Collaborative research: Radiocarbon dating of North American terrestrial gastropod shells

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Project Summary

Terrestrial gastropods are one of the most successful animal groups on Earth. They occupy and thrive in incredibly diverse habitats, ranging from marshes and grasslands to upland forests and arctic tundra. Their distribution in the fossil record is equally diverse. Gastropod shells are commonly found in lake, wetland, alluvial, loess, and glacial deposits, as well as in sediments at archeological sites worldwide. Yet despite their widespread occurrence in the fossil record and the fact that they contain ~12% by weight carbon, gastropod shells are usually avoided for ^{14}C dating because many taxa incorporate ^{14}C-deficient (or "dead") carbon from limestone when building their shells. Geochronologists refer to this as the "Limestone Problem" because the amount of dead carbon incorporated in gastropod shells is variable at all taxonomic levels and can cause ^{14}C ages to be up to 3,000 years too old. However, our preliminary results from the American Southwest suggest that some small (maximum body dimension <10 mm) gastropods avoid limestone even when it is readily available. Moreover, these same taxa appear to remain closed systems with respect to carbon over geologic timescales in arid environments. Thus, at least in dry conditions, some small terrestrial gastropod shells may in fact provide reliable ^{14}C ages. The primary research objective of this study is to clearly identify gastropod taxa that are capable of consistently yielding reliable ^{14}C ages, regardless of local lithology, environmental conditions, climate, or ecological habitat. To this end, we will conduct a systematic analysis of the ^{14}C content of a suite of modern and fossil terrestrial gastropods that are endemic to North America. We have targeted more than 30 extant species that will be used to answer the following research questions: (1) do individuals of a specific taxon always avoid limestone when building their shells, and (2) if so, do their shells remain closed systems over time regardless of local environmental conditions? The wide taxonomic, ecological, and taphonomic scope of our study will allow us to determine what types of gastropod shells can be used to reliably date Quaternary sediments. Moreover, this approach will help other investigators identify additional target species, including those outside North America, by providing *a priori* guidelines for the identification of taxa that use only metabolically-generated carbon in shell construction, and that will hence provide accurate ^{14}C ages.

INTRODUCTION

Terrestrial gastropods are one of the most successful animal groups on Earth. They occupy and thrive in incredibly diverse habitats, ranging from marshes, wet meadows, and grasslands to upland forests and arctic tundra. Their modern distribution spans from Greenland to the Caribbean to Patagonia, and includes all continents except Antarctica. Their distribution in the fossil record is equally diverse. Gastropod shells are commonly preserved in lacustrine, wetland, alluvial, loess, and glacial deposits, as well as in sediments at archeological sites worldwide (e.g., EVANS, 1972). Despite their widespread occurrence and the fact that their shells contain ~12% by weight carbon, gastropod shells are usually avoided for ^{14}C dating because many taxa incorporate ^{14}C-deficient (or "dead") carbon from limestone when building their shells. This phenomenon, referred to as the "Limestone Problem" by GOODFRIEND and STIPP (1983), can cause ^{14}C ages of gastropod shells to be as much as ~3,000 years too old.

Despite the Limestone Problem, geochronologists have continued to investigate the possibility of using gastropod shells for ^{14}C dating because of their tremendous potential for dating Late Quaternary sediments (FRYE and WILLMAN, 1960; LEIGHTON, 1960; RUBIN et al., 1963; TAMERS, 1970; EVIN et al., 1980; GOODFRIEND and HOOD, 1983; GOODFRIEND and STIPP, 1983; GOSLAR and PAZDUR, 1985; YATES, 1986; GOODFRIEND, 1987; BRENNAN and QUADE, 1997; ZHOU et al., 1999; YATES et al., 2002; PIGATI et al., 2004). Prior to the mid-1990's, ^{14}C studies of gastropod shells generally focused on relatively large taxa, typically >20 mm in maximum dimension (length or diameter), and found that the large gastropods consistently incorporated carbon from limestone or other carbonate rocks when it was available. For decades, the observed ^{14}C deficiencies were thought to apply to all gastropods, large and small. BRENNAN and QUADE (1997), however, found that fossil shells of small[1] gastropods generally yielded reliable ^{14}C ages for the Late Pleistocene. PIGATI et al. (2004) followed by measuring the ^{14}C inventory of a suite of small gastropods living in alluvium dominated by Paleozoic carbonate rocks and found that, while some of the small gastropods did incorporate carbon from limestone when building their shells, others did not.

