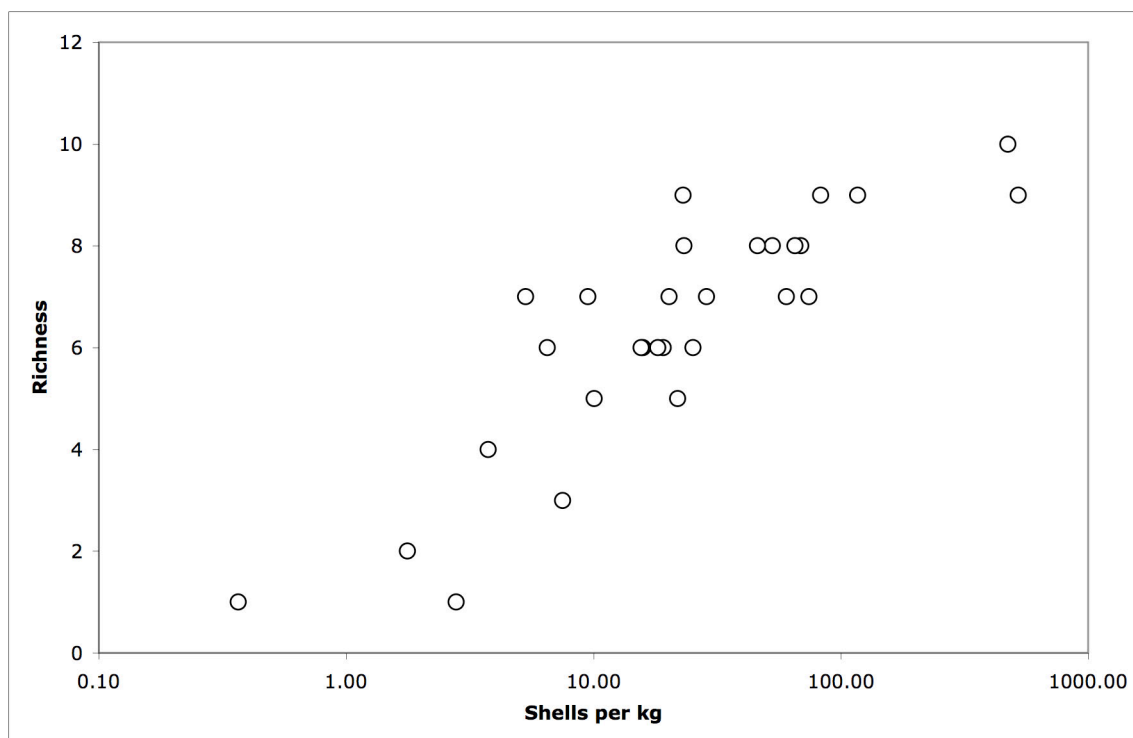


Figure 4.5. Semi-log plot of Shells per kg versus richness for all samples.

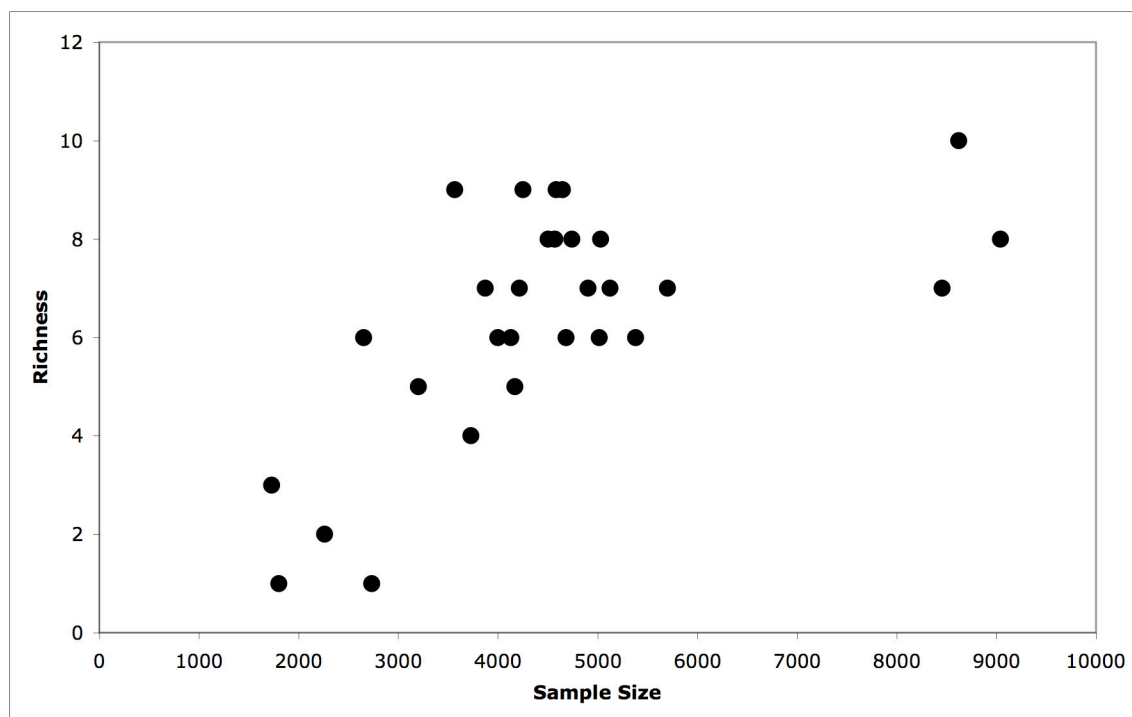


Figure 4.6A. Richness versus sample size.

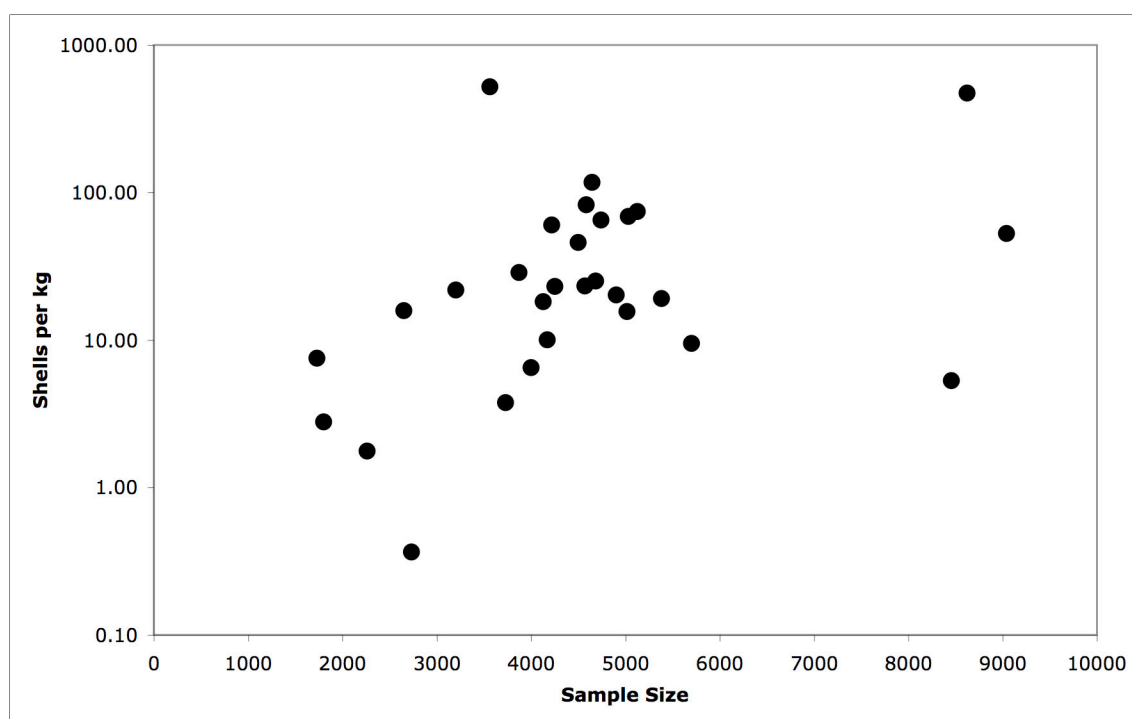


Figure 4.6B. Shells per kg versus sample size.

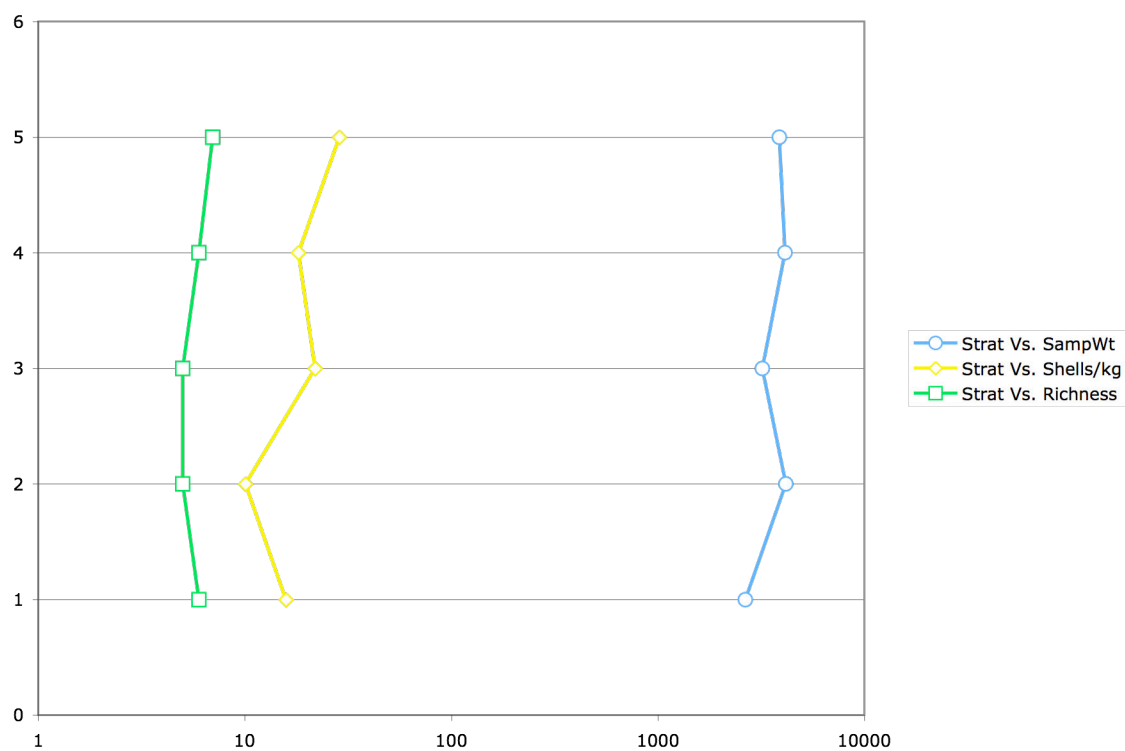


Figure 4.7A. Stratigraphic variation in Richness, Shells/kg and Sample Weight at Hwy-JJ.



Figure 4.7B. Stratigraphic variation of Richness, Shells/kg, and Sample Weight in Kulas Quarry Samples.

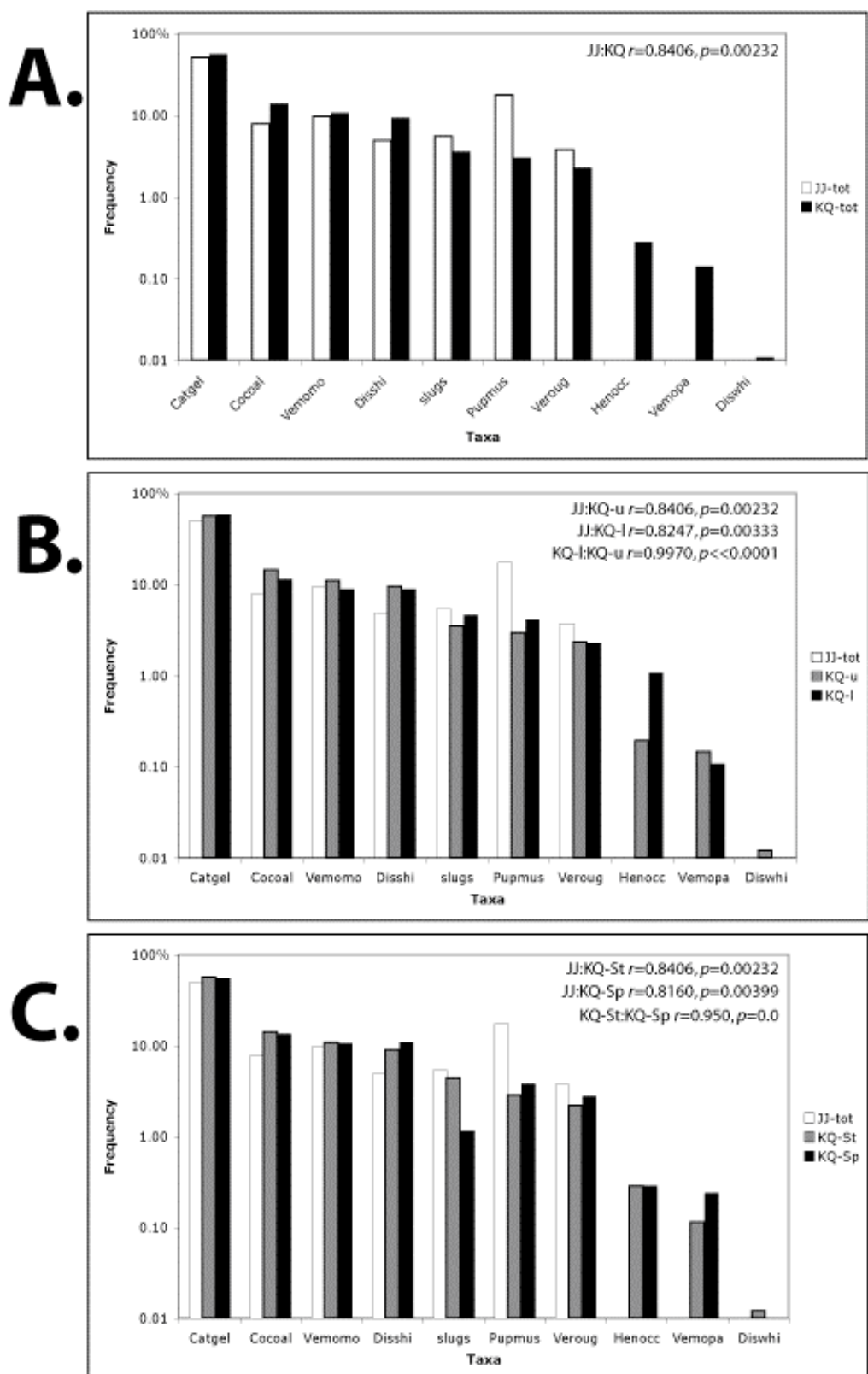


Figure 4.8. Rank abundance of terrestrial gastropod taxa from Hwy-JJ and Kulas Quarry sample groups. Spearman rank (ρ) represents the comparison between sample groups.

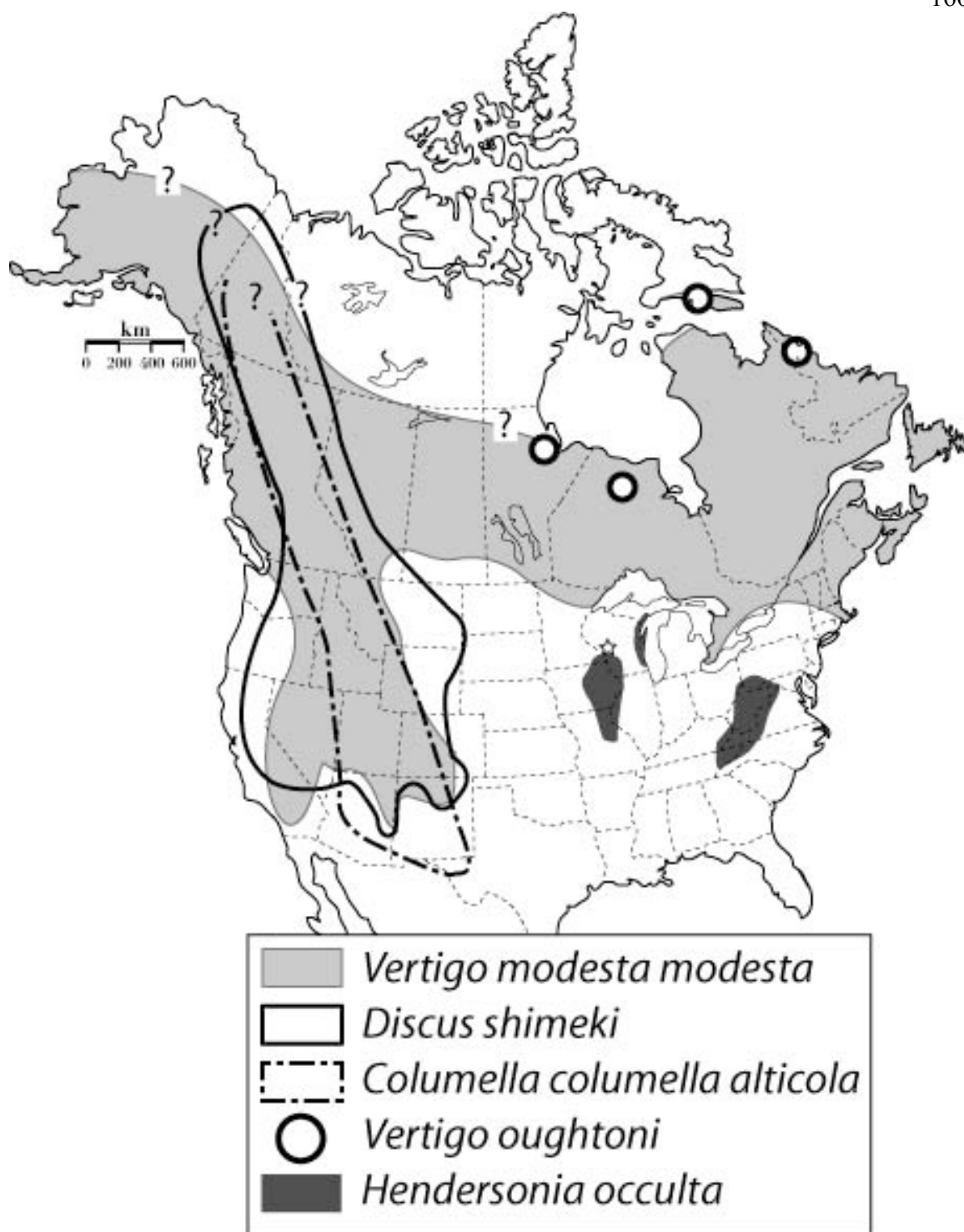


Figure 4.9. Range Map showing modern range distributions of selected gastropod taxa.



Figure 4.10. North American distribution of *Dicrostonyx* sp. (collared lemming).

Chapter 5

Summary and Conclusions

5.1 RESULTS SUMMARY

5.1.1 Overview

This dissertation represents the first systematic study of late Pleistocene terrestrial gastropod fossils in the Driftless Area since Chamberlin and Salisbury (1885), including the northernmost full-glacial biotic assemblage in the Midwest (Kuchta et al., 2007a). Several of the gastropod taxa described represent the first records of these species in Wisconsin (e.g. *Discus shimeki*, *Columella columella alticola*, *Vertigo oughtoni*). The relationships between the fossil assemblages and stratigraphic architecture suggest that fossil assemblages should be similar throughout the region, and will help constrain the timing of important depositional episodes within the UMV. The amino acid racemization analysis demonstrates that this technique can be used to identify gastropods that did not coexist and provides a baseline from which to extend an amino acid geochronology into other fossiliferous deposits in Wisconsin and Minnesota.

The late Pleistocene gastropod fauna from the Upper Mississippi Valley is dominated by Cordilleran-Boreal taxa, such as *Discus shimeki* and *Columella columella alticola* (Figure 5.1). This compares to the modern gastropod fauna, which is dominated by Eastern Deciduous Forest gastropods including *Anguispira alternata* and *Neohelix albolabris* (Figures 5.2 and 5.3). One of the most striking differences between the snails living in the UMV today, and the late Pleistocene gastropod fauna is the much wider range in body size of individual shells (Figure 5.4A, 5.4B). It is also interesting to note

that Foley (1984) reported *Anguispira* sp. from Moscow Fissure. The distribution of late Pleistocene *A. alternata* fossils is restricted to the Gulf Coast (Hubricht, 1985; Figure 5.3). Based on the results from this study, the typical species in late Pleistocene assemblages are considerably different than those reported from Moscow Fissure. If Moscow Fissure is full-glacial in age, it represents a remarkable gastropod refugium. However, Moscow Fissure may predate the full-glacial period (Richard Slaughter, personal communication 2006), which has considerable implications for the response of terrestrial gastropods to climate change.

5.1.2 Sedimentology and Stratigraphy

Late Pleistocene sediments within the UMV provide important insights into the depositional mechanisms that preserved an abundant gastropod fauna. The thickest and most fossiliferous deposits include clast-supported and matrix-supported diamictos along hillslopes that grade into silty and sandy alluvial sediments filling the river valleys. The depositional context of the fossiliferous sediments within the UMV provides insight into the potential age distribution and taphonomic filters that control what types of gastropod shells are preserved.

Radiocarbon data from this and previous studies suggest that hillslope mass wasting and valley aggradation were most active between approximately 24,000 and 16,000 cal yr BP. Most sediment exposures that crop out below the late Pleistocene Savanna Terrace surface show aggradational features during this period. Several sites within the Latch Valley of Trempealeau County display diverse associations of lithofacies and sedimentary structures. This pattern consists of matrix-supported

diamicton and massive silts on the hillslopes that grade into laminated silt along the valley margins with sandy lithofacies closer to the valley axis. The fine colluvial silt may consist of reworked loess and some bedrock clasts, while the fine laminated silt and clay along the valley edges is characteristic of floodplain deposits with interbedded sheet sands as a result of overbank floods and slack water deposits. Root casts within the fine-grained lithofacies suggest the floodplains were vegetated. Sandy lithofacies closer to the valley axis indicate that active braided stream type aggradation was the primary mode of sediment deposition. Large trough cross-beds suggest individual channels were about 0.5-1.5 m deep and 1-3 meters wide. Two fining upward parasequences visible at Kulas Quarry suggest the active channel belt moved laterally across the floodplain, exposing previously active channels and loess might have been able to accumulate on the floodplain surface during this hiatus. The sand and gravel-sized fraction of the sediments consist of well-rounded quartz, glauconite, muscovite, and bedrock fragments. Sediment within the Latch Valley was mostly derived from weathered Cambrian bedrock (Tunnel City Group and Wonewoc Formation) although some silt was probably introduced from outside the valley as loess.

Downcutting into the Savanna Terrace surface likely began by approximately 16,100 cal yr BP based on the age data from Hideaway Lane plus additional radiocarbon data from Knox (1996; 2005). This incision does not correspond to well-constrained outburst events from glacial lake Aggasiz, long thought to have controlled much of the incision into the late Pleistocene floodplain of the UMV (Knox, 2009). Based on the red clay rip-up clasts, it is likely that the earliest incision was a result of sudden drainage of Glacial Lake Duluth or (in addition) Lake Lind, which emptied into the UMV via the St.

Croix River valley. Colluvial sedimentation continued during this initial phase of downcutting, as indicated by radiocarbon results from Limery Coulee and additional results from Mason and Knox (1997). The data from this study supports the conclusions by previous authors that most sedimentation ceased after 16,000 cal yr BP (Knox, 1996; Mason and Knox, 1997; Knox 2005).

5.1.3 Amino Acid Racemization

The results from amino acid racemization analyses (AAR) of gastropod shells demonstrate both the potential applications and sources of uncertainty for this technique. Shells from gastropod genera with “older” looking shells (*Succinea*, *Catinella*, *Discus*, *Vertigo*, *Columella*, *Pupilla*, and *Vallonia*) had D/L Asp values from 0.300 to 0.350, characteristic of late Pleistocene ages, whereas “young” shells (*Helicodiscus*, *Hawaiiia*, *Glyphalina*, *Pupoides*) had D/L Asp values between 0.060 and 0.170, indicating these shells were introduced into the assemblage after its deposition, some shells could have been incorporated quite recently; only a few hundred years ago. The total variance in D/L Asp for succineid shells was less than that expected as a result of analytical uncertainty and multiple ^{14}C dates from single horizons were in close agreement. While the D/L Asp values yielded little variability, the radiocarbon results shows that there could be several hundred years difference between the ages of individual succineid shells.

Principal component analysis (PCA) of the AAR data showed that the majority of the variance (PC1) positively correlated with D/L ratios of fast-racemizing amino acids (serine, aspartic acid) and negatively correlated with the concentration of L-Ser. The next largest variance (PC2) correlated positively with Depth and negatively with slower

racemizing amino acids (glutamic acid, alanine). The negative correlation between depth and D/L Glu and D/L Ala indicates that either L-Ala and L-Glu are preferentially removed (by leaching free amino acids) or D-Ala and D-Glu are introduced near the surface. D/L Asp – the most commonly used indicator of age – did not correlate, or showed a slight negative correlation with depth. Surface heating may explain stratigraphic aberrations in D/L Asp values. The anomaly in Glu and Ala may be a result of surface contamination from bacteria, as the peptidoglycan in the cell walls of many bacteria is enriched in D-Ala and D-Glu.

These results suggest that: 1) some non-analog species found within fossil deposits were introduced long after the assemblage formed. 2) Relative and ^{14}C age data suggest time averaging was less than 1000 years. 3) Variation within succineid AAR data can be attributed largely to diagenetic alteration, either leaching of D-AAs or contamination from L-Ser, heat-induced racemization, or D-Ala and D-Glu contamination (perhaps from bacterial peptidoglycan). The D-Ala, D-Glu anomaly has not previously been observed in terrestrial gastropod AAR studies, but has significant implications for future gastropod-based amino acid geochronologic studies – especially where D/L Glu is used as an independent or longer interval (e.g. beyond radiocarbon utility) estimate.

5.1.4 Paleoecology

The colluvial and alluvial sediments from Hwy-JJ and Kulas Quarry within the Latch Valley, Trempealeau Co., Wisconsin, provided an opportunity to compare the fossil gastropod assemblages within two distinct yet coeval depositional settings. These

sites contained abundant terrestrial gastropod fossils and some vertebrate remains.

Identifiable dental elements from small rodents include those of *Dicrostonyx* sp. a tundra-dwelling lemming. The gastropod fauna is complex, and includes taxa with modern boreal-cordilleran affinities such as *Discus shimeki*, *Columella columella alticola*, and *Vertigo modesta*, which are not found in the region today. Other gastropods include species that prefer open, xeric habitats, and those that inhabit deciduous forests such as *Hendersonia occulta*, an endangered snail that inhabits the UMV today. While most shells were recovered as both intact and broken specimens, *H. occulta* was only recovered as fragmentary pieces. This suggests that this taxon was incorporated into the deposit via an alternate taphonomic pathway. The shell fragments may be a result of preferential destruction either during transport or deposition, or the shell fragments could be reworked from older material.

Succineid gastropod shells yielded radiocarbon ages between 16,100 and 18,000 RCYBP and indicate the fauna is full-glacial in age. The differences in species richness observed between sites and samples can be largely attributed to the total number of shells within each sample. Samples with high numbers of shells per kilogram of matrix were the richest, while samples with few shells yielded few species. The rank order of abundance was nearly identical for all samples; the primary differences were between upland and floodplain samples, the former yielded a greater abundance of *Pupilla muscorum*, while the latter contained a larger number of rare species. This similarity in gastropod composition suggests a community that was largely unchanged throughout this time interval. The gastropod fauna from the Latch Valley is the northernmost full-glacial fauna in the UMV, located less than 100 km from the terminal moraine of the Chippewa Lobe

of the Laurentide Ice Sheet. The age range of this deposit appears to coincide with a minor retreat of the Chippewa Lobe between the Stanley and Late Chippewa advances. These results generally agree with the ecological interpretations from other regional fossil localities of a tundra-like environment, however the presence of *H. occulta* at this site (if not reworked from older deposits) suggests the presence of minor amounts of deciduous vegetation within topographically controlled microhabitats. It is likely that the Driftless Area of the UMV served as an important refuge for temperate species during the full-glacial period, much as it serves as an important refuge for northern species today.

5.2 CONCLUSIONS

The results of this dissertation have provided much needed groundwork regarding the utility and context of late Pleistocene terrestrial gastropod fossils from the UMV. Terrestrial gastropod fossils are the most abundant biotic material within these sediments, and they have the potential to answer important questions related to the interaction between the landscape, climate, and biological communities. The fossil assemblages described in this study are late full-glacial to early late-glacial in age (ca. 24,000-18,000 and 18,000-13,000 cal yr BP respectively). In addition, there is little evidence for significant time averaging within succineid shells; age differences were undetectable with AAR and only a few hundred years separated radiocarbon dates from the same interval. Species with well-preserved shells had significantly lower D/L amino acid values compared to those species with opaque, worn shells. Burial and preservation of this fauna was largely a result of the sedimentary processes active at the time. The lack of older

fossil assemblages may be due to their lack of exposure, or a reduced sedimentation rate prior to this interval.

The gastropod fauna preserved is complex; it is dominated by species with Cordilleran and Boreal habitat affinities but also contains several taxa that prefer eastern deciduous forest habitats. Given the proximity to the Laurentide Ice Sheet, the mixture of habitat preferences within these assemblages is striking. It is probable that the strong topographic contrasts in this region provided a refuge for many species throughout the last glacial period. It is possible that the formation of the Driftless Area at some earlier point in the Pleistocene had a profound effect upon the biotic response to subsequent climatic changes.

5.3 SUGGESTIONS FOR FUTURE RESEARCH

5.3.1 Locate additional sites

These results suggest avenues for future research, some of which are underway and are described in more detail within Appendix B. Several fossiliferous sites were identified during the survey period of this study, but were not sampled or described in detail. Despite extensive exploration, I was only able to cover a fraction of the total area in the UMV and many more exposures remain to be found, especially given the recent flooding in Minnesota and Wisconsin. The highest priority exposures are those rich in species with a long record of sedimentation and sites from age ranges not covered in this project. Knox (2005) described a shelly layer 4.5 m below the Savanna Terrace from an exposure along the Grant River dated at approximately 17,000 cal yr BP. Mason (1995) and Baker et al. (1999) mentioned the presence fossiliferous sediments at Jore-1, a

cutbank exposure along a tributary of the Root River in southeastern Minnesota. A spruce log, which was dated to approximately 22,400 cal yr BP. Recovery of additional material over a broad range of ages, especially prior to the last glacial maximum or from the earliest Holocene, will be helpful in determining arrival and extirpation dates for individual gastropod species.

5.3.2 Determine taphonomic influences

Fossil-based paleoenvironmental reconstruction depends on separating the climatic influences from depositional and taphonomic ones. The preferential preservation and destruction of fragile gastropod shells will have a significant impact upon the composition of the gastropod assemblage. Many important differences between regional sites may exist at scales not measured by species richness (e.g. diversity). Taphonomic filters such as preferential shell destruction may provide insight into how individual shells are incorporated into a deposit and allow for more detailed environmental interpretations.

5.3.3 Extend the chronology of amino acid racemization in Wisconsin

This project demonstrated the potential applications of amino acid racemization in Wisconsin. Future studies should consider this technique to study the chronology of Quaternary deposits that lie beyond the range of radiocarbon, such as the problematic, eroded deposits of pre-Wisconsinan glacial sediments. In addition, more work is required to characterize the potential for bacterial contamination and alteration of measured AAR results within fossil assemblages. Shells may be pitted, or contain other microscopic

evidence of bacterial activity, in addition, it may be possible to culture the bacteria responsible for contamination and determine their influence on shell protein diagenesis (e.g. Child et al., 1993). Moscow Fissure (Foley, 1984) is widely cited as a full-glacial mammal fauna from southern Wisconsin. However, both the gastropod and mammal fauna are not characteristic of tundra-forest conditions. Revisiting Moscow Fissure with the purpose of radiocarbon and amino acid racemization analyses of the fossils may help resolve the anomalies within this deposit.

5.3.4 Refine gastropod biogeography

Gastropods remain an understudied group, especially in the UMW (Hubricht, 1985; Jass, 2004). In order to make useful environmental interpretations from fossils, it will be necessary to have detailed information on the modern autecology for terrestrial gastropods. I have begun collaborating with Kathryn Perez and James Theler at the University of Wisconsin – La Crosse to build a database for terrestrial gastropods in Wisconsin and expand our understanding of the fauna by conducting new surveys. As of this writing, we have received funding from the Wisconsin DNR to create GIS-based maps and predictive habitat models for the terrestrial gastropods in Wisconsin. These results are expected to aid in fossil-based environmental reconstructions of the late Pleistocene. Finally, the late Pleistocene gastropod fauna in the UMW is dominantly Cordilleran and Boreal in its composition. Combining multiple sites into a regional map may provide insight into where and when species adjusted their ranges across North America (e.g. FAUNMAP, 1996 for mammals).

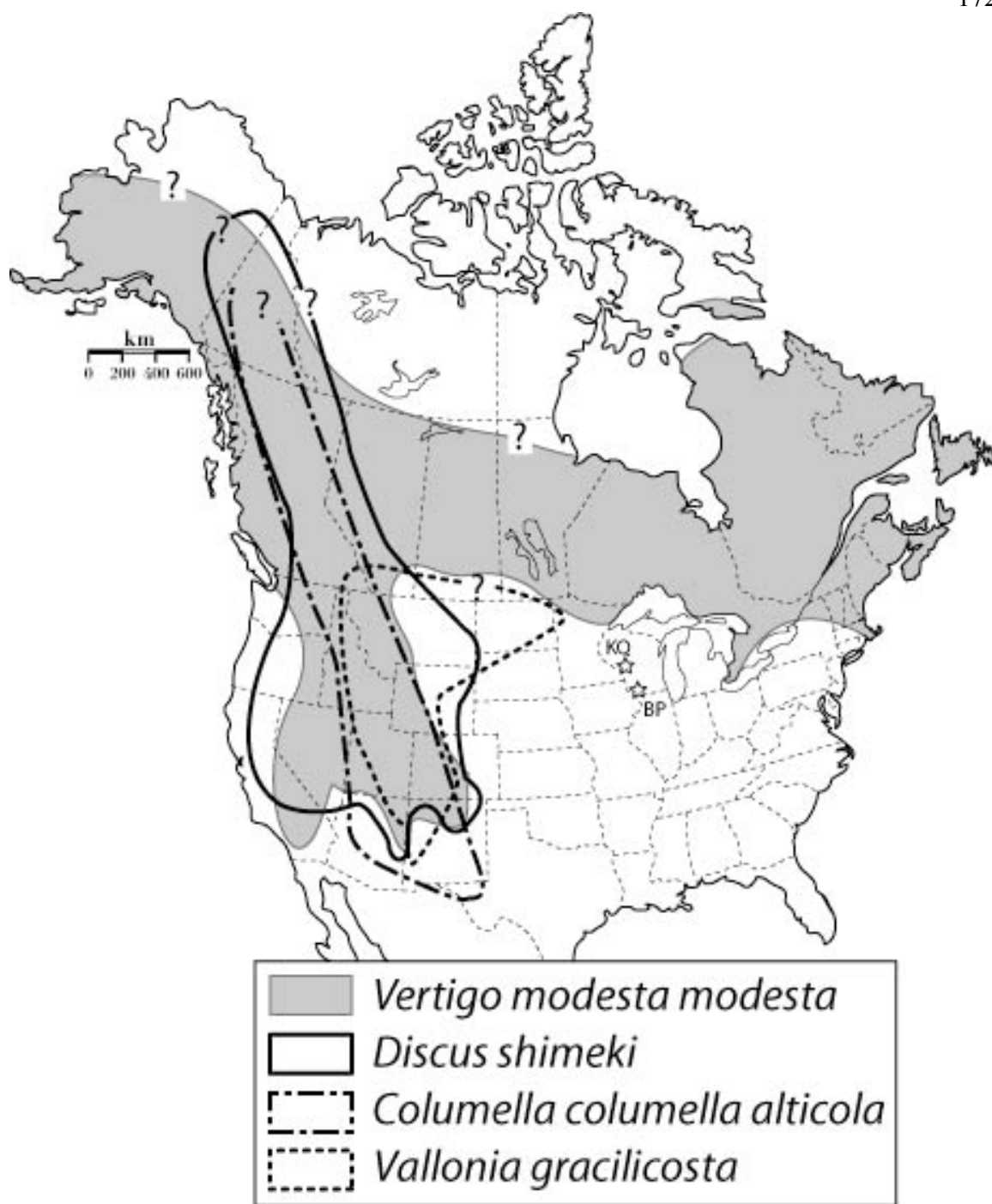


Figure 5.1. Modern distribution of gastropods that occur in the UMV as late Pleistocene fossils.



Figure 5.2. Distribution of *Anguispira alternata*; a common snail in the Eastern Deciduous Forest, but only found along the Gulf Coast as a late Pleistocene fossil.



Figure 5.2. Distribution of *Neohelix albolabris*; a common snail in the Eastern Deciduous Forest, that is restricted to the Gulf Coast as a late Pleistocene fossil.

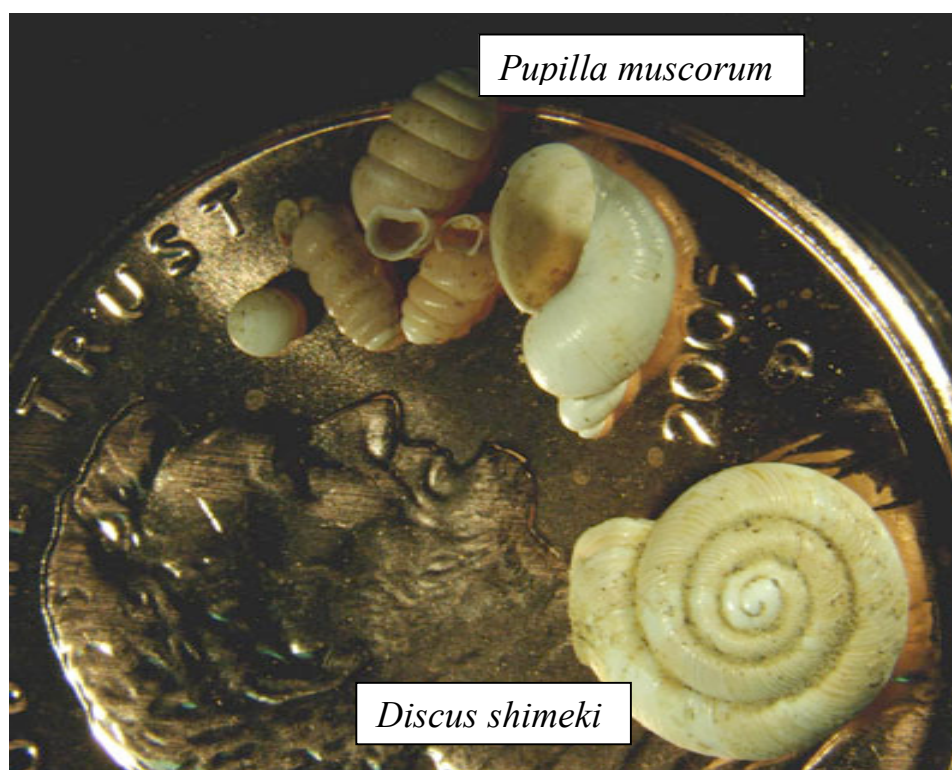


Figure 5.4A. Photograph of typical full-glacial gastropods from the UMV.

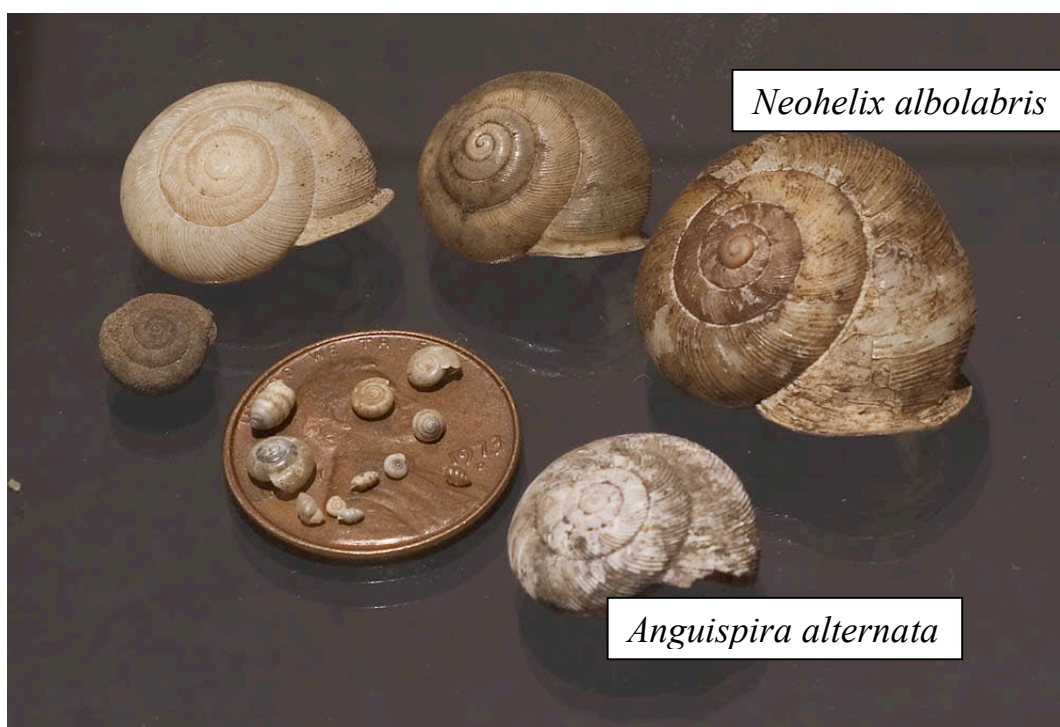


Figure 5.4B. Photograph of common gastropods found in the UMV today. Note the size range compared to the full-glacial taxa.