Based on these initial positive results, small gastropod shells are currently being used to date Late Quaternary ground-water discharge deposits in the American Southwest (PEDONE and RIVERA, 2003; PIGATI et al., in prep.) and loess deposits in the Great Plains (D. Muhs, pers. comm.). However, it is unclear if the results obtained from a limited number of localities in the American Southwest can be extrapolated to all geologic and climatic environments. Several outstanding questions must be satisfied before we can confidently use small gastropod shells for ^{14}C dating. For example, were the results obtained from the American Southwest the rule or the exception for the taxa that were investigated? Was there something about the local conditions that prevented certain taxa from incorporating limestone-derived carbon in their shells? Or are there underlying physical, biochemical, and/or phylogenetic traits that allow some small taxa to avoid limestone when others clearly depend on it? If so, at what taxonomic levels do these forcing mechanisms operate? What are the limits of generalization? Can the results from the Southwest be applied to other populations within the same species, regardless of local geologic

[1] Malacologists categorize gastropods by their maximum body dimension (length or diameter) as follows: large (>20 mm), medium (10-20 mm), small (5-10 mm), minute (2-5 mm), and micro (<2 mm). Although the size of the gastropods targeted for study in this proposal range from small to micro, for simplicity, we refer to them collectively as "small". All of the gastropods targeted for study in this proposal belong to Phylum Mollusca, Class Gastropoda, Subclass Pulmonata, Order Stylommatophora (see Figure 1 for some examples).

or environmental conditions? What about other species within the same genus? Or even other genera within the same family?

Even if some small gastropods always manage to avoid the Limestone Problem regardless of local environmental or geologic conditions, there is still another hurdle that must be overcome before we can confidently use their shells for ^{14}C dating. That is, their shells must remain closed systems with respect to carbon after burial. For reliable ^{14}C dating of gastropod shells, the pool of carbon atoms measured during the ^{14}C dating process must consist solely of carbon atoms that originally resided in the shell. Thus, following burial, the shells must resist the addition or exchange of ^{14}C atoms with the local environment. Although the initial results from the American Southwest indicate that small gastropod shells are, in fact, closed systems with respect to carbon over geologic (<50 ka) timescales in arid environments, this issue has not been addressed for fossil shells in more temperate or humid environments.

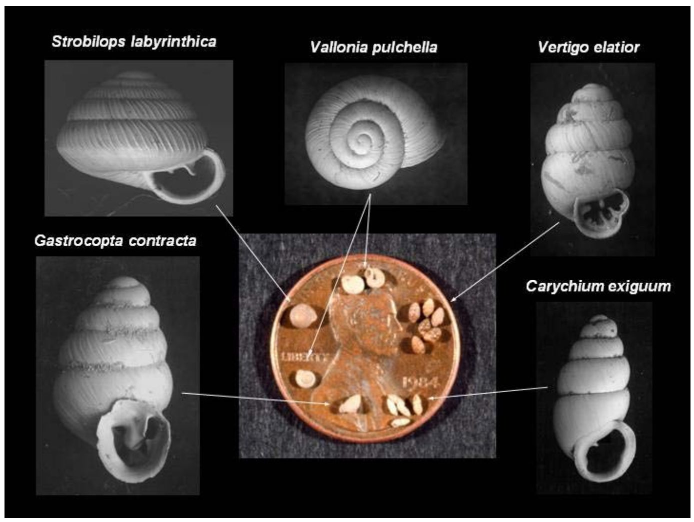

Figure 1 Scanning electron microscope (SEM) photomicrographs of selected small gastropod shells with a Lincoln penny for scale.

PROPOSED WORK AND SIGNIFICANCE

This project is a collaborative endeavor between geologists specializing in geochronology and Quaternary sedimentology (Pigati and Rech), and a community ecologist who specializes in the distribution and ecology of North American land snails (Nekola). Together, we propose to conduct a systematic analysis of the ^{14}C content of a suite of modern and fossil gastropods to determine conclusively under what circumstances gastropods can or cannot be used for radiocarbon dating. Although gastropod shells are often used for ^{14}C dating when other, more desirable organic materials are absent, lack of knowledge of the carbon source in shell material creates large uncertainties in ^{14}C ages derived from gastropod shells. In turn, this limits the usefulness of such data for answering fundamental research questions that require accurate and precise age control.