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AAR Raw Data for Chapter 3

UAI	Sample	Trans	sample characteristics			DL			peak areas			Concentration (pHing shell)			Proportion of [Sum]			L-Ser			
			ARCS	area	norm	ppm	DL	DL	Area	DL	DL	Area	DL	DL	Area	DL	DL				
6302A	BPC1a	Sucrose	1	1	35	3	0.314	0.103	0.614	0.171	727	236	70	272	87	609	115	761	0.291	0.333	
6302B	BPC1a	Sucrose	1	1	35	3	0.300	0.102	0.493	0.160	520	156	509	52	209	103	416	70	760	0.291	0.333
6302C	BPC1a	Sucrose	1	1	35	3	0.318	0.099	0.575	0.177	821	261	726	72	273	157	621	110	746	0.291	0.333
6302D	BPC1a	Sucrose	1	1	35	3	0.289	0.095	0.467	0.167	927	268	904	66	366	171	683	114	733	0.291	0.333
6302E	BPC1a	Sucrose	1	1	35	3	0.337	0.101	0.619	0.161	1207	326	624	63	226	140	528	101	728	0.291	0.333
6302F	BPC1a	Sucrose	1	1	35	3	0.285	0.105	0.453	0.165	1227	320	869	104	419	190	814	159	772	0.291	0.333
6302G	BPC1a	Sucrose	0	1	35	3	0.365	0.105	0.549	0.310	874	319	736	71	295	182	578	179	743	0.291	0.333
6302H	BPC1a	Sucrose	0	1	35	3	0.338	0.111	0.598	0.218	736	249	729	81	271	182	570	124	753	0.291	0.333
6302I	BPC1a	Sucrose	0	1	35	3	0.338	0.103	0.586	0.161	851	288	809	83	295	173	629	114	755	0.291	0.333
6302J	BPC1a	Sucrose	0	1	35	3	0.338	0.103	0.586	0.161	851	288	809	83	295	173	629	114	755	0.291	0.333
6302K	BPC1a	Sucrose	0	1	35	3	0.322	0.103	0.488	0.166	698	212	658	68	254	124	526	98	690	0.291	0.333
6302L	BPC1a	Sucrose	0	1	35	3	0.316	0.102	0.563	0.228	698	212	658	68	254	124	526	98	690	0.291	0.333
6302M	BPC1a	Sucrose	0	1	35	3	0.327	0.097	0.567	0.245	698	224	741	72	264	144	564	138	720	0.291	0.333
6302N	BPC1a	Sucrose	0	1	35	3	0.335	0.104	0.587	0.287	698	234	700	73	264	144	564	138	720	0.291	0.333
6302O	BPC1a	Sucrose	0	1	35	3	0.314	0.315	0.535	0.230	732	230	732	75	270	156	625	137	718	0.291	0.333
6302P	BPC1a	Sucrose	0	1	35	3	0.307	0.097	0.578	0.219	795	232	777	75	270	156	625	137	718	0.291	0.333
6302Q	BPC1a	Sucrose	0	1	35	3	0.327	0.100	0.591	0.273	810	265	814	81	289	163	640	175	719	0.291	0.333
6302R	BPC1a	Sucrose	0	1	35	3	0.316	0.100	0.529	0.220	775	245	767	77	289	163	640	175	719	0.291	0.333
6302S	BPC1a	Sucrose	0	1	35	3	0.311	0.104	0.520	0.253	779	242	712	74	277	144	592	147	710	0.291	0.333
6302T	BPC1a	Sucrose	0	1	35	3	0.336	0.096	0.571	0.218	729	245	738	71	281	149	591	129	693	0.291	0.333
6302U	BPC1a	Sucrose	0	1	35	3	0.326	0.101	0.583	0.233	827	270	772	78	271	158	621	145	681	0.291	0.333
6303A	BPC1b	Sucrose	1	2	60	3	0.321	0.101	0.570	0.181	343	110	367	37	149	85	332	60	769	0.291	0.333
6303B	BPC1b	Sucrose	1	2	60	3	0.313	0.099	0.542	0.188	307	96	292	29	118	64	240	45	755	0.291	0.333
6303C	BPC1b	Sucrose	1	2	60	3	0.336	0.099	0.601	0.186	753	253	788	78	278	167	606	113	741	0.291	0.333
6303D	BPC1b	Sucrose	1	2	60	3	0.342	0.095	0.568	0.182	802	274	733	70	284	150	560	102	726	0.291	0.333
6303E	BPC1b	Sucrose	1	2	60	3	0.338	0.092	0.599	0.179	678	229	698	64	237	142	520	93	737	0.291	0.333
6303F	BPC1b	Sucrose	0	2	60	3	0.382	0.099	0.619	0.178	1159	443	1217	121	409	253	869	155	604	0.291	0.333
6303G	BPC1b	Sucrose	0	2	60	3	0.344	0.097	0.561	0.169	971	334	1038	101	362	203	752	127	620	0.291	0.333
6303H	BPC1b	Sucrose	0	2	60	3	0.332	0.097	0.558	0.172	1068	355	1068	104	369	206	734	126	640	0.291	0.333
6303I	BPC1b	Sucrose	0	2	60	3	0.328	0.101	0.577	0.232	728	239	726	73	267	154	573	133	736	0.291	0.333
6303J	BPC1b	Sucrose	0	2	60	3	0.340	0.096	0.569	0.170	603	205	710	68	260	148	554	94	649	0.291	0.333
6303K	BPC1b	Sucrose	0	2	60	3	0.327	0.091	0.454	0.253	841	275	846	77	359	163	648	164	750	0.291	0.333
6303L	BPC1b	Sucrose	0	2	60	3	0.360	0.111	0.610	0.182	884	318	857	95	326	199	674	123	675	0.291	0.333
6303M	BPC1b	Sucrose	0	2	60	3	0.344	0.095	0.565	0.169	700	241	628	79	276	156	605	102	658	0.291	0.333
6303N	BPC1b	Sucrose	0	2	60	3	0.351	0.098	0.598	0.201	777	273	772	76	271	162	592	119	745	0.291	0.333
6303O	BPC1b	Sucrose	0	2	60	3	0.337	0.101	0.534	0.221	719	242	660	70	266	142	569	126	732	0.291	0.333
6303P	BPC1b	Sucrose	0	2	60	3	0.323	0.103	0.542	0.172	718	232	779	80	295	160	604	104	652	0.291	0.333
6303Q	BPC1b	Sucrose	0	2	60	3	0.344	0.100	0.559	0.163	834	287	834	83	311	174	635	116	733	0.291	0.333
6303R	BPC1b	Sucrose	0	2	60	3	0.317	0.097	0.507	0.150	676	214	710	69	272	138	572	86	675	0.291	0.333
6303S	BPC1b	Sucrose	0	2	60	3	0.312	0.083	0.385	0.176	820	256	931	77	417	152	680	120	736	0.291	0.333
6303T	BPC1b	Sucrose	0	2	60	3	0.342	0.106	0.580	0.174	738	273	875	93	283	170	645	112	725	0.291	0.333
6303U	BPC1b	Sucrose	0	2	60	3	0.334	0.106	0.564	0.263	727	241	660	72	259	146	525	138	704	0.291	0.333
6303V	BPC1b	Sucrose	0	2	60	3	0.321	0.090	0.583	0.251	671	217	671	67	258	153	606	152	701	0.291	0.333
6303W	BPC1b	Sucrose	0	2	60	3	0.284	0.087	0.326	0.155	586	170	624	54	304	99	452	70	702	0.291	0.333

LAL	Sample	Taxon	sample characteristics			DL			peak areas										Concentration (palling shell)			Proportion of (Sum)			L-Ser/																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																
			Address	Str	Depth	Ten	DL	Asp	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL	DL

UAL	Sample	Taxon	AARSP	Strat	Rank	Depth	Type	D/L			Peak areas										Concentration (µg/mg)			Proportion of [Sum]			L-Ser			
								D:Asp	D:Glu	D:Ser	L:Asp	L:Glu	L:Ser	L:Asn	L:Gln	L:Leu	L:Val	L:Ala	L:Pro	L:Thr	L:Met	L:His	L:Ile	L:Tyr	L:Trp	L:Arg		L:Pro	L:Thr	L:Met
6847A	KQ-10	Catnella	0	6	350	3	0.331	0.072	0.497	0.125	1198	396	1411	101	636	316	1169	146	736	433	411	259	357	1460	0.297	0.281	0.177	0.245	0.399	0.474
6847B	KQ-10	Catnella	0	6	350	3	0.331	0.090	0.495	0.139	1237	410	1072	96	570	282	906	126	892	416	395	215	281	1187	0.351	0.249	0.181	0.220	0.346	0.488
6847C	KQ-10	Catnella	0	6	350	3	0.317	0.101	0.499	0.152	864	274	821	83	429	214	672	102	852	267	212	151	182	812	0.329	0.261	0.186	0.224	0.377	0.475
6847D	KQ-10	Catnella	0	6	350	3	0.304	0.069	0.484	0.128	864	299	1033	71	508	246	894	114	724	354	305	208	278	1146	0.309	0.266	0.182	0.243	0.396	0.460
6847E	KQ-10	Catnella	0	6	350	3	0.330	0.073	0.519	0.148	1224	404	1308	95	568	284	1293	152	860	348	213	293	1259	0.321	0.277	0.170	0.233	0.348	0.403	
6847F	KQ-10	Catnella	0	6	350	3	0.301	0.069	0.486	0.127	1108	333	1157	80	535	260	920	117	768	375	322	207	270	1174	0.320	0.274	0.176	0.230	0.371	0.432
6848A	KQ-12	Catnella	0	5	380	3	0.327	0.073	0.554	0.136	1484	486	1632	119	769	434	1395	190	791	488	443	304	401	1646	0.303	0.269	0.185	0.244	0.390	0.439
6848B	KQ-12	Catnella	0	5	380	3	0.321	0.075	0.529	0.130	744	239	815	61	344	182	339	83	792	248	221	133	182	785	0.316	0.282	0.169	0.232	0.350	0.393
6848C	KQ-12	Catnella	0	5	380	3	0.326	0.074	0.510	0.119	764	249	852	63	396	202	756	90	745	272	246	161	227	905	0.300	0.271	0.177	0.251	0.391	0.433
6848D	KQ-12	Catnella	0	5	380	3	0.307	0.091	0.510	0.142	862	265	849	77	406	207	733	104	781	289	237	157	214	897	0.322	0.264	0.175	0.239	0.360	0.438
6848E	KQ-12	Catnella	0	5	380	3	0.341	0.078	0.473	0.136	888	296	859	67	410	194	893	93	807	288	229	150	192	860	0.335	0.267	0.174	0.224	0.352	0.443
6848F	KQ-12	Catnella	0	5	380	3	0.329	0.077	0.527	0.136	1065	350	1095	82	509	268	922	125	763	371	301	204	274	1150	0.323	0.262	0.177	0.239	0.360	0.444
6328A	KQ-15	Catnella	0	4	280	3	0.346	0.077	0.392	0.137	1181	409	1221	94	688	270	991	136	1216	262	216	158	185	821	0.319	0.264	0.192	0.226	0.433	0.523
6328B	KQ-15	Catnella	0	4	280	3	0.309	0.077	0.432	0.133	1438	444	1629	125	895	387	1370	182	1135	332	309	226	273	1140	0.291	0.271	0.198	0.240	0.476	0.510
6328C	KQ-15	Catnella	0	4	280	3	0.321	0.091	0.499	0.139	1341	430	1491	136	773	386	1328	185	1111	319	393	209	272	1093	0.292	0.268	0.191	0.249	0.436	0.475
6328D	KQ-15	Catnella	0	4	280	3	0.352	0.082	0.497	0.147	1767	622	1595	128	915	455	1237	182	1245	394	272	220	228	1104	0.348	0.246	0.199	0.207	0.383	0.540
6328E	KQ-15	Catnella	0	4	280	3	0.315	0.080	0.451	0.119	1241	391	1217	97	641	289	1078	128	1191	274	221	156	203	853	0.321	0.259	0.183	0.237	0.393	0.488
6849A	KQ-17	Catnella	0	3	250	3	0.315	0.066	0.489	0.131	1406	443	1550	103	777	380	1291	169	779	475	424	297	375	1571	0.302	0.270	0.189	0.239	0.420	0.470
6849B	KQ-17	Catnella	0	3	250	3	0.333	0.071	0.516	0.123	999	333	983	70	548	283	920	101	806	331	261	206	229	1027	0.322	0.255	0.201	0.223	0.411	0.520
6849C	KQ-17	Catnella	0	3	250	3	0.327	0.069	0.475	0.129	1324	433	1244	86	602	286	912	118	769	457	346	231	288	1302	0.351	0.266	0.177	0.206	0.343	0.453
6849D	KQ-17	Catnella	0	3	250	3	0.354	0.126	0.505	0.187	364	129	380	48	198	100	343	64	860	115	100	69	95	378	0.303	0.263	0.183	0.250	0.402	0.463
6849E	KQ-17	Catnella	0	3	250	3	0.334	0.085	0.468	0.179	1223	409	1200	102	605	292	922	165	778	420	335	231	279	1265	0.332	0.265	0.183	0.221	0.371	0.465
6849F	KQ-17	Catnella	0	3	250	3	0.332	0.073	0.512	0.138	1259	418	1294	95	603	309	1013	140	789	425	352	231	292	1301	0.327	0.271	0.178	0.225	0.360	0.434
6850A	KQ-18	Catnella	0	2	280	3	0.303	0.064	0.391	0.143	1196	362	1234	79	688	269	938	134	776	402	338	247	276	1263	0.318	0.268	0.195	0.219	0.442	0.524
6850B	KQ-18	Catnella	0	2	280	3	0.316	0.068	0.403	0.124	1122	354	1239	84	718	289	986	122	757	390	350	266	293	1298	0.300	0.269	0.205	0.225	0.486	0.543
6850C	KQ-18	Catnella	0	2	280	3	0.270	0.058	0.310	0.109	1394	430	1902	110	725	389	1469	160	801	565	302	410	407	1625	0.277	0.275	0.225	0.223	0.620	0.624
6850D	KQ-18	Catnella	0	2	280	3	0.293	0.063	0.349	0.112	1306	383	1515	95	890	311	1098	123	754	448	427	319	324	1518	0.295	0.281	0.210	0.213	0.527	0.553
6850E	KQ-18	Catnella	0	2	280	3	0.302	0.070	0.421	0.145	1275	365	1334	93	730	307	1064	154	784	423	384	265	311	1383	0.311	0.267	0.194	0.228	0.440	0.512
6850F	KQ-18	Catnella	0	2	280	3	0.303	0.085	0.391	0.150	960	291	845	72	596	233	705	166	789	317	232	210	206	965	0.329	0.241	0.218	0.213	0.476	0.650
6851A	KQ-20	Catnella	0	1	250	3	0.330	0.077	0.560	0.137	1473	486	1344	104	623	345	1304	179	801	489	382	243	370	1484	0.334	0.247	0.168	0.253	0.318	0.430
6851B	KQ-20	Catnella	0	1	250	3	0.323	0.077	0.595	0.132	1377	445	1579	121	650	397	1307	172	797	497	427	260	371	1515	0.302	0.286	0.172	0.245	0.357	0.382
6851C	KQ-20	Catnella	0	1	250	3	0.344	0.076	0.580	0.150	1301	516	1576	19	683	396	1331	200	801	594	423	269	382	1579	0.319	0.268	0.171	0.242	0.339	0.403
6851D	KQ-20	Catnella	0	1	250	3	0.355	0.080	0.576	0.138	1283	455	1091	87	545	314	897	120	783	444	298	219	252	1214	0.366	0.246	0.161	0.208	0.314	0.467
6851E	KQ-20	Catnella	0	1	250	3	0.366	0.087	0.674	0.142	1060	395	1221	95	467	335	856	136	777	360	339	214	282	1214	0.315	0.279	0.176	0.232	0.337	0.378
6851F	KQ-20	Catnella	0	1	250	3	0.346	0.087	0.593	0.147	1225	424	1095	95	545	316	897	132	778	424	366	222	285	1216	0.349	0.252	0.182	0.218	0.331	0.458
6437	HP1	Helicodiscus	0	1	35	2	0.162	0.049	0.104	0.070	1428	231	1113	54	654	129	819	57	713	465	327	222	246	1261	0.369	0.260	0.176	0.195	0.400	0.569
6438	HP2	Helicodiscus	0	1	35	2	0.165	0.046	0.103	0.078	1110	184	980	45	574	111	703	55	729	395	261	188	208	1032	0.344	0.272	0.182	0.201	0.444	0.559
6439	HP3	Helicodiscus	0	1	35	2	0.152	0.039	0.104	0.068	1410	210	1165	46	665	121	905	55	689	471	352	226	250	1299	0.363	0.271	0.174	0.192	0.405	0.563
6440	HP4	Helicodiscus	0	1	35	2	0.113	0.038	0.135	0.065	1066	120	890	36	617	83	599	39	726	393	266	184	185	944	0.348	0.271	0.209	0.203	0.550	0.745
6441	HP5	Helicodiscus	0	1	35	2	0.098	0.044	0.115	0.066	2230	220	1741	76	933	168	1382	81	722	674	500	415	405	1994	0.338	0.261	0.208	0.203	0.552	0.645
6442	HP6	Helicodiscus	0	1	35	2	0.108	0.038	0.139	0.057	725	78	591	22	409	57	439	35	726	221	166	139	139	644	0.344	0.258	0.199	0.199	0.509	0.678
6566A	HP7	Helicodiscus	0	1	35	2	0.161	0.060	0.202	0.088	19902																			

UAL	Sample	Taxon	sample characteristics				DL		peak areas										Concentration (pM/mg shell)					Proportion of [Sum]					L-Ser/		
			AltDep	Strat Rank	Depth	Type	DL Asp	DL Ser	L-Asp	D-Asp	L-Glu	D-Glu	L-Ser	D-Ser	L-Ala	D-Ala	n-His	[Asp]	[Glu]	[Ser]	[Ala]	[Sum]	Asp	Glu	Ser	Ala	His	D-L-Asp/D-L-Glu			
6555A	C2DS1	<i>Discus-shi</i>	0	1	40	3	0.352	0.093	0.523	0.211	1992	702	2393	222	777	406	1192	252	732	736	714	323	395	2168	0.339	0.330	0.149	0.182		0.288	0.297
6555B	C2DS1	<i>Discus-shi</i>	0	1	40	3	0.354	0.101	0.537	0.206	1482	524	1729	175	561	301	973	200	755	531	504	228	311	1575	0.337	0.320	0.145	0.197		0.280	0.295
6555C	C2DS1	<i>Discus-shi</i>	0	1	40	4	0.355	0.087	0.470	0.179	844	300	1079	94	384	171	569	102	799	286	294	134	168	882	0.325	0.333	0.152	0.190		0.318	0.310
6556A	C3DS1	<i>Discus-shi</i>	0	1	40	3	0.342	0.085	0.505	0.205	1335	456	1550	132	556	281	786	161	766	468	439	219	247	1373	0.341	0.320	0.159	0.180		0.310	0.331
6556B	C3DS1	<i>Discus-shi</i>	0	1	40	3	0.317	0.081	0.457	0.202	1051	333	1391	113	452	252	677	137	791	350	380	203	206	1139	0.307	0.334	0.178	0.181		0.399	0.367
6556C	C3DS1	<i>Discus-shi</i>	0	1	40	3	0.295	0.077	0.423	0.152	1168	344	1294	100	454	192	735	112	806	375	346	160	210	1092	0.344	0.317	0.147	0.193		0.300	0.326
6853	C2DW	<i>Discus-whi</i>	0	2	80	3	0.300	0.092	0.435	0.194																					
6558A	C2VM1	<i>Vertigo</i>	0	1	40	3	0.320	0.114	0.523	0.268	1403	449	1410	161	398	208	982	266	964	384	326	126	261	1097	0.350	0.297	0.115	0.238		0.215	0.253
6558B	C2VM1	<i>Vertigo</i>	0	1	40	3	0.327	0.112	0.498	0.278	2761	903	2833	316	578	487	2227	618	954	768	660	307	596	2332	0.329	0.283	0.132	0.256		0.267	0.311
6558C	C2VM1	<i>Vertigo</i>	0	1	40	3	0.338	0.115	0.529	0.297	1232	417	1353	155	393	208	965	287	918	359	329	131	273	1092	0.329	0.301	0.120	0.250		0.258	0.261
6559A	C3VM2	<i>Vertigo</i>	0	1	40	3	0.332	0.109	0.474	0.303	1086	964	1370	150	428	203	899	272	897	326	339	141	261	1066	0.305	0.318	0.132	0.245		0.293	0.282
6559B	C3VM2	<i>Vertigo</i>	0	1	40	3	0.341	0.109	0.451	0.281	2100	717	2307	251	761	343	1593	448	820	687	624	269	498	2078	0.331	0.300	0.130	0.240		0.270	0.297
6559C	C3VM2	<i>Vertigo</i>	0	1	40	3	0.357	0.108	0.586	0.277	1256	448	1763	191	495	290	1178	326	891	382	439	176	338	1335	0.387	0.329	0.132	0.253		0.290	0.253
6855	BP-GI	<i>Glyptalmia</i>	0	1	35	1	0.139	0.040	0.166	0.050																					
6854	C2-HM	<i>Hawalia</i>	0	2	80	2	0.081	0.060	0.049	0.046																					
6856A	BP-HM	<i>Hawalia</i>	0	1	35	2	0.071	0.037	0.097	0.042																					
6856B	BP-HM	<i>Hawalia</i>	0	1	35	2	0.130	0.033	0.140	0.058																					
6856C	BP-HM	<i>Hawalia</i>	0	1	35	2	0.122	0.048	0.172	0.068																					
6856D	BP-HM	<i>Hawalia</i>	0	1	35	2	0.172	0.050	0.180	0.089																					
6557A	PM1	<i>Pupilla</i>	0	1	40	3	0.321	0.120	0.555	0.311																					
6557B	PM2	<i>Pupilla</i>	0	1	35	3	0.343	0.149	0.482	0.403																					
6557C	PM3	<i>Pupilla</i>	0	1	35	4	0.354	0.102	0.455	0.283																					
6557D	PM4	<i>Pupilla</i>	0	1	40	4	0.332	0.125	0.524	0.324																					
6560	PA1	<i>Pupoides</i>	0	2	80	2	0.081	0.032	0.118	0.032																					
6561A	EF1	<i>Eucornutus</i>	0	2	80	3	0.308	0.105	0.522	0.221																					
6561B	EF2	<i>Eucornutus</i>	0	2	80	3	0.317	0.112	0.518	0.220																					
6567A	VG1	<i>Valonia</i>	0	1	35	4	0.330	0.091	0.413	0.159																					
6567B	VG2	<i>Valonia</i>	0	1	40	3	0.335	0.094	0.505	0.155																					
6567C	VG3	<i>Valonia</i>	0	1	40	4	0.253	0.064	0.182	0.133																					
6567D	VG4	<i>Valonia</i>	0	2	80	3	0.219	0.049	0.331	0.114																					
6567E	VG5	<i>Valonia</i>	0	2	80	3	0.300	0.074	0.414	0.144																					
6568A	C3CA1	<i>Columnella</i>	1	1	40	3	0.287	0.125	0.399	0.283																					
6568B	C3CA2	<i>Columnella</i>	1	1	40	4	0.306	0.127	0.490	0.301																					
6568C	C3CA3	<i>Columnella</i>	1	1	40	3	0.283	0.107	0.391	0.265																					
6568D	C3CA4	<i>Columnella</i>	1	1	40	3	0.286	0.117	0.401	0.256																					
6569A	C3CA1	<i>Columnella</i>	1	1	40	3	0.292	0.125	0.480	0.294																					
6569B	C3CA2	<i>Columnella</i>	1	1	40	3	0.322	0.125	0.501	0.314																					

Notes: * = Rejected based on screening criteria; *flagged by one screening test, but not rejected; AARdep-more than 50 cm below exposure face; StratRank 1 = highest; Depth = cm below top of exposure; Notes: total = 2.36 shells analyzed; All shells except *Catnella* are from Big Blatte (BP) KQ=Kulus Quarry.

Notes: **Rejected based on screening criteria; *Flagged by one screening test, but not rejected; AltDep=more than 50 cm behind exposure face; StratRank 1 = highest; Depth = cm below top of exposure; total = 236 shells analyzed; All shells except *Columnella* are from Big Plate (BP) KQ=Kulus Quarry.

Appendix B

Data Screening

Non-temporal sources of variation (contamination, leaching, etc.) can have a profound effect on the AAR data. Understanding the source of this variation can identify outliers that are truly aberrant, as opposed to older, reworked shells. Identification of AAR outliers is on an empirical basis, but no universal standard for recognizing and rejecting outliers exists. A set of screening criteria for one taxon may not be applicable to others. Kaufman (2003) used a cutoff of L-Ser/L-Glu ratios > 1.0 to reject ostracod AAR data, whereas values of L-Ser/L-Asp > 0.8 (> 1.5 in degraded samples) resulted in rejection of foraminiferal AAR data (Kaufman, 2006). Kosnik and Kaufman (2008) discuss outlier analysis in detail, by comparing transformed marine mollusk AAR data to linear models and flagging residuals greater than a specified cutoff value.

I followed the suggestions of Kaufman (2000), Kaufman (2006), and Kosnik et al. (2008) to systematically identify outliers in *Succinea*, *Catinella*, and *Helicodiscus*. The remaining taxa consisted of too few individuals to provide reliable estimates. The outlier screens presented here are a modification of those described in the literature (e.g. Kaufman, 2006; Kosnik and Kaufman, 2008) based on empirical analysis of the Big Platte and Kulas Quarry data sets. To reduce the influence of screening on the inferred age-population of the shells, I only flagged samples whose residuals were more than three standard deviations outside the mean for a normal distribution. Samples that were flagged by more than one screening test were rejected.

Tests for outliers included: 1) the covariance of L-Ser/(L+D Asp) versus D/L Glu. Values of the labile L-Ser should be small; samples with abnormally high L-Ser may

indicate modern contamination (e.g. Kaufman, 2000). 2) Covariance of L-Ser/(L+D Glu) versus D/L Asp is a quasi-independent test compared to 1 (*sensu* Kosnik and Kaufman, 2008). Both tests used values calculated from the peak areas measured during HPLC. 3) The concentration of [Asp] and [Glu] should covary as a function of time. Departures from this relationship may indicate aberrant behavior. Concentration was calculated as the sum of the peak D+L areas within each sample, calibrated to an internal spike of the non-protein amino acid L-*h*Arg (Kaufman, 2000). 4) Finally, D/L Asp and D/L Glu should both increase over time (D/L Asp at a faster rate) and samples that do not display this well-documented covariance may indicate an unusual diagenetic pathway (e.g. Kaufman, 2003). 5) In addition to univariate tests, I used the “Outlier Analysis” option in PC-ORD 5.0 (McCune and Mefford, 2006) to analyze the entire data matrix for outliers within rows (samples). This method creates a frequency distribution for the calculated average distances between all entities in the matrix and flags multivariate outliers from this distribution at user-defined cutoffs. I transformed the data matrix by subtracting the mean from each variable and dividing by its standard deviation. This transformed matrix represents the total variation within each column. The distances between individual samples were measured using the Euclidean distance measure. I flagged samples whose average distance was more than three standard deviations above the mean average distance for all samples.

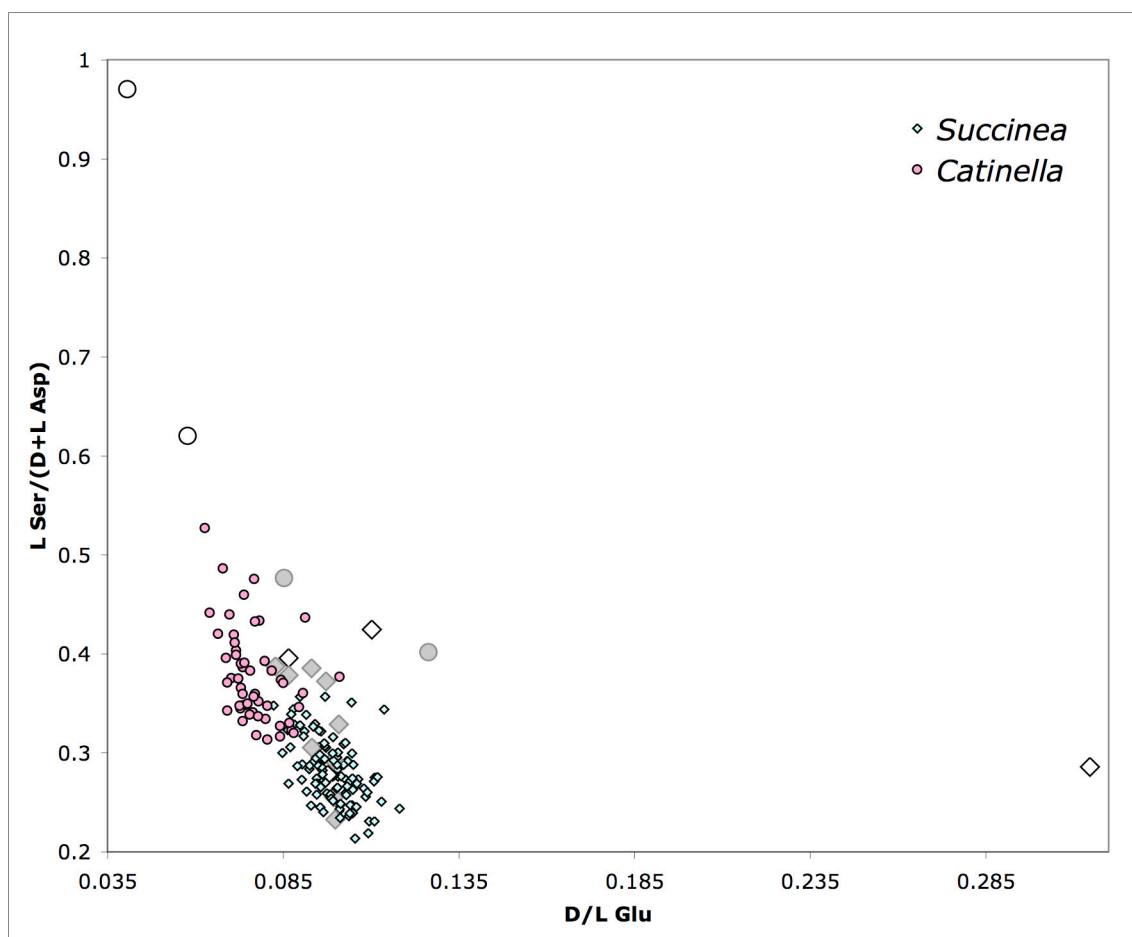


Figure B1. Covariance of D/L Glu versus L-Ser/(D+L Asp) for succineid shells. Outliers in gray, rejected outliers are open symbols.

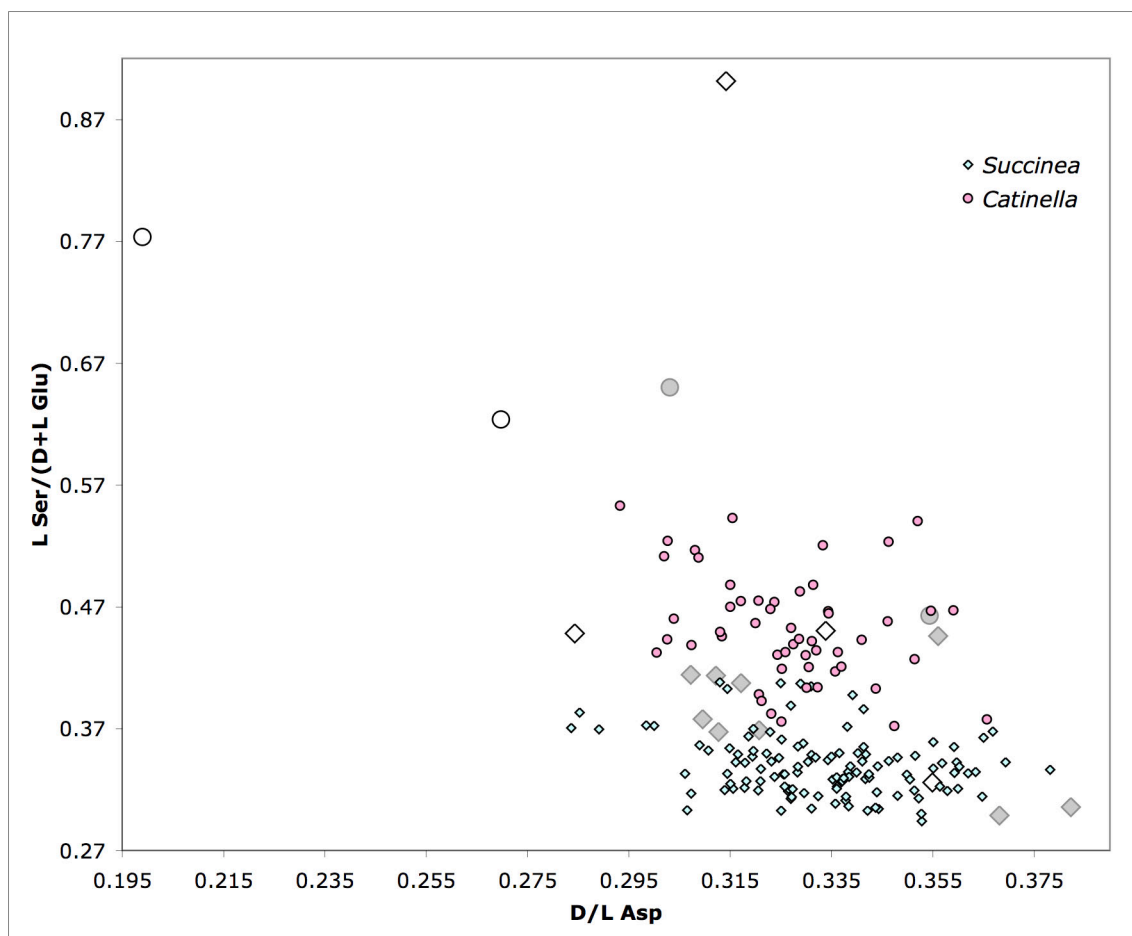


Figure B2. Covariance of D/L Asp versus L-Ser/(D+L Glu) for succineid shells. Outliers in gray, rejected outliers are open symbols.

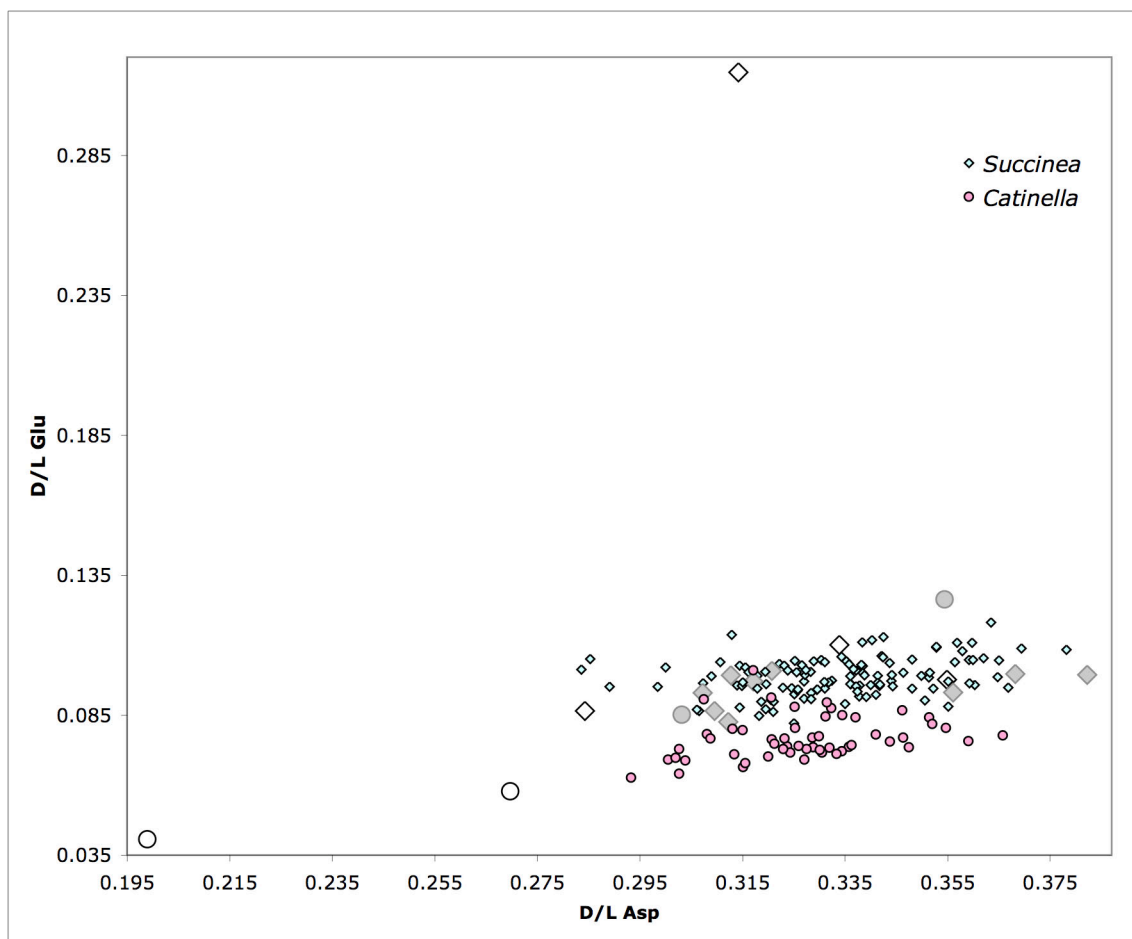


Figure B3. Covariance of D/L Asp versus D/L Glu for succineid shells. Outliers in gray, rejected outliers are open symbols.

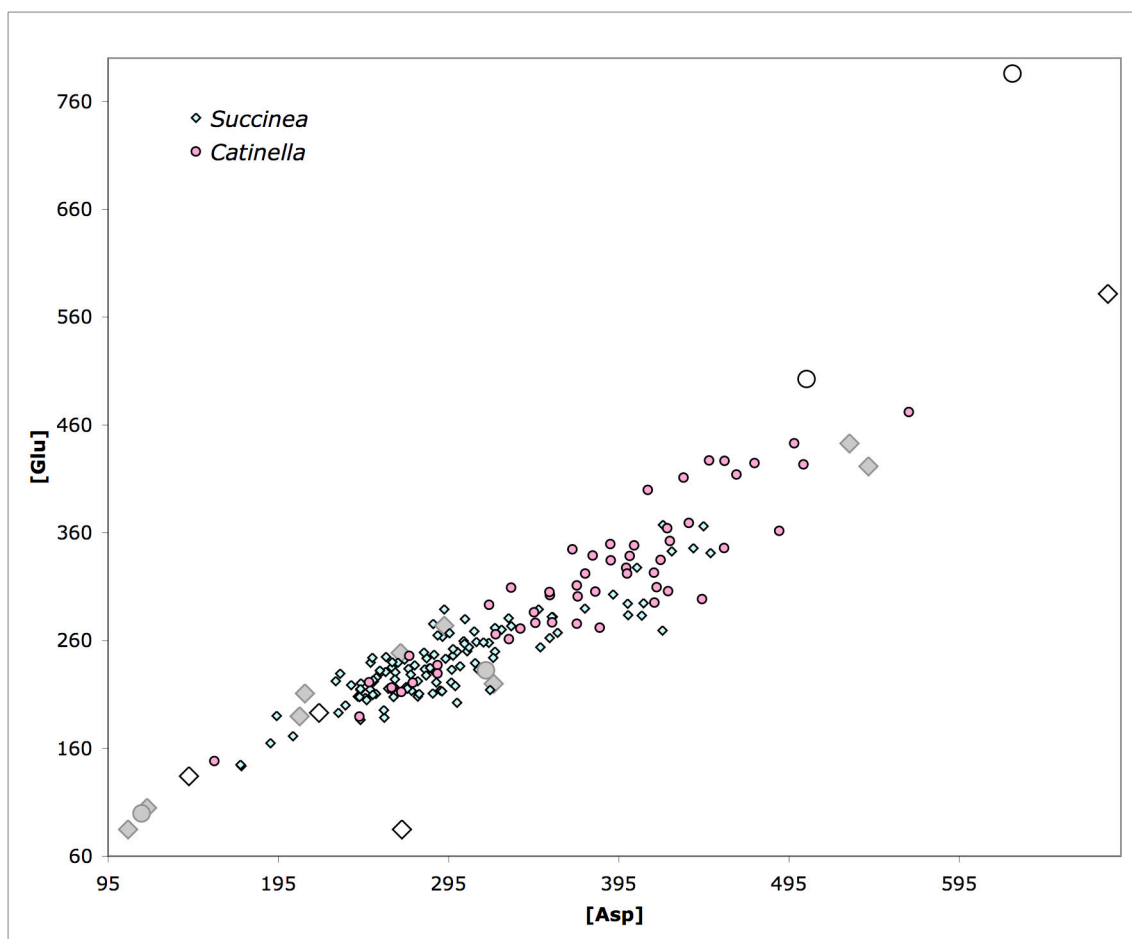


Figure B4. Covariance of L-Ser/(D+L Asp) for succineid shells. Outliers in gray, rejected outliers are open symbols.