Our proposed study addresses these problems by considering the following research questions: (1) Do certain types of small gastropods avoid the use of bedrock-derived carbon for shell construction under all geologic and environmental conditions? (2) Do these shells remain closed systems with respect to carbon over geologic timescales, again regardless of the geologic and environmental conditions? (3) Can taxa that avoid use of bedrock-derived carbon for shell construction be predicted based on their phylogeny, physical characteristics, or ecological range? Answering these questions will not only determine the general utility of small land snails for geochronologic studies, but will help investigators identify other potential target species by providing *a priori* guidelines for identification of taxa that use only metabolically-generated carbon in shell construction, and that will hence provide accurate ^{14}C ages.

Previous ecological sampling by PI Nekola has resulted in an extensive collection of modern gastropods from North America, constituting 246 taxa and over 470,000 individuals from 1025 modern environments ranging from Hudson Bay to Florida to Arizona (Fig. 2).

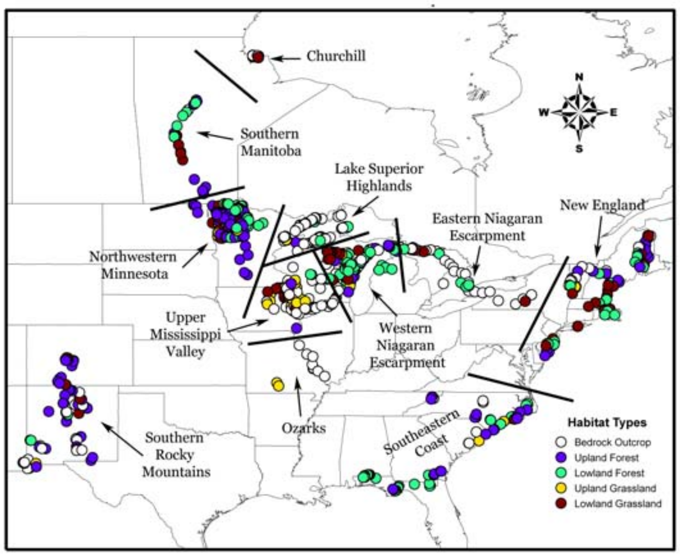

Figure 2 Distribution of localities for modern gastropods in P.I. Nekola's collection

Measuring the ^{14}C content of this entire suite of taxa is unreasonable in terms of both time and expense. Moreover, many of these taxa are not well represented in the Quaternary fossil record. In this study, we propose to measure the ^{14}C content of small gastropod shells that meet three criteria, thereby keeping costs and personnel time to a minimum while at the same time maximizing the potential benefits to Quaternary geologists. First, the small gastropod shells chosen for study must be commonly preserved in the Quaternary fossil record. Second, their modern distribution must include both carbonate and non-carbonate terrains. Finally, they must be either contained in PI Nekola's existing collection or can be easily obtained with a minimum of field sampling. In total, we have identified 44 different species of terrestrial and semi-aquatic gastropods that meet each of these criteria.

We also propose to measure the ^{14}C inventory of a suite of fossil small gastropods shells recovered from well-dated Quaternary deposits in the American Midwest to determine if their shells remain closed systems with respect to carbon over geologic timescales in more temperate environments. We are focusing this part of our work on the Midwest because of the broad distribution and diversity of gastropods in this region, the presence of calcareous substrate (Paleozoic limestone and calcareous till and loess), the abundance of fossil gastropod shells in Quaternary deposits, and the continued prevalence of humid conditions since the last glacial maximum. We have identified three well-dated Quaternary deposits that contain abundant small gastropod shells; the Oxford Glacial Outcrops in southern Ohio (ECKBERG et al., 1993), the Conklin Quarry site in southeastern Iowa (BAKER et al., 1986), and the Two Creeks Forest Bed in northern Wisconsin (BROECKER and FARRAND, 1963; KAISER, 1994). These sites range in age from ~11,000 to 22,000 ^{14}C years and cumulatively contain at least 20 different gastropod taxa.

The current proposal represents a significant advancement over previous studies that have investigated a small number of either live or fossil specimens (never both) from only single environmental settings. The wider taxonomic, ecological, and taphonomic scope of our proposed study will allow for the determination of the validity of using small terrestrial gastropods to date Quaternary sediments across a wide array of taxa, climatic conditions, ecological habitats, and geologic substrates. The extensive modern distribution of small gastropods (for example, see Fig. 3) gives an indication of the potential of ^{14}C dating gastropod shells in Quaternary sediments. Today, these gastropods live in diverse environmental conditions and exploit a variety of microhabitats, from leaf litter and grassy areas to areas under limestone boulders and rotting wood. Based on our experience with small gastropods in the fossil record in the American Southwest and Midwest, it appears that they likely exploited many of the same niches in the past.

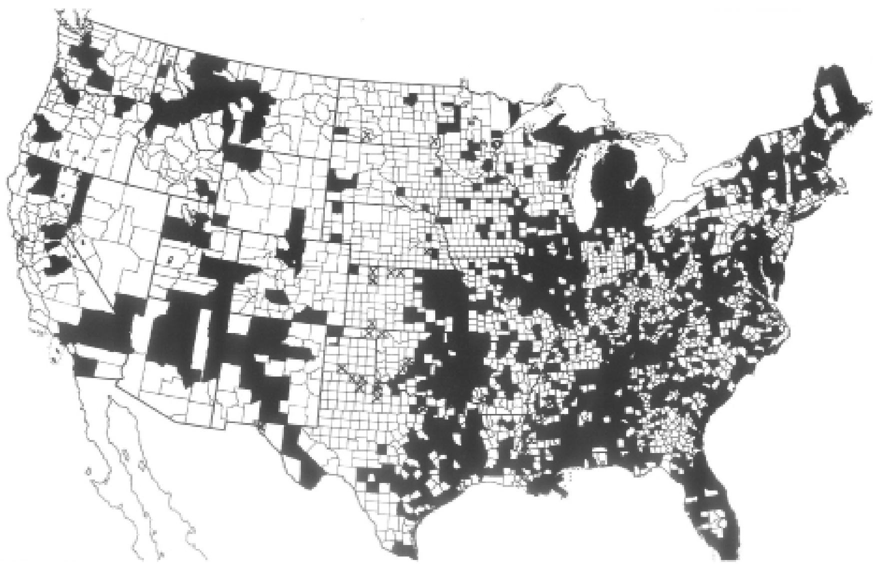

Figure 3 Modern distribution (shaded by county) of *Zonitoides arboreus* (after HUBRICHT, 1985).

The identification of a new material (small terrestrial gastropod shells) that yield ^{14}C ages that are as reliable as those obtained from well-preserved plant macrofossil and charcoal will be an extremely important addition to the relatively small list of materials that consistently yield robust ^{14}C ages. Among many potential applications in Quaternary research, ^{14}C dating of small terrestrial gastropod shells could be used to revolutionize our understanding of paleohydrologic conditions in the American Southwest, the Middle East, North and East Africa, Central and South America, and Australia since the last glacial maximum. Spring discharge deposits, which demarcate the position of past water tables on the landscape (QUADE, 1986) and are therefore sensitive to climate change, often contain fossil terrestrial gastropod shells. Radiocarbon dating of these shells could be used to improve chronologic constraints for changes in water table elevations through time, which, in turn, would allow researchers to determine how hydrologic systems around the world responded to high-frequency climate variations, such as the Younger Dryas cold event and Dansgaard-Oeschger cycles. Similarly, improved temporal control of loess, alluvial, and glacial deposits would allow researchers to better understand the response these and other geomorphic systems to past climate change.