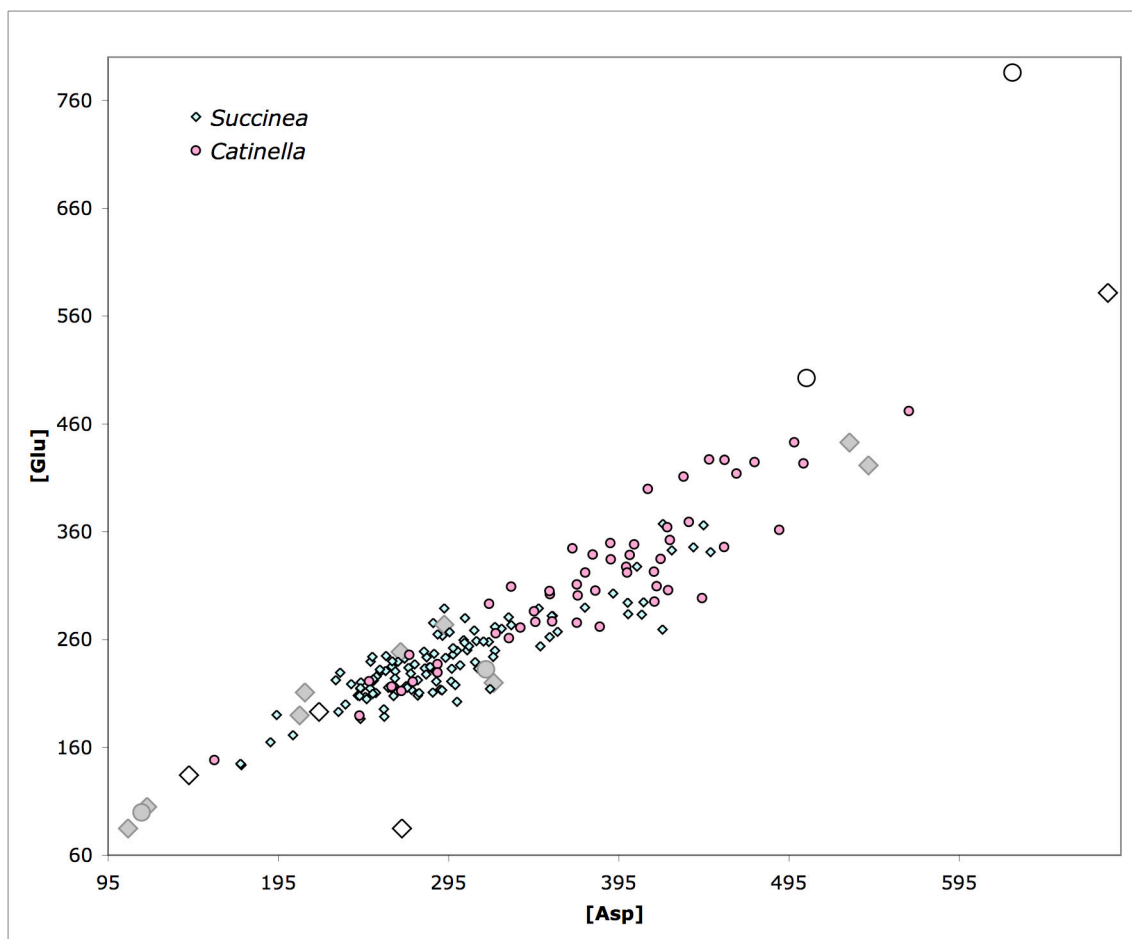


Figure B5. Covariance of [Asp] versus [Glu] for succineid shells. Outliers in gray, rejected outliers are open symbols.

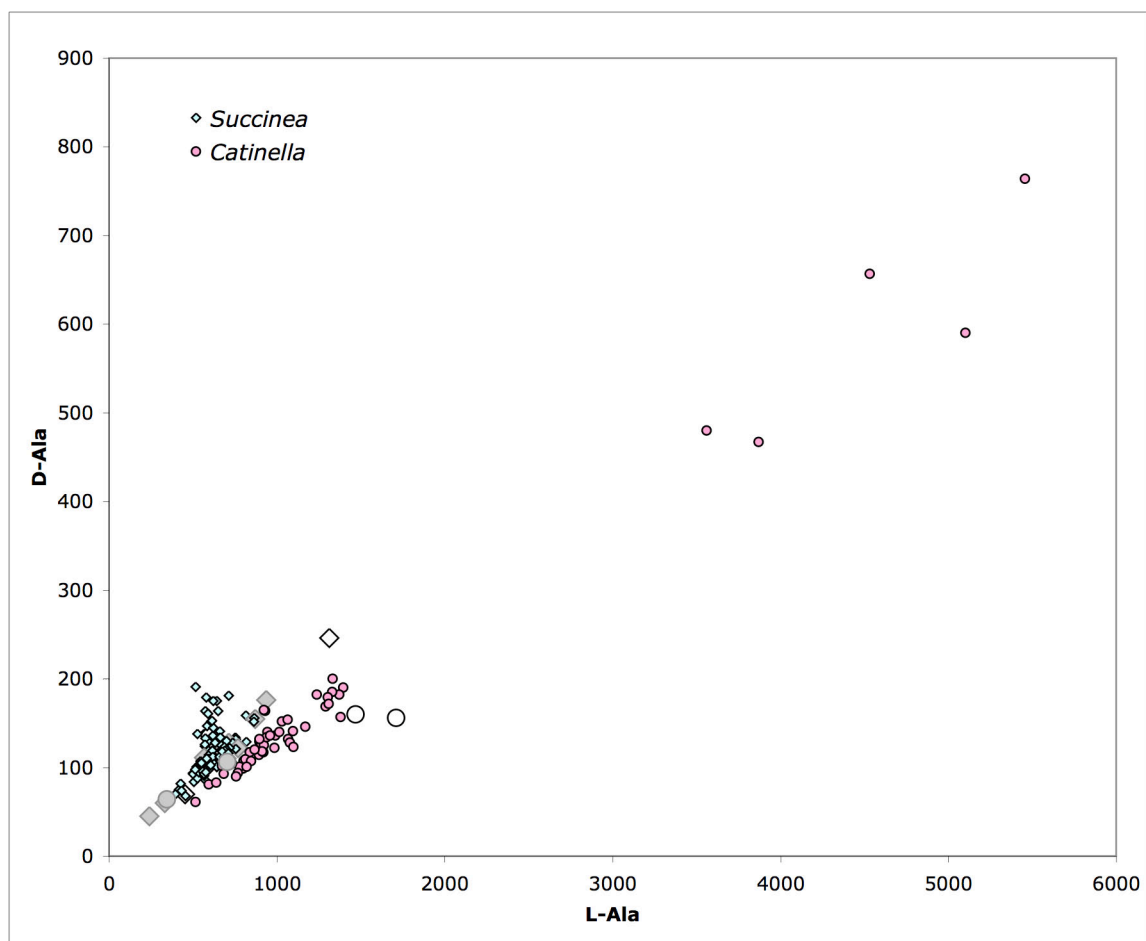


Figure B6. Covariance of L-Ala versus D-Ala for succineid shells. Outliers in gray, rejected outliers are open symbols. This analysis was not used in data screening. Note that several shells (“*Succinea*” represented with blue diamonds) that do not fit the general linear covariance of L- and D-Ala are not flagged as outliers by these screening tests.

Appendix C

Gastropod Species Descriptions

This appendix provides a general morphological and ecological description of the species found at the study localities and discussed within the text. The descriptions are generalized from Pilsbry (1948), Leonard (1952), Burch (1962), Frest and Dickson (1986), and Forsythe (2001) with updates and suggestions from Nekola (2003; personal communication, 2007). The taxonomy of terrestrial gastropods has been subject to frequent revision (e.g. Turgeon et al., 1998), and a systematic hierarchy is not discussed here. For detailed descriptions and identification, refer to the key from Barthel and Nekola (2000), which includes detailed photographs. Range maps represent compilations of Hubricht (1985) and Leonard (1952) with revisions by Nekola (2003) and Forsythe (1999). This is not intended as a detailed review of the literature, but instead represents the general understanding of the habitat preferences of the taxa discussed in this dissertation.

It is interesting to note the general pattern of modern versus fossil distributions. Late Pleistocene deposits from the Midwest contain abundant Cordilleran-Boreal taxa, while large Eastern Deciduous Forest taxa such as *Anguispira alternata* are restricted further south. The modern distributions likely reflect a complex interaction between the snails' dispersal capabilities and their habitat preference. Cordilleran-Boreal taxa dispersed to the North and West, while Eastern Deciduous Forest taxa expanded their range North and East. This compares with the changes in vegetation after the Pleistocene;

the Eastern Deciduous Forest expanded from a restricted range along the Gulf (e.g. Webb et al, 2004).

***Hendersonia occulta* (Say)**

Description:

Shell somewhat depressed, with solid, conical spire. Five, nearly flat whorls; surface dull, with fine, transverse growth striae. Periphery more or less keeled; aperture oblique, subtriangular to semicircular; peristome narrowly expanded, strongly thickened with a rounded edge. Umbilicus closed, covered by thick callus. Diameter variable from 5 – 8 mm, height 6 – 8 mm.

Remarks:

Common late Pleistocene fossil from Nebraska to Ohio and southward to Alabama and Louisiana (Figure C-1). Frest and Fay (1980) considered this species to be characteristic of the Midwest Biome, an extinct gastropod fauna typical of late Pleistocene fossil assemblages in Iowa. Currently restricted to the Driftless Area and UMV, the Niagaran Escarpment in eastern Wisconsin and the Upper Peninsula of Michigan, and the Appalachian Piedmont (van der Schalie, 1939; Pilsbry, 1948; Nekola, 2003; Pearce, 2007). A calciphile that prefers well-shaded sites with sufficient leaf litter.

Considered a state endangered species in Wisconsin and species of concern in Michigan and Pennsylvania. Its occurrence as a late Pleistocene fossil in Wisconsin may represent a relict population, or the fragmentary remains may be reworked from earlier, pre-glacial material. As of this writing, amino acid racemization analyses of the shell has

not been performed, but samples are prepared and awaiting study. Additional genetic analysis of the Driftless Area populations are also being considered (K. Perez, personal communication, 2009). Map C1.

***Vallonia gracilicosta* (Reinhardt)**

Description:

Shell minute, diameter 2.5 mm. Almost flat spiral, 2.5 whorls, convex, with deeply impressed suture. Surface sculpture consists of fine riblets obliquely transverse to whorls. Constantly increasing whorls with body whorl rapidly enlarging toward aperture. Aperture descending with strongly reflected peristome; thickened, with approaching terminations connected by callus.

Remarks:

Common in the Rocky Mountain region today, some relict populations in the Paleozoic Plateau in Minnesota and Iowa (Frest and Dickson, 1986). Abundant fossil in loess deposits of Iowa, Nebraska, and Kansas (Leonard, 1950; 1952). Map C2.

***Pupilla muscorum* (Linne)**

Description:

Shell large for pupillid, height 3.9 – 4 mm. Cylindrically ovate shell with six to seven whorls, convex but not inflated; rimate and finely striate. Prominent crest parallels the peristome, separated by a groove. Aperture truncated slightly oblique oval.

Occasionally, parietal tooth may be present (not observed in Wisconsin fossil specimens), peristome sharply everted, terminations approaching connected by thin callus.

Remarks:

Frest and Dickson (1986) describe *P. muscorum* as a northern species with a few disjunct populations in the Interior and Cumberland regions east of the Mississippi River. Common loess fossil in Iowa, Nebraska and Kansas. Nekola (personal comm., 2007) regards this species as consisting of both native and introduced (from Europe) populations. Map C3.

***Pupoides albilabris* (C. B. Adams)**

Description:

Height 3.7 – 5.6 mm. Shell elongate, tapering from last whorl to obtuse apex. Rimate with 4.5-6.5 whorls; finely striate. Peristome broadly reflected, heavily thickened within. Fresh shell often translucent reddish brown with opaque white peristome.

Remarks:

A common species throughout the eastern Interior of North America, found as a late Pleistocene fossil in Texas and other southern states (Pilsbry, 1948; Hubricht, 1985). Current Wisconsin distribution is unknown, but I have found it at several locations in Grant County at depths of up to 50 cm. Amino acid D/L Asp values indicate this species has only recently (Holocene?) been in Wisconsin. Generally found in areas of open ground (see also Frest and Dickson, 1986; Theler, 1997). Map C4.

***Vertigo modesta modesta* (Say)**

Description:

One of the largest *Vertigo* species, shell height between 2.0 – 2.3 mm. Shell ovately conical, summit convex. Four to five rimate, convex whorls. Nuclear whorls finely granular, remaining whorls with distinct, irregular and coarse striae; body whorl more than half the height of the shell. Aperture ovate, outer peristome barely indented with three to four denticles, including a low, slightly elongate parietal lamella, low tubercular upper palatal fold, a large, somewhat elongate lower palatal fold, and a low, short disposed coluellar fold. Palatal folds not on callus. Peristome not everted, margins slightly rounded.

Remarks:

Very common late Pleistocene fossil throughout Midwest (Leonard, 1950; 1952; Frest and Dickson, 1986; Woodman et al., 1996). Currently found in Northern and Rocky Mountain regions west of the Mississippi River. A holarctic species, it is typically found as different “races” that share distinct shell morphologies. Wells and Steward (1987) described the distribution of this and *V. m. parietalis* as Cordilleran-Boreal. Nekola (2003) reported isolated relict populations in northern Wisconsin, this species was not previously known as a late Pleistocene fossil in the state. Map C5.

***Vertigo modesta parietalis* (Ancy)**

Description:

Shell nearly identical to *V. m. modesta*, but with a fifth parietal lamella.

Remarks:

Rare late Pleistocene fossil, currently found in the Yukon and elsewhere in northern Canada (Woodman et al., 1996; Forsythe, 2001). Locally common in a few fossil localities in Iowa (Frest and Dickson, 1986). Nekola (1996) reported an isolated, relict colony in the Upper Peninsula of Michigan. Not previously reported as a late Pleistocene fossil in Wisconsin. Woodman et al. (1996) reported it as a fossil from an assemblage in northeastern Iowa at Elkader.

***Vertigo oughtoni* (Pilsbry)**

Description:

Shell smaller than *V. modesta*, rarely more than 2 mm in height. Shell volume 1/3 to 1/2 that of *V. modesta*. Subcylindric pupilliform shell with 4.5 whorls; strongly convex with well-incised sutures. Aperture ovate to subcircular containing up to three indistinct denticles. No depression on exterior of shell over palatal lamellae. Peristome rounded to slightly reflected, parietal callus absent or weak.

Remarks:

Previously described as *V. alpestris oughtoni* Pilsbry, Nekola (personal communication, 2007) and Forsythe (2001) consider it a separate species. Frest and Dickson (1986) describe this species as an uncommon loess fossil found near the glacial

margin. Currently restricted to the moist Tundra and Muskeg habitats of northern Canada.

Map C6.

***Columella columella alticola* (Ingersoll)**

Description:

Shell cylindrical 2.5 – 3 mm in height, six to seven whorls; striate. Shell distinctly columnar with high spire and blunt apex. Pentultimate whorl smaller than adjacent whorls, body whorl often rounded. Sutures deeply impressed, small subcircular aperture, peristome simple, slightly thickened. Peristome slightly reflected at termination near umbilicus.

Remarks:

Hubricht (1985) and Bequart and Miller (1973) regard this species as a North American subspecies of the holarctic, European *C. columella*. In North America, it is known only as a late Pleistocene fossil east of the Mississippi River. Common in the North and Rocky Mountain regions, Wells and Stewart (1987) consider it typical of the Cordilleran-Boreal gastropod fauna. Pilsbry (1948) reports this species only occurs at high elevations (>2,000 m) in the southern portion of its range. Barthel and Nekola (2000) describe this species as common in “willow scrub” and dwarf birch stands near the treeline. Not previously reported as a Wisconsin fossil. Map C7.

***Succinea bakeri* (Hubricht)**

Description:

Shell elongatedly oval, body whorl inflated and accounts for up to 90% of total shell height. Two to four whorls, 15 – 19 mm in height, sculpture consists of fine growth striae. Aperture ovate with height more than double the width. Simple peristome with no callus or thickening.

Remarks:

The most widespread fossil succineid throughout the Midwest. Considered extinct (Frest and Dickson, 1986), however morphologically similar to *S. ovalis*. Given the phenotypic variability of this family, additional work is necessary to assign species (even genera) designations to this group. Chamberlin and Salisbury (1885) reported *S. obliqua* from sites in Grant County, Wisconsin, which may be synonymous with “*S. cf. bakeri*” from this dissertation.

***Catinella gelida* (F. C. Baker)**

Description:

Slender shell, length 7 – 11 mm, nearly twice diameter. Three to four whorls, deeply impressed sutures with coarse, wrinkled growth striae. Aperture ovate to subcircular, apertural height less than twice the width. Body whorl accounts for half to three-quarters total shell length (less than *S. bakeri*). Simple peristome, somewhat thicker than *S. bakeri*.

Remarks:

Widespread late Pleistocene fossil throughout Midwest. Frest (1987) reported a few relict populations in the Driftless Area and UMV. Nekola (personal communication, 2007) reported that shells of *Oxyloma groenlandica* are identical to fossil *C. gelida*. As with *S. bakeri*, fossil succineids represent a taxonomic conundrum: the only currently reliable identification is by soft tissue dissection. However, amino acid composition of shell proteins may yield additional insight (see Chapter 3 and Appendix A of this dissertation).

***Discus whitneyi* (Newcomb, 1864)**

Description:

Shell small, 6.7 mm in width. Depressed heliciform, low spire with 4.5 whorls; convex or subangular (especially in juveniles). Deep suture, protochonc smooth, strong equally spaced axial riblets along outer whorls that extend onto base. Aperture rounded, peristome simple without callus. Umbilicus large, more than 33% the shell width.

Remarks:

Common fossil snail south of Minnesota and Wisconsin from Nebraska to Ohio and southward (Frest and Dickson, 1986). Common in floodplains and forested wet habitats. This species can still be found in the region today. Typical of cool climates, but more cosmopolitan than *D. shimeki* or *D. macclintocki* (Frest and Dickson, 1986; Nekola, 2003). Previously described as *D. chronkhitei* (e.g. Baker et al., 1986; Frest and Dickson, 1986), but *D. whitneyi* predates the former name. Similar to the European *D. ruderatus* in size and morphology (Forsythe, 200?). Chamberlin and Salisbury (1885)

reported this species (as *Patula striatella* Anthony) in Crawford County, Wisconsin from alluvial sediment near the Bridgeport Terrace along the Wisconsin River. Map C8.

***Discus shimeki* (Pilsbry)**

Description:

Shell small, generally 6.5 mm in width, slightly depressed heliciform with elevated spire. Periphery rounded to subangular (especially in juveniles), 4 – 4.5 whorls, robust. Sculpture consists of prominent, fine ribs above, which disappear along the base of the whorls. Aperture subcircular with simple peristome. Circular umbilicus is narrower than *D. whitneyi* (less than 33% of the shell width).

Remarks:

Sometimes referred to as *D. shimekii*, it is a common late Pleistocene fossil in Iowa and Wisconsin (Frest and Dickson, 1986; Kuchta et al., 2007a, b). Currently found in the Rocky Mountains, often at high elevations, especially at the southern end of its range. In Arizona, Bequaert and Miller (1973) reported it at altitudes above 2,000 m. Not previously reported for Wisconsin. Often found with *D. whitneyi*, but can be differentiated from the former by its narrower umbilicus and fine to absent axial striae along the base of the whorls (Barthel and Nekola, 2000). Map C9.

***Anguispira alternata* (Say)**

Description:

Shell helicoids, 5-5.5 whorls, widely umbilicate with simple peristome. Live specimens have a tan shell with bold red-brown markings. These markings are often discernable in fossil shells. Diameter of adult shells is about 20 mm.

Remarks:

A common, typical woodland species that lives under leaf litter or under decaying wood. Mostly occurs as a late Pleistocene fossil in the south, along the Gulf Coast in Louisiana and Mississippi. Occasional older fossils occur west in Kansas and north in Iowa. Map C10.

Helicodiscus parallelus (Say)

Description:

Shell small; diameter 3 – 4 mm. Planispiral to slightly convex, umbilicus broad and shallow. 4 to 4.5 parallel whorls, outer whorls conspicuously marked with numerous raised spiral lirae. Periphery flattened. Peristome simple, with thin callus. Two small denticles inside body whorl not visible on exterior.

Remarks:

Late Pleistocene fossil in some regions of the Midwest, common throughout the Eastern and Interior regions of North America east of the Mississippi River today (Hubricht, 1985). Typically found in decaying leaf litter or decaying wood, it has been reported burrowing deep into the soil (Pilsbry, 1948). Results from this dissertation show

that it was not likely a late Pleistocene fossil in Wisconsin, but rather burrowed into the soil at depths up to 1 m. Map C4.

***Glyphalinia indentata* (Say)**

Description:

Shell slightly depressed, deeply umbilicate 4.5 – 5.5 mm in diameter. Sculpture consists of numerous radial grooves which are missing on base of whorls. 3.5 to 4 whorls that rapidly increase in size. Aperture ovoid-lunate, simple, thin peristome.

Remarks:

Abundant in the Eastern Deciduous Forest. Burch (1962) considered it typical of the Interior province. Hubricht (1985) suggested this name was applied to several species with similar shells. Theler (1997) reported this species along bluffs in the Driftless Area. Amino acid D/L Asp values indicate this taxon was not a late Pleistocene fossil in Wisconsin. Map C4.

***Hawaiiia miniscula* (Binney)**

Description:

Shell minute 2.2 – 2.8 mm in diameter. Umbilicate, spire slightly depressed and convex. Four whorls strongly convex, slowly enlarging in size toward aperture. Shell surface smooth with irregular, fine striae above and smooth below. Aperture nearly round, simple thin peristome.

Remarks:

One of the most common terrestrial gastropods in the United States (Hubricht, 1985). Generally prefers deciduous forest habitats. Found in open areas in western Iowa (Frest and Dickson, 1986). Leonard (1952) regarded *H. miniscula* as very common and cosmopolitan in habitat preference. Based on amino acid racemization analysis, this species was not a late Pleistocene fossil in Wisconsin.

***Euconulus fulvus* (Müller)**

Description:

Shell thin, diameter 3.2 mm. Subconic-heliciform, width slightly greater than height. Spire moderately elevated with an obtuse apex. 5.5 whorls slightly convex, somewhat deep sutures; periphery rounded to subangular, especially along body whorl. Close axial striae become indistinct along the base of the whorls. Aperture narrow, crescent-shaped without denticles. Peristome simple with closed umbilicus.

Remarks:

Favors cool habitats, found in moist and shaded woodlands in northern regions, but also in drier grasslands to high elevations generally (Pilsbry, 1948; Frest and Dickson, 1986). Leonard (1952) regarded *E. fulvus* as inhabiting sites with abundant organic debris. Burch (1962) described it as inhabiting Northern and Interior provinces. Wells and Stewart (1987) considered this species typical of the Eastern Deciduous Forest habitats despite being widespread throughout North America. Some authors recognize *E. fulvus alaskensis* as a separate species (e.g. Lauriol et al., 2002).

***Deroceras laeve* (Müller)**

Description:

Shell about 4 mm, ovoid, flattened plate with concentric growth lines. Left margin more convex than right, nucleus not quite terminal on left posterior.

Remarks:

The small, flattened internal slug plates are found in moist habitats. Previous authors (Leonard, 1950; 1952; Baker et al., 1986; Frest and Dickson, 1986; Woodman et al., 1996) assigned these plates to *D. laeve*. The slug plates found in late Pleistocene sediments in Wisconsin may be identical to those described, but reliable taxonomic identification is difficult for slugs (Nekola, personal communication, 2007). All slug plates found from this study are unassigned at this time.



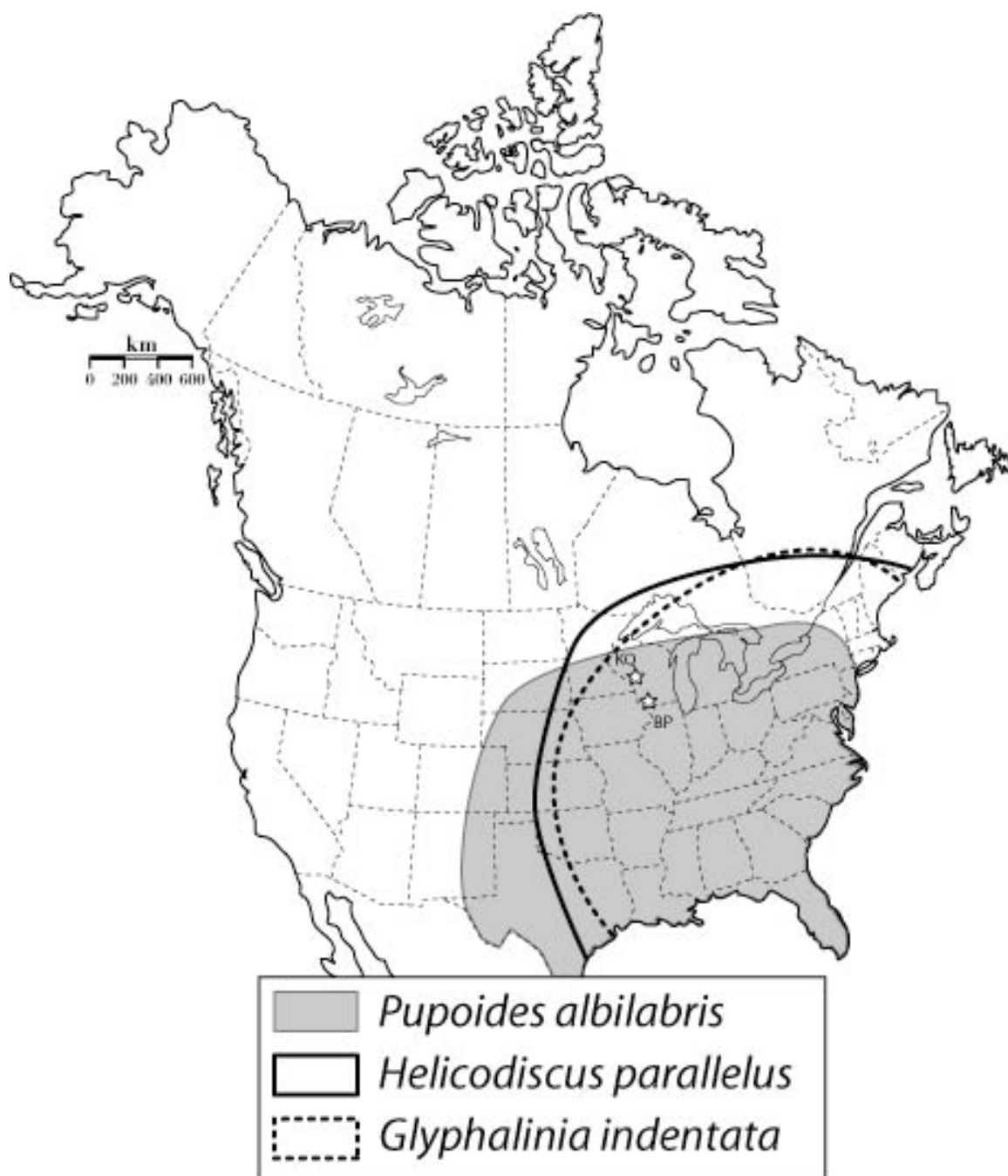
Map C1: *Hendersonia occulta*



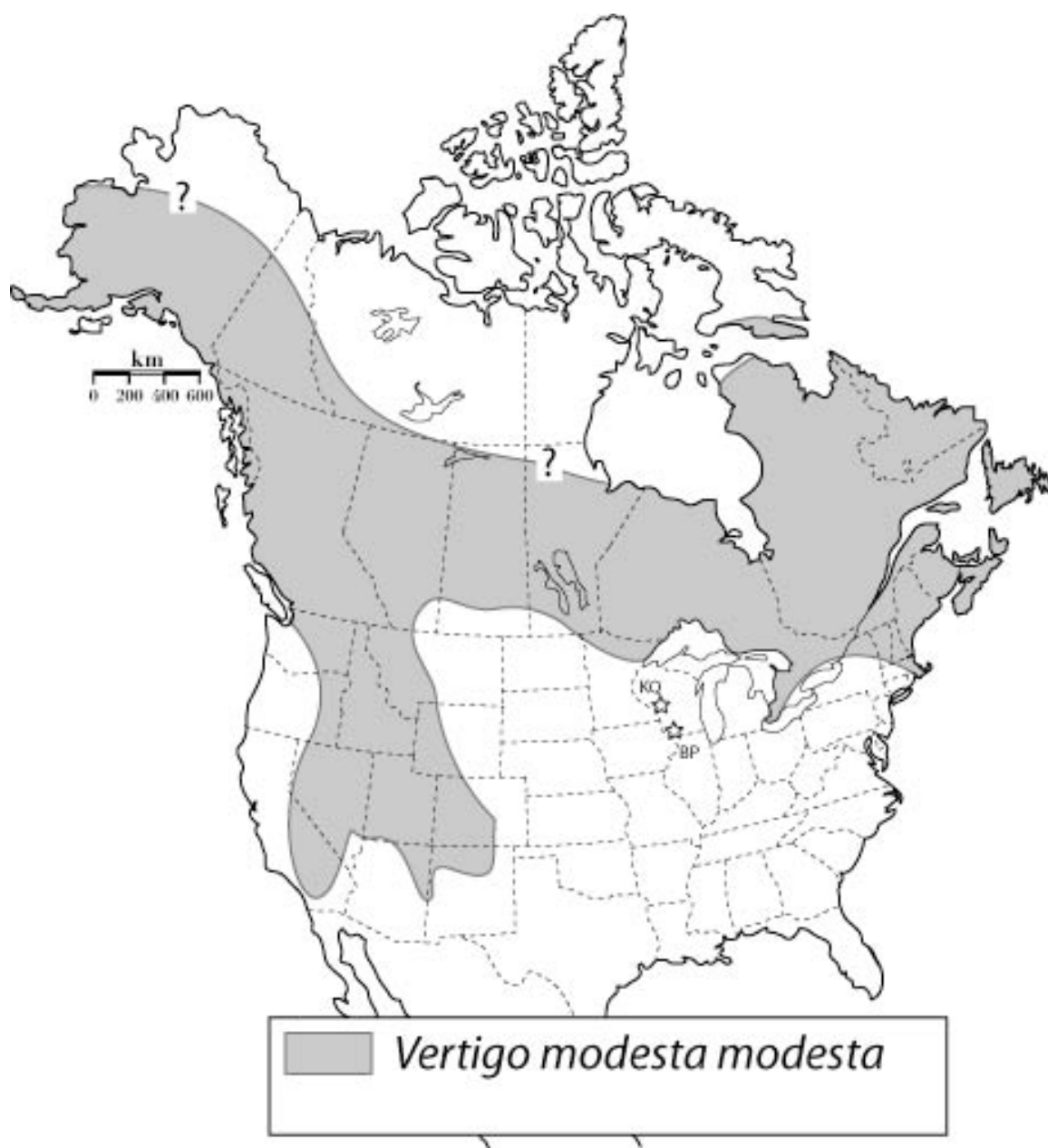
Map C2: *Vallonia gracilicosta*



Map C3: *Pupilla muscorum*



Map C4: *Pupoides albilabris*, *Helicodiscus parallelus*, *Glyphalinia indentata*



Map C5: *Vertigo modesta modesta*



Map C6: *Vertigo oughtoni*



Map C7: *Columella columella alticola*



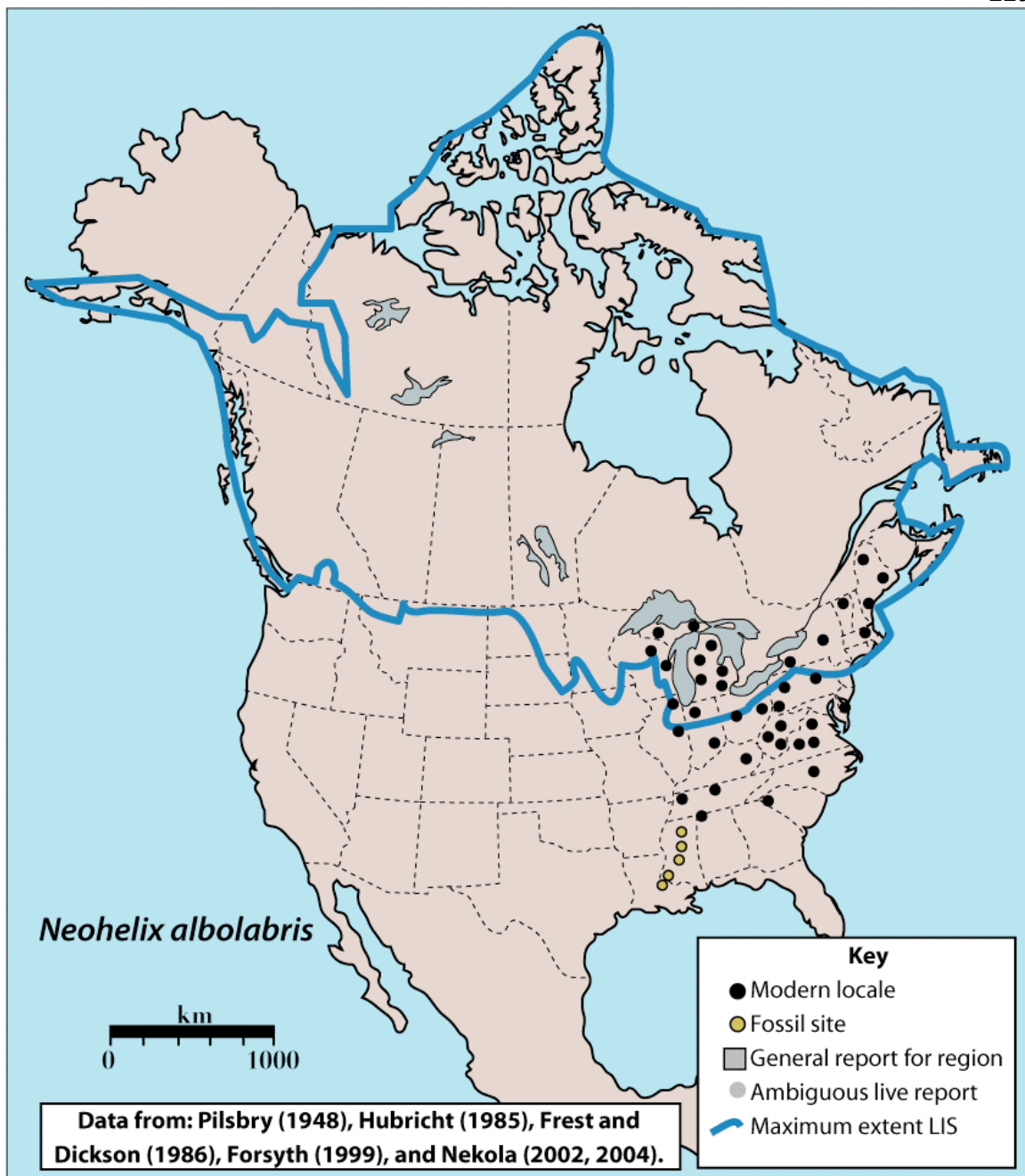
Map C8: *Discus whitneyi*



Map C9: *Discus shimeki*



Map C10: *Anguispira alternata*

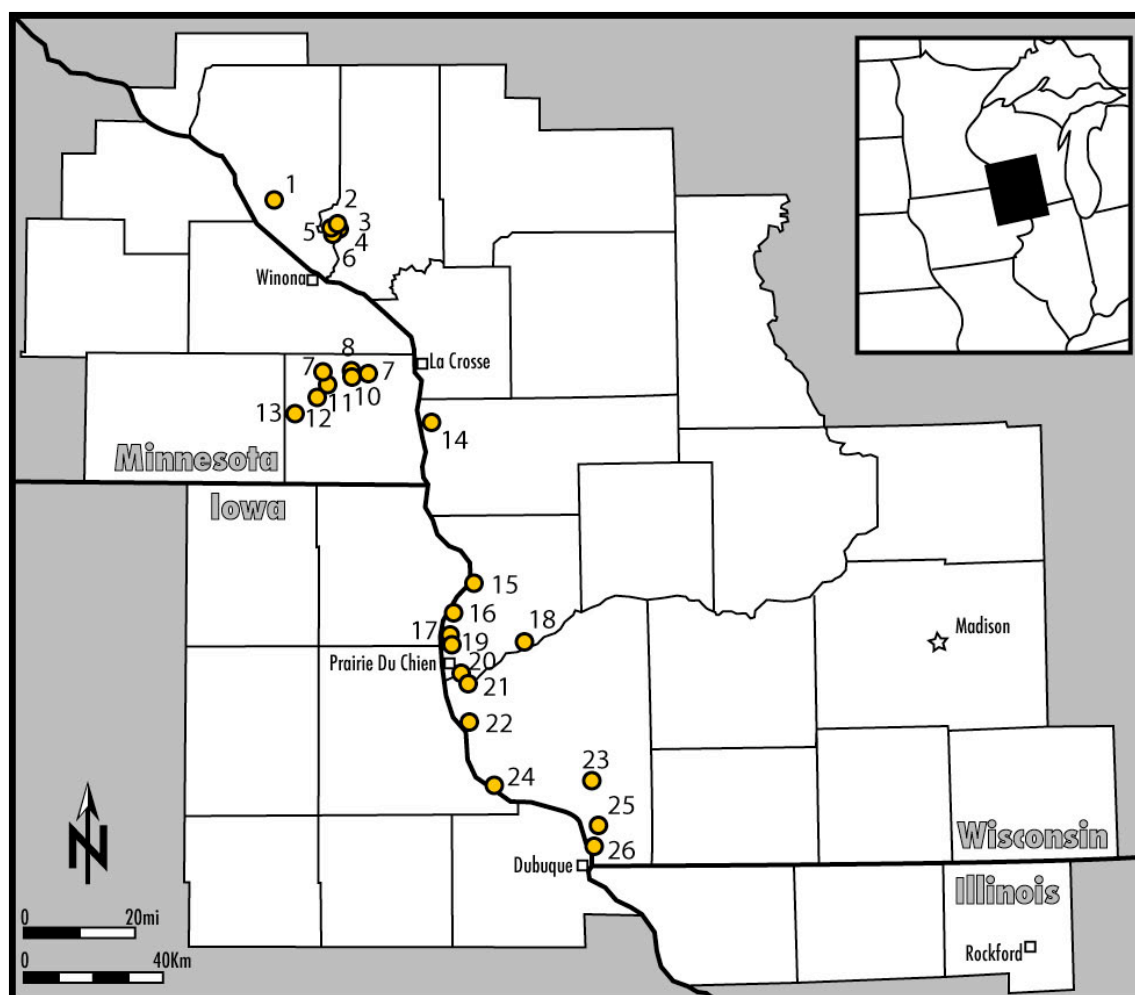


Map C11: *Neohelix albolabris*

Appendix D

Site descriptions and locations.

Numerous sites with late Pleistocene gastropods were located during the field surveys in 2005 and 2006. The map below (Map D1) shows the relative location of all sites surveyed (Table D1). A presence/absence table for selected sites is also included (Table D2). The most accessible and abundant sites are discussed in the dissertation; however, this is intended as a guide to future survey and sampling work. Sites were identified by systematically driving along roadways looking for exposures of unconsolidated sediments. Many locations were identified by the presence of broken shell fragments weathering onto the surface. Some sites, however, yielded identifiable material only after processing the sediment.



Map D1: Site location map. See description in Table D1.

Sites described/discovered in 2004-2006 field seasons.

Map#	Site Name	Lat	Lon	Age*	Type**	Notes
1	Waumandee Valley	44.246	-91.766	FG	A	
2	Kulas Quarry	44.173	-91.548	17,000	A	Northernmost full-glacial fossil locality in midwest
3	Kulas-2	44.17	-91.548	FG	A	
4	Kulas-1	44.169	-91.542	FG	A	
5	Hwy-JJ	44.168	-91.557	16,100	C/A	
6	JX	44.158	-91.554	FG	C/A	
7	Doblar Road	43.799	-91.589	FG	A	
8	Storer Valley	43.796	-91.485	FG	A	
9	Root River	43.792	-91.424	15,800	C/A	Gastropods dated by Mason and Knox (1997)
10	Storer Creek	43.787	-91.483	15,500	A	
11	Houston Nature Center	43.765	-91.57	Holocene	A	Recent floodplain material.
12	Thorson Quarry	43.731	-91.606	FG	A	
13	Yucatan	43.691	-91.689	FG	C	Stratigraphy described by Mason (1995)
14	Hideaway Lane	43.666	-91.198	13,200	A	
15	Lynxville	43.247	-91.056	LG?	A	
16	Charme Sioux Coulee	43.169	-91.123	FG	C	
17	Mill Coulee	43.111	-91.129	FG	C/A	
18	Wauzeka	43.095	-90.865	FG	C	Clast-supported colluvium, with occasional fossils
19	Limery Coulee	43.09	-91.127	13,400	C	
20	Old 18	43.012	-91.095	FG?	A	
21	Tubbs Farm	42.988	-91.065	LG?	A	
22	Sandy Creek	42.889	-91.068	LG?	C/A	
23	Big Platte	42.731	-90.634	15,800	C	Richest full-glacial locality in Wisconsin
24	Cassville Manor	42.716	-90.988	LG?	C/A	
25	Dickeyville Quarry	42.634	-90.599	?	L	No gastropod fossils, abundant rhizocretions
26	Bluff Road	42.559	-90.633	LG?	A	

*Dates in ¹⁴C YR; LG=Late Glacial, FG=Full Glacial, age estimates based on gastropod fauna

**A=Alluvium, C=Colluvium, C/A=reworked colluvium, L=Loess

Table D1: Site name, location, type, and approximate age. Numbers refer to locations marked on Map D1.