BACKGROUND

The "extreme plasticity and adaptability" of the Molluscan body plan (BARNES et al., 1993) has lead to their remarkable evolutionary success, representing at least 100,000 extant species. Gastropods are the most diverse of molluscan groups, with at least 70,000 taxa occupying terrestrial, marine and freshwater habitats. Globally, terrestrial gastropods encompass at least 35,000 species (BARKER, 2001), span 4-5 orders of magnitude in volume, and represent a variety of trophic levels, including polyphagous detritivores, herbivores, omnivores, and carnivores (KERNEY and CAMERON, 1979; BURCH and PEARCE, 1990). Species are known from all continents, save Antarctica, and occupy almost all vegetation types except for extreme desert. Gastropods are so exceptionally diverse in their appearance, ecology, and physiology that determining their phylogenetic relationships from conchological and/or anatomical characteristics remains difficult and controversial (e.g., PONDER and LINDBERG, 1997 and references therein). However, it is clear that terrestrialism in North American gastropods has independently developed in three of six basal clades (Neritomorpha, Caenogastropoda, and Heterobranchia), with the informal (and polyphyletic) group Pulmonata representing over 99% of the continental fauna. Of the Pulmonata, the most frequent size class in both modern and fossil assemblages are individuals with adult shells <10 mm in maximum dimension (NEKOLA, 2005).

^{14}C activities of potential carbon sources

All materials (organic or inorganic) that yield reliable ^{14}C ages have two common characteristics. First, the initial ^{14}C activity of the material – a plant, for example – was in equilibrium with atmospheric ^{14}C at the time that it was alive. In other words, the ^{14}C activity of a plant that lived *T* years ago was the same as the ^{14}C activity of the atmosphere *T* years ago[2]. Second, after death, the material behaves as a closed system; that is, carbon was neither added nor removed from the sample material through time. If both of these criteria are met, then the measured ^{14}C activity is a function of only two parameters: (1) the initial ^{14}C activity of the atmosphere, and (2) the amount of time elapsed since the material was isolated from the atmosphere (e.g., since the death of the organism). The measured ^{14}C inventory and the age of the material are related by the familiar decay equation $A=A_oe^{-\lambda t}$, where A and A_o are the measured and initial ^{14}C activities of the material, respectively, λ is the decay constant ($\ln 2/t_{1/2}$), the half-life of ^{14}C is 5,730 years, and t is the time elapsed since the death of the organism. Measured ^{14}C ages are converted to calendar year ages to account for variations in the ^{14}C activity of the atmosphere (A_o) through time (e.g. STUIVER et al., 1998).

Sources of gastropod shell carbon

In order to evaluate the validity of a ^{14}C age of any material, the original source(s) of the carbon must be known. The carbon in gastropod shell carbonate originates from as many as four different sources – atmospheric CO_2, food, water, and carbonate rocks.

Atmospheric CO_2

Gastropods incorporate CO_2 from the atmosphere through respiration. Respired CO_2 is introduced to the bicarbonate pool in the gastropod's hemolymph and passed along to the

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[2] This statement is valid if measured ^{14}C activities are corrected for fractionation. Fractionation (or isotopic enrichment) occurs along chemical and biological pathways because of the differences in the rates of reaction for different molecular species. By convention, all measured ^{14}C activities are normalized to a δ^{13}C value of -25‰$_{VPDB}$.

extrapallial fluid, from which the shell carbonate is ultimately precipitated. Estimates of the contribution of atmospheric CO_2 to gastropod shell carbonate vary between negligible (STOTT, 2002) and 30-60% (GOODFRIEND and HOOD, 1983).

Food

Carbon from various gastropod food sources (e.g. fungi, organic detritus, living plants, animals) is incorporated into the extrapallial fluid through two mechanisms: direct digestion and breakdown of urea. When gastropods consume and digest food, carbon is introduced to the hemolymph and passed along to the extrapallial fluid in the same manner as atmospheric CO_2. There it mixes with atmospheric carbon before becoming incorporated in the shell carbonate.

Carbon derived from urea takes a more indirect pathway. Urea that is not expelled by the gastropod breaks down into CO_2 and NH_3 via a urease reaction (STOTT, 2002). The resulting CO_2 is then reintroduced directly to the extrapallial fluid and ultimately incorporated in the shell carbonate. Estimates of the amount of carbon derived from plants, either directly or indirectly, range from 25-40% (GOODFRIEND and HOOD, 1983) to ~100% (STOTT, 2002).

In most environments, the ^{14}C activity of live plants and animals is in equilibrium with global atmospheric values (plants living near volcanic vents are an exception). Gastropods that obtain their shell carbon entirely from the atmosphere and live plants, therefore, should yield reliable ^{14}C ages. Gastropods consuming fungi and/or organic detritus do not pose a problem for ^{14}C dating because the time between plant death, its incorporation into decomposing fungi, and ultimate consumption by gastropods is usually quite short, on the order of years to decades. Exceptions include situations in which organic matter is preserved at the ground surface for centuries to millennia or where fossil organic matter is exhumed and made available for consumption. Although relatively limited in geographic importance, this effect is most pronounced in areas where decomposition is hindered by aridity or elevated water tables. While few snails survive in hyperarid conditions, they are abundant in tundra and peatland habitats, which suggests that this factor could be an important confounder in such depositional settings.

Water

Gastropods consume water from several sources, including surface water, dew, and rain, all of which contain some amount of dissolved inorganic carbon (DIC). Water is taken up through the foot of the gastropod by contact rehydration (BALAKRISHNAN and YAPP, 2004) and introduced to the hemolymph before being passed on to the extrapallial fluid. The amount of carbon in terrestrial gastropod shells that is derived from water is unknown, although it is probably not significant.

Pigati *et al*. (2004) found that aqueous carbon sources account for ~10% of the shell carbon for the semi-aquatic gastropod *Succineidae*. It is not known if this value is constant across other wetland terrestrial gastropod taxa. Regardless, the ^{14}C activity of surface waters is typically at or near equilibrium with atmospheric ^{14}C. Exceptions include spring water emerging from deeply circulating carbonate aquifers or from active volcanic areas where ^{14}C-deficient CO_2 is abundant. As long as these environments are avoided, water is unlikely to introduce a significant error to measured ^{14}C ages from either terrestrial or semi-aquatic gastropods.

Carbonate rocks

Some gastropods are able to directly ingest small granules of carbonate rocks (limestone, dolomite, soil carbonate), which dissolve in their stomach acid to produce CO_2 (GOODFRIEND and STIPP, 1983). This CO_2 then dissolves in the hemolymph, is passed on to the extrapallial fluid, and is ultimately incorporated in the shell carbonate. Other gastropods are able to dissolve carbonates outside their bodies and take the ^{14}C-deficient carbon in through their foot where it is introduced to the hemolymph, passed on to the extrapallial fluid, and ultimately incorporated in the shell carbonate.

The incorporation of ^{14}C from limestone and other carbonate rocks presents the most significant problem for ^{14}C dating of gastropod shells. The ^{14}C activity of atmospheric carbon, plants, and most water bodies is essentially the same, 100 pMC (i.e., “live” carbon). In contrast, the ^{14}C activity of limestone is 0 pMC (i.e., “dead” carbon). Thus, for ^{14}C dating, the magnitude of the potential error introduced by limestone is a direct function of the amount of dead carbon that is incorporated in the shell. For example, if 10% of the shell carbon is derived from limestone, then the initial ^{14}C activity will be 10% deficient. If 20% of the shell carbon is derived from limestone, then the initial ^{14}C activity will be 20% deficient, and so on. Goodfriend and Stipp (1983) found that up to 30% of shell carbon can be derived from limestone, which would cause a measured ^{14}C age to be ~3,000 years too old! Unfortunately, a simple correction that accounts for the incorporation of ^{14}C-deficient carbon is not possible because we cannot know *a priori* how much of the shell carbon was derived from carbonate rocks versus other sources. Thus, to be confident in ^{14}C ages from gastropod shells, it is imperative that we are able to identify and avoid taxa that incorporate carbon derived from carbonate rocks altogether.

Previous ^{14}C dating of terrestrial gastropods

Fossil gastropod shells are abundant in Quaternary deposits in North America and have been the focus of numerous studies dating back to the early 20th Century. Initial studies focused on the use of gastropod assemblages as a paleoenvironmental indicator (e.g., SHIMEK, 1913; BAKER, 1920; LEONARD and FRYE, 1960; MILLER and BAJC, 1989), whereas later studies used gastropod shells for ^{14}C dating of sediments (e.g., SNOWDEN and PRIDDY, 1968; PYE and JOHNSON, 1988; OCHES et al., 1996) or for comparison with ^{14}C dates obtained from wood or other organic material (IVES et al., 1964; WILLMAN and FRYE, 1970; COLEMAN, 1972; COLEMAN and LIU, 1975). Still other studies used ^{14}C ages of gastropod