Site	<i>Succinea</i> cf. <i>bakeri</i> <i>Catinella</i> cf. <i>gelida</i> SLUG PLATES			<i>Vertigo oughtoni</i>	<i>Discus shimeki</i>	<i>Columella columella alticola</i>	<i>Pupilla muscorum</i>	<i>Vertigo modesta modesta</i>	<i>Vertigo modesta parietalis</i>	<i>Vallonia gracilicosta</i>	<i>Discus whitneyi</i>	<i>Euconulus fulvus</i>	<i>Hendersonia occulta</i>	Cal Age (ka)	Depo.	R
Hideaway Lane	X	X	X		X	X	X	X	X	X	X	X		16.1-17.0	A	11
Limery Coulee		X	X	X	X	X	X	X	X	X		X	X	16.4	C	11
Storer Creek		X	X		X	X	X	X	X					19.0-20.3	A	7
Root River		X			X	X	X	X	X					19.1	A	6
Big Platte	X	X			X	X	X	X	X	X	X	X		19.0-19.1	C	10
Hwy-JJ		X	X	X	X	X	X	X	X					19.2	C	8
Kulas Quarry ¹		X	X	X	X	X	X	X	X		X		X	19.9-20.6	A	10
Kulas Quarry ²		X	X	X	X	X	X	X	X				X	21.0-21.7	A	9
Biome	P	P	W	T	C	CB	CB	CB	CB	CB	CBE	CBE	EF			
Temp./Cold			C	C	C	C	C	C	C	C	C	T	T			
Drier/Wetter		?	W	W	b	W	D	W	W	D	b	b	W			
Open/Shade			S	O	b	S	O	S	S	O	S	b	S			

Table D2. Gastropod fossils recovered from selected sites.

Appendix E

If it ain't broke, then what? Taphonomic filters of late Pleistocene

Terrestrial Gastropod fossils in the Upper Mississippi Valley

Abstract

This chapter analyzes terrestrial gastropod shell breakage patterns in late Pliocene sediments from the Upper Mississippi River Valley in order to characterize potential taphonomic biases within four different sedimentary facies. Taxon abundance within each sample was compared to the proportion of those shells that represent broken individuals. These preliminary results show that taphonomic biases were related to shell morphology: tall, narrow shells were the most vulnerable, while some taxa did not show any significant difference in breakage patterns.

Introduction

Late Pleistocene gastropod assemblages from the Upper Mississippi Valley (UMV) present an underutilized proxy record to characterize the regional climate. However, the taphonomic modification of these assemblages must be understood before any ecological interpretation can be made. It is widely recognized that fossil taxa are recovered in unequal proportions. These proportions reflect taphonomic modification of ecological abundance patterns. Much work has been done to characterize the taphonomy of marine shelly deposits (e.g. Flessa et al., 1993), however the influences on continental mollusks remain understudied (Goodfriend, 1992). Previous work on continental mollusk taphonomy is often geared towards recognizing autochthonous versus allochthonous fossil assemblages (La Rocque, 1970; Miller and Bajc, 1990).

The goal of this appendix is to present the preliminary findings of abundance patterns related to the proportion of broken gastropod shells for late Pleistocene fossil

taxa from the UMV. I will describe the influence of factors such as abundance, depositional energy, and morphology upon the proportion of broken individuals in samples of late Pleistocene sediment

Methods

I used the PAST software program (Hammer et al., 2001) to analyze the relationship between facies type and frequency of broken individuals using one-way ANOVAs. I used box plots to represent the central tendencies of the data graphically using box plots. Pearson correlation coefficients were calculated for abundance and broken frequencies using the web-based “Free Statistics Software” interface of Wessa (2008). I excluded singletons from the analysis to avoid overrepresentation of individual shells either whole or broken.

Results

Dataset Overview

The results are summarized in Tables 1-3. The six sites (Figure E1) represent four different depositional facies and radiocarbon results indicate most sites are late full-glacial in age (ca. 16,000 RCYBP), while Limery Coulee dates to the middle late-glacial (ca. 13,400 RCYBP) (Table E1). The 43 samples, weighing a total of 182.4 kg, yielded a total of 12,983 individuals (Table E2). Succineids were the dominant group, accounting for roughly 51% of all specimens recovered. Four genera, *Columella*, *Vertigo*, *Pupilla*, and *Discus* were also abundant, representing nearly 49% of the remaining fraction. The

remaining genera were absent at most sites, occurring within a small number of samples (Table E3).

The sites are grouped into four facies associations with varying proportions of coarse-grained sediment. The trough cross-bedded facies is and tabular cross-bedded sand, fine-grained facies colluvium, and fine-grained alluvial silt. The greatest number of samples came from colluvium (n=16), while both alluvial silt and tabular cross-bedded sand were the least sampled (n=7; Table E2). Shell abundance, however, was highest in trough cross-bedded sand facies (n=6,772) and lowest in alluvial silt facies (n=572).

Variation in facies grain size

Grain size significantly varied ($P=0.00001477$; Figure E2). Samples from the trough cross-bedded sand facies had the highest median weight percent residuum followed by tabular cross-bedded sands, then colluvium, and alluvial silt, with the least residuum weight percent. The variability of sample residuum weight percent also decreases, with trough cross-bedded facies being the most variable in residuum weight percent and alluvial silt are the least.

Variation in taxon breakage The proportion of broken individuals between all four facies per sample significantly varied for *Columella* ($P=0.0001518$; Figure E3). In addition, the variability (e.g. intraquartile range) of samples within facies increased as depositional energy decreased. Similarly, the proportion of broken shells varied significantly for *Pupilla* ($P=0.01103$; Figure E4) when the comparison occurs between the higher energy and lower energy depositional facies, but decreased when all four

facies were analyzed separately ($P=0.07239$). Samples from high-energy depositional settings that contained shells of *Discus* display no significant variation ($P=0.4662$; Figure E5). The pattern of increasing variability in lower energy facies seen in *Columella* and *Pupilla* may be present, but only two samples of alluvial silt contained *Discus* shells. In addition, the small sample size likely contributes to the lowered statistical significance. Additional work may be necessary to determine if the weak statistical significance is due to low numbers of specimens, or other factors. Specimens of *Vertigo* showed no variability between facies ($P=0.9146$) both with median or range.

Discussion

Depositional Energy

It is possible to characterize the potential depositional energy of each facies by using the proportion of residuum. Samples with a larger fraction of coarse (>0.425 mm) material correspond to greater energy required for sediment transport (Figure E1). The highest median values of trough cross-bedded samples represent high depositional energy while alluvial silts represent low depositional energy.

Shell breakage patterns

I interpret the pattern of breakage, visible in three of the most common taxa, of decreasing variability between samples as residuum weight increases as the effect of increased reworking of shells as depositional energy increases. The likelihood of shell breakage increases with the energy of the deposition and transport mechanism, which would also increase proportion of broken individuals incorporated into the fossil

assemblage. While the trend itself is unsurprising, it is important to note that it is not expressed equally among all taxa.

The proportion of broken individuals of both *Pupilla* and *Columella* significantly varied between facies, while *Discus* and *Vertigo* did not (Figures E2-E6). Sparks (1964) noted the vulnerability of *Columella* shells, but suggested that *Pupilla* much more robust. He noted that, although the shell is rather thin, the ratio of its height to its width is relatively low, making breakage due to asymmetric stress on the shell less likely. Similarly, Briggs et al. (1990) also noted few broken *Pupilla* shells in braided stream habitats in the Austrian Alps. Carter (1990) found that there was differential preservation in the aperture of *Pupilla* in temperate, humid soils. The results of this study suggest that *Pupilla* is among the more vulnerable of taxa, however whether the shells are broken as a result of external influences such as soil moisture or depositional energy or related to shell structure is not known. *Pupilla* is often associated with xeric, open habitats (Pilsbry, 1948; Leonard, 1952), which may be located further away from active floodplains where trough and tabular cross-bedded sands are deposited. Shells of *Pupilla* may be transported further distances relative to other taxa.

Shells of *Discus* weakly follow the pattern of increased variability in broken proportions with decreased depositional energy (Figure E5). Sparks (1964) noted that relatively small, discoidal shells were most often broken as a result of sediment compaction. It is unlikely that sediment compaction affects *Discus* breakage in the trough cross-bedded facies, since coarser sediments do not compact as much as finer sediments. The lack of *Discus* shells may be a result of ecological factors that limit its abundance in areas of alluvial silt deposition.

It is interesting to note that *Vertigo* does not display any significant variation in the number of broken individuals per sample between facies (Figure E6). Sparks (1964) mentioned this genus was relatively resistant to breakage because of its shape. Shells of *Vertigo* are relatively small and oval in shape, which may provide some resistance to breakage. It may also be that *Vertigo* may not pass through similar taphonomic “filtering” as compared to other pupillids such as *Columella* and *Pupilla* (c.f. Behrensmeyer et al. 2000), or that the process of shell breakage is more random. Alternatively, it may be that *Vertigo* shells were transported relatively short distances due to the fact they inhabited areas of deposition for all four sampled facies.

Rare genera such as *Vallonia* and *Euconulus* were obtained as mostly and entirely complete shells, respectively (Table E3). *Hendersonia*, however, is represented by exclusively broken shells. It may be that the threshold for detecting fragments of *Vallonia* and *Euconulus* is high. One needs nearly whole shells to retain sufficient shell characters for identification. *Hendersonia*, however, has a very unique shell with thick, flattened whorls and a distinct apertural callus that remain identifiable even with very small (ca. 2mm) fragments. Rare species with morphologically indistinct shells may be hard to detect as broken fragments, while distinct shells, such as *Hendersonia*, will be easy to recover.

Hendersonia may also represent a unique taphonomic pathway. Its shell is relatively large, especially compared to other full-glacial gastropods and may occur as exclusively broken fragments as the result of selective predation or as a result of reworked, older material. An amino acid racemization analysis of these fragments is planned for the summer of 2009.

The abundance of succineid gastropods may represent the supply-side influence of taphonomy (e.g. reproduction rate) or reflect high local abundance in a wide variety of depositional settings (c.f. Frest and Dickson, 1986). Succineid gastropods produce far more individual shells than any other taxa. Detailed analysis of this possibility is beyond the scope of this study, but it may be related to the reproductive mode of gastropod taxa. There is some evidence to suggest that many succineids reproduce semelparously, whereas most other species are iteroparous (Pilsbry, 1948). Semelparous species will tend to produce fewer shells per generation; while iterparous species will produce many offspring once and then die, adding more dead shells compared to iteroparous taxa.

Conclusions

The results from this study show that the highest proportion of broken individuals occurred within samples from high-energy trough cross-bedded and tabular cross-bedded sand facies as compared to samples from the lower energy colluvium and alluvial silt facies (e.g. *Columella* Figure 3). The range of values was also lower in higher energy facies compared to the lower energy facies. This trend likely reflects the increased probability that higher energy depositional mechanisms will break the shell. The higher proportion of broken individuals in higher energy facies is a result of more broken individuals, while the narrower range could be due to a closer balance between input of whole shells and their subsequent destruction.

Site	Facies	¹⁴ C Age	Lab Number	No. Samples
Kulas Quarry (KQ)	TAB/TRO	17,550±70 16,670±60	Beta-	20
Hwy-JJ (JJ)	COLL	16,120±60	Beta-	6
Big Platte (BP)	COLL	15,710±50 15,890±50 15,800±100	Beta-	8
Storer Creek (SC)	SILT	15,800±50	Beta-	5
Root River (RR)	SILT	15,983±136*	*	2
Limery Coulee (LC)	COLL	13,430±70 13,460±50	Beta-	2

Tab = Tabular Cross-Bedded Sand, Tro = Trough Cross-Bedded Sand, COLL = Colluvium, SILT = Alluvial Silt

*Age data from Mason and Knox (1997)

Table E1. Sedimentary facies, radiocarbon age, and number of samples obtained from sites discussed in text. Date for Kulas Quarry represents an upper section and lower section date, while remaining dates obtained from base of site exposures.

Facies	No. Samples	Total Weight (Kg)	Total No. Shells
Trough Cross-Bedded Sand	13 (30.2%)	56.25 (30.8%)	6,772 (52.1%)
Tabular Cross-Bedded Sand	7 (16.3%)	24.61 (13.5%)	2,038 (15.7%)
Colluvium	16 (37.2%)	75.84 (41.6%)	3,601 (27.7)
Alluvial Silt	7 (16.3%)	25.70 (14.1%)	572 (4.4%)
Total	43	182.41	12,983

Table E2. Number of samples, weight, and total number of individual shells obtained from the four sedimentary facies discussed in the text.

Taxon	Tot Shells (% Broken)	Sites						
		KQ-TRO	KQ-TAB	JJ	BP	RR	SC	LC
<i>Succinidae</i> *	6726 (6.6%)	3991 (7.4%)	1158 (18.4%)	298 (9.7%)	813 (1.4%)	102 (4.9%)	250 (7.6%)	99 (1%)
<i>Vertigo</i>	2028 (25.8%)	929 (25.9%)	283 (25.4%)	79 (22.8%)	631 (18.2%)	66 (19.7%)	52 (23.1%)	265 (16.2%)
<i>Columella</i>	1886 (73.8%)	999 (84.7%)	284 (81.3%)	46 (65.2%)	373 (50.1%)	49 (51%)	15 (33.3%)	120 (56.7%)
<i>Discus</i>	1807 (16.3%)	633 (19.7%)	228 (14%)	29 (24.1%)	517 (13.9%)	16 (6.3%)	1 (0%)	383 (15.1%)
<i>Pupilla</i>	669 (77.1%)	200 (89%)	79 (82.3%)	104 (78.8%)	95 (49.5%)	14 (85.7%)	7 (42.9%)	169 (75.7%)
<i>Vallonia</i>	179 (6.1%)	-	-	-	28 (21.4%)	-	-	151 (3.3%)
<i>Hendersonia</i>	27 (100%)	20 (100%)	6 (100%)	-	-	-	-	1 (100%)
<i>Euconulus</i>	11 (0%)	-	-	-	8 (0%)	-	-	3 (0%)
Total Shells	12983	6772	2038	556	2465	247	325	1191
r^2	0.0165	0.2851	0.1163	0.0915	0.0007	0.2772	0.1669	0.1096
P (1-sided)	0.3534	0.08645	0.2042	0.28002	0.4276	0.18104	0.2474	0.17503

*Four samples (three from KQ-TRO and one from KQ-TAB) were not used to calculate broken percentage due to high (>1000) abundance of succineid shells. Counting was also halted at 1000 individuals for each sample.

r^2 and P values calculated via Pearson Correlation of taxon frequency abundance and broken proportion

Table E3. Summary table of all taxon abundance and proportion of broken individuals at each site discussed in the text. Kulas Quarry split into two separate facies. P and r^2 values calculated via Pearson correlation of taxon frequency abundance and proportion of broken individuals.

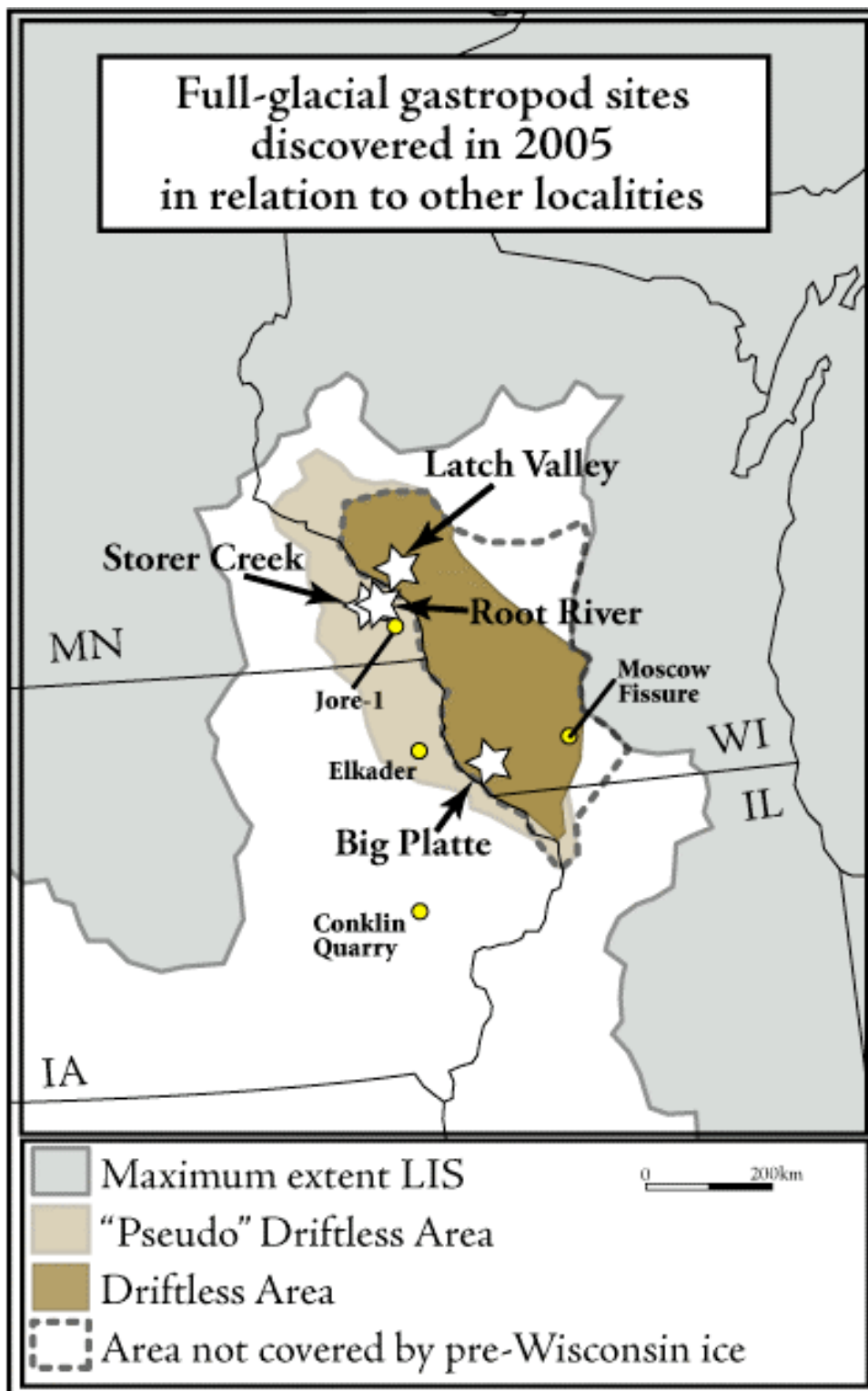


Figure E1. Field sites referred to in Appendix D.

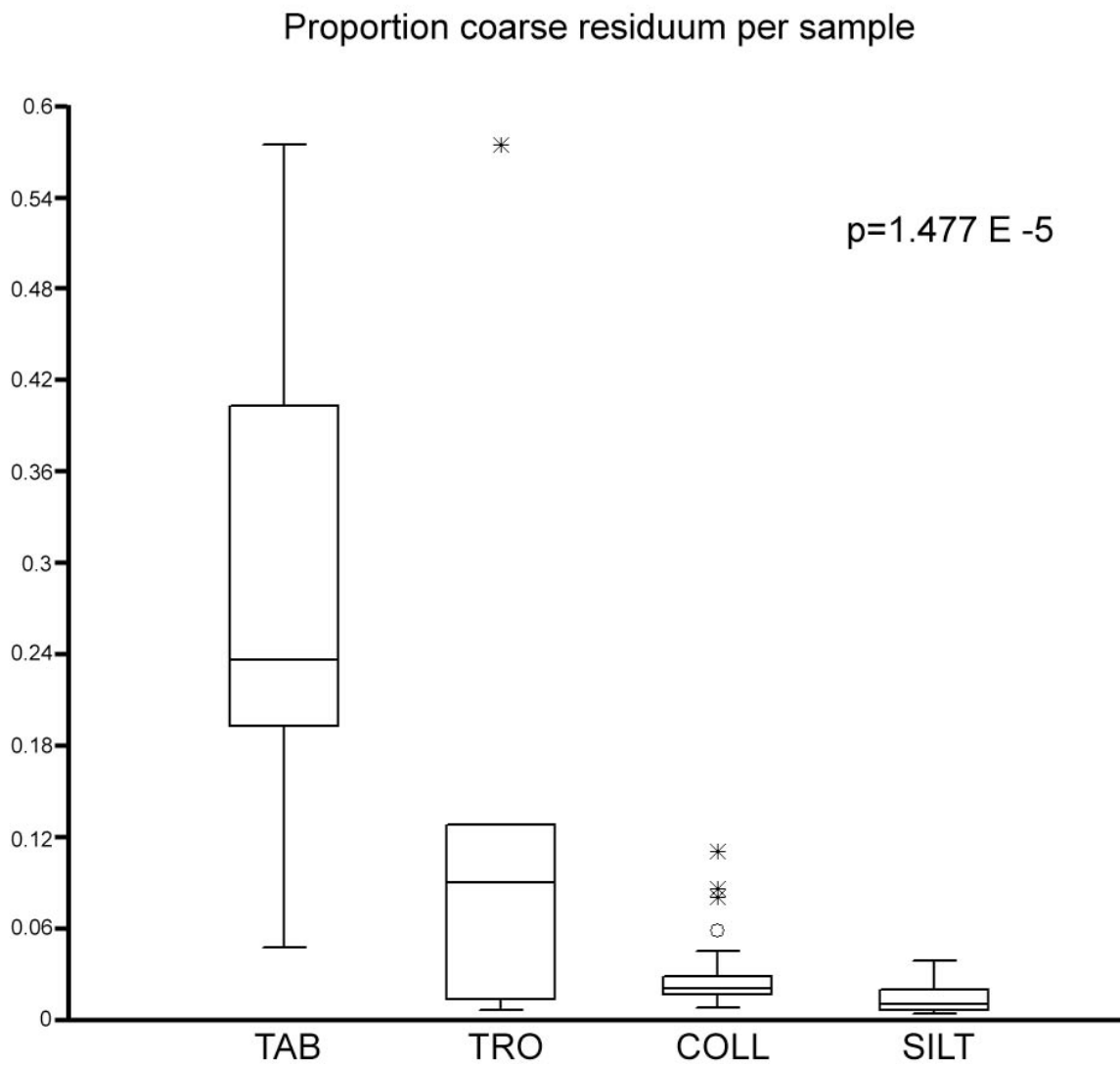


Figure E2. Box plot showing proportion of residuum per sample from all four facies discussed in text. P value calculated via one-way ANOVA.

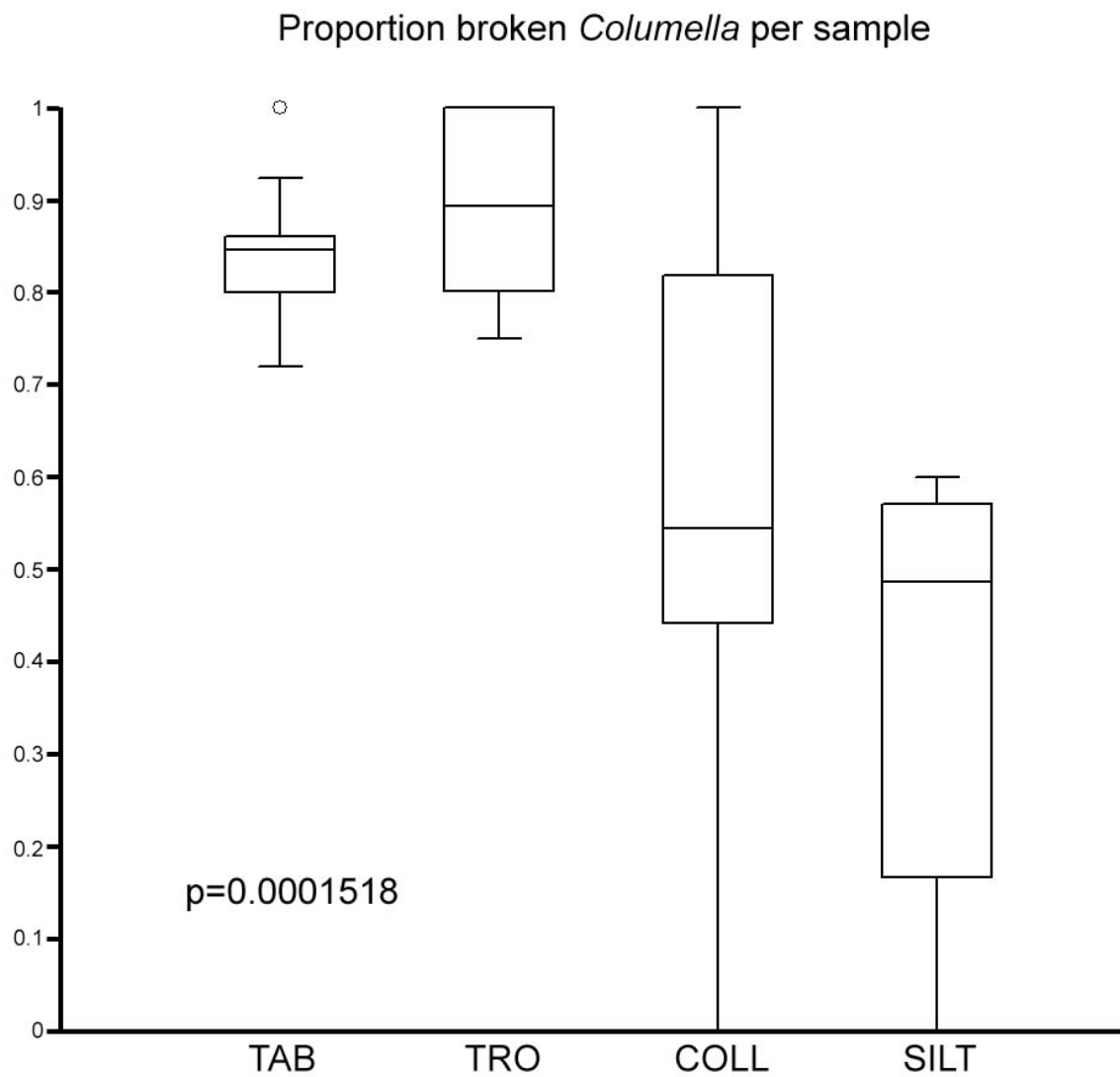


Figure E3. Box plot showing the proportion of broken *Columella* per sample within depositional facies. P value calculated via one-way ANOVA.

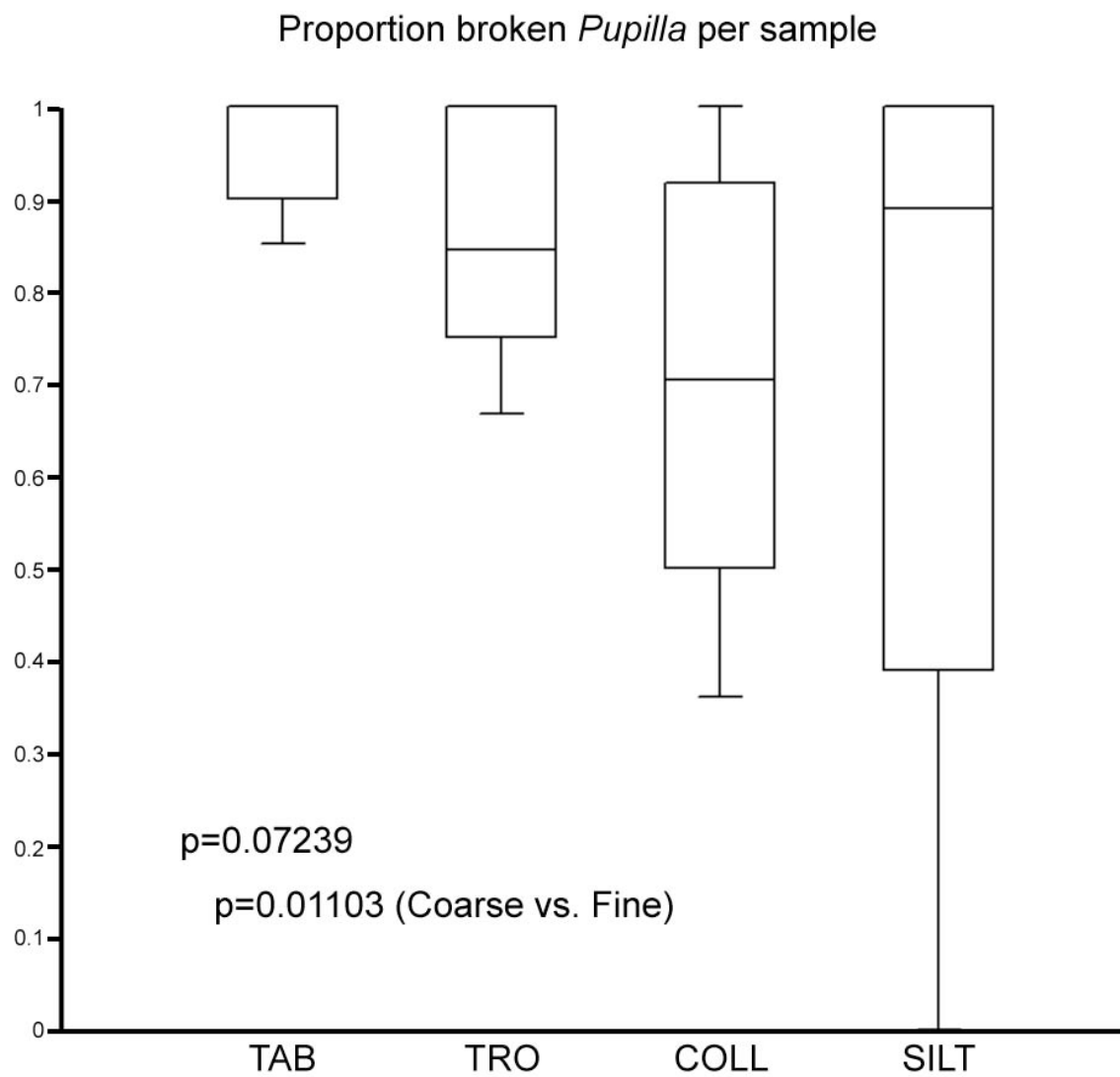


Figure E4. Proportion of broken *Pupilla* shells per sample from all four facies discussed in text. P values calculated from one-way ANOVA.

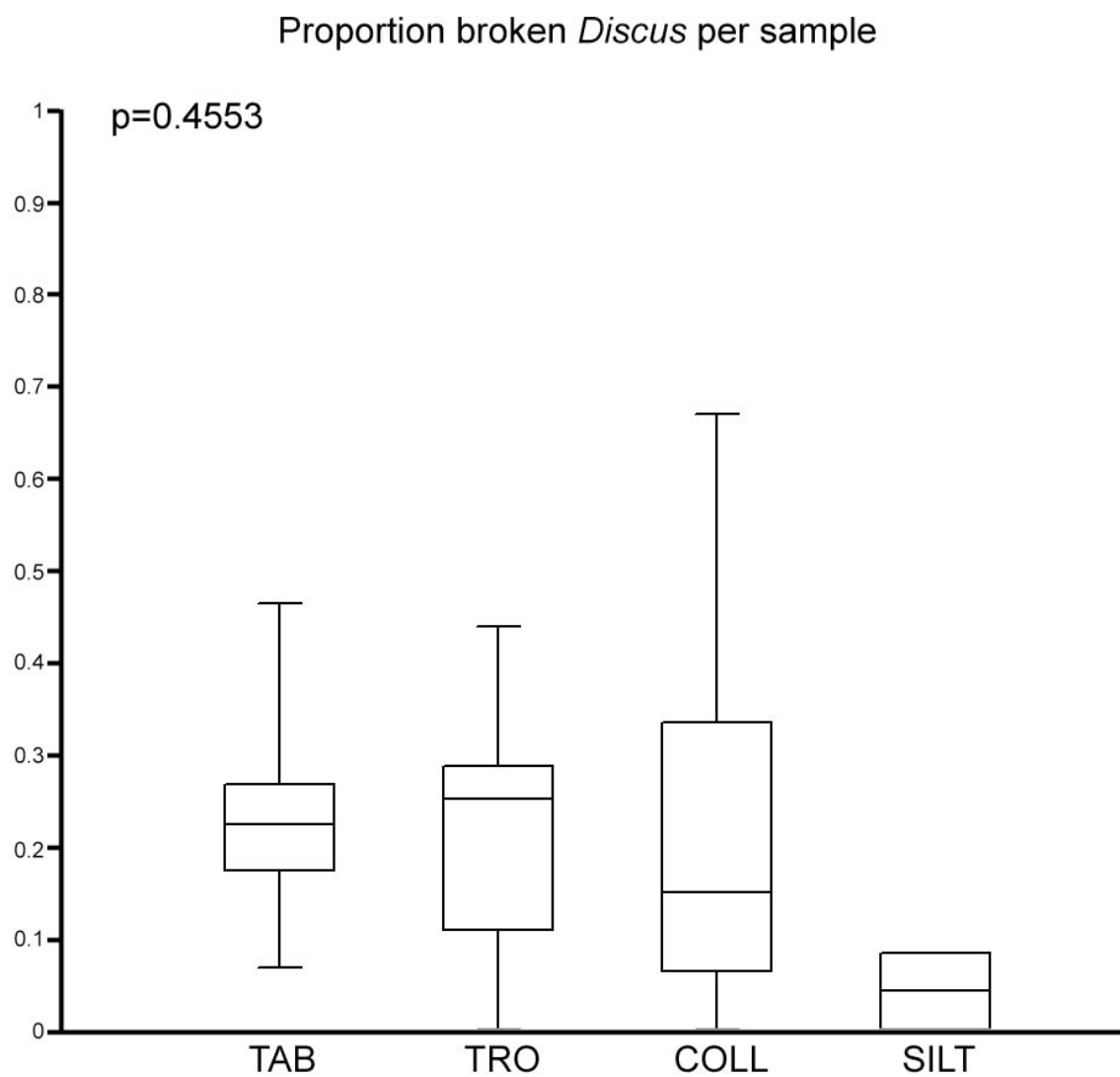


Figure E5. Proportion of *Discus* shells broken per sample among each facies. P value calculated via one-way ANOVA.

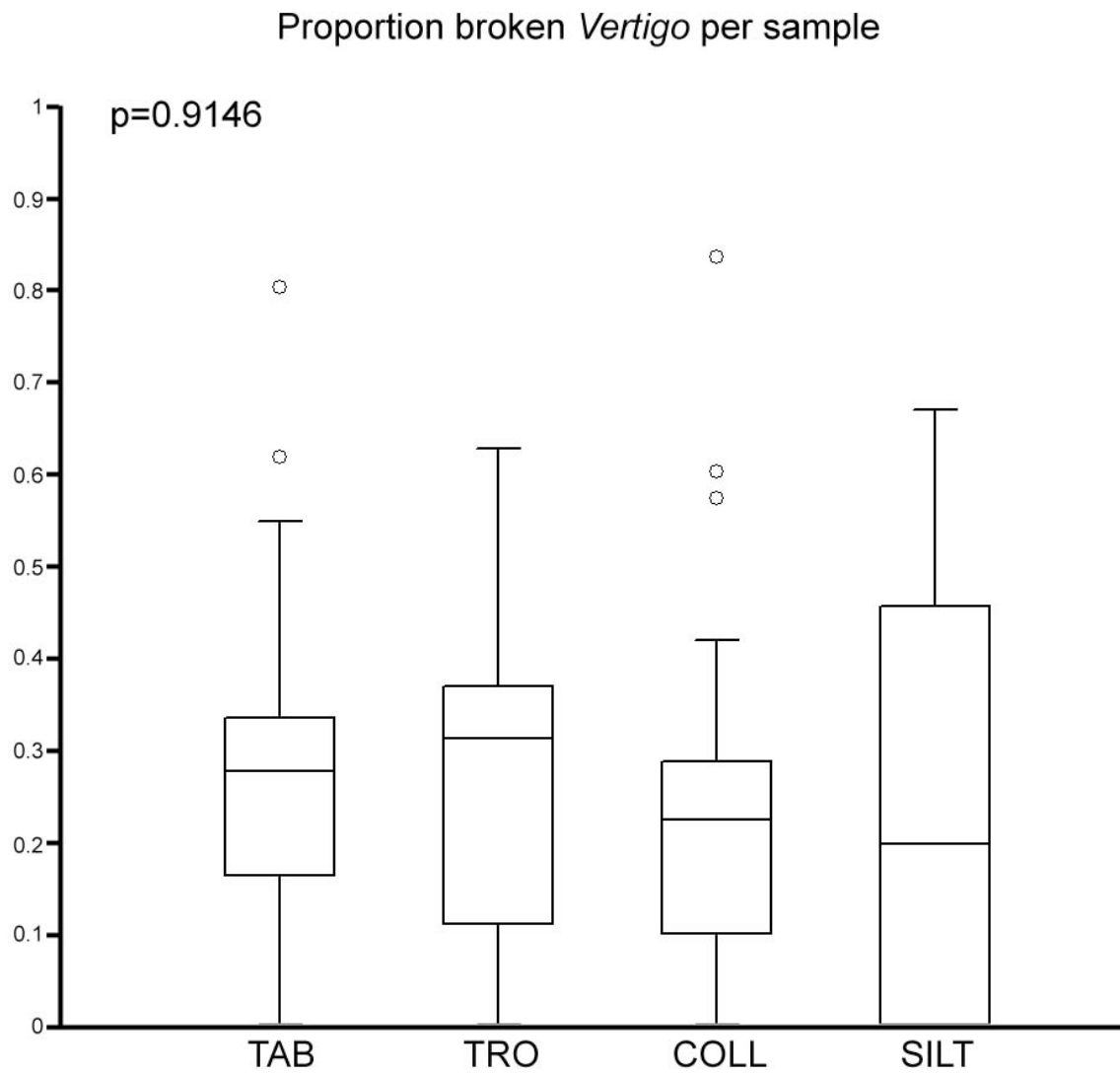


Figure E6. Proportion of *Vertigo* shells broken per sample among each facies. P value calculated via one-way ANOVA.

Appendix F

Converting Site numbers to UW repository numbers

The sites and samples discussed in the body of the dissertation are filed in the University of Wisconsin-Madison, Department of Geology and Geophysics under the file number UW1987. Each site has its own identification number, and samples from each site are numbered sequentially.

Site	UW
Kulas Quarry	UW1987/01
Hwy-JJ	UW1987/02
Root River	UW1987/03
Storer Creek	UW1987/04
Hideaway Lane	UW1987/05
Limery Coulee	UW1987/06
Big Platte	UW1987/07

Note: samples within each site are numbered sequentially by sample (e.g. UW1987/01.01 = KQ01, etc.)

Site (Field-Code)	Site (UW)	Sample (Field)	Sample (UW)
Kulas Quarry (KQ)	1987/01	KQ01 (KQ-U)	1987/01.01
		KQ02 (KQ-T)	1987/01.02
		KQ03 (KQ-Q)	1987/01.03
		KQ04 (KQ-L)	1987/01.04
		KQ05 (KQ-G)	1987/01.05
		KQ06 (KQ-F)	1987/01.06
		KQ07 (KQ-C)	1987/01.07
		KQ08 (KQ-I)	1987/01.08
		KQ09 (KQ-D)	1987/01.09
		KQ10 (KQ-E)	1987/01.10
		KQ11 (KQ-S)	1987/01.11
		KQ12 (KQ-J)	1987/01.12
		KQ13 (KQ-M)	1987/01.13
		KQ14 (KQ-B)	1987/01.14
		KQ15 (KQ-A)	1987/01.15
		KQ16 (KQ-N)	1987/01.16
		KQ17 (KQ-K)	1987/01.17
		KQ18 (KQ-P)	1987/01.18
		KQ19 (KQ-H)	1987/01.19
		KQ20 (KQ-O)	1987/01.20
		KQ21 (KQ-R)	1987/01.21
Hwy-JJ (JJ)	1987/02	JJ01	1987/02.01
		JJ02	1987/02.02
		JJ03	1987/02.03
		JJ04	1987/02.04
		JJ05	1987/02.05
		JJ06	1987/02.06
		JJ07	1987/02.07
		JJ08	1987/02.08
Root River (RR)	1987/03	RR01	1987/03.01
		RR02	1987/03.02
Storer Creek (SC)	1987/04	SC01	1987/04.01
		SC02	1987/04.02
		SC03	1987/04.03
		SC06	1987/04.04
		SC07	1987/04.05
Hideaway Lane (HL)	1987/05	HL01	1987/05.01
Limery Coulee	1987/06	LC-A	1987/06.01
		LC-B	1987/06.02
Big Platte (BP)	1987/07	BP-Bulk	1987/07.01
		BPst_15-35, BPC1a	1987/07.02
		BPst_40-60, BPC1b	1987/07.03
		BPst_65-85, BPC1c	1987/07.04
		BPst_100-120, BPC1d	1987/07.05
		BPC2_10-40, BPC2a	1987/07.06
		BPC2_50-80, BPC2b	1987/07.07
		BPC3_10-40, BPC3a	1987/07.08
		BPC3_50-80, BPC3b	1987/07.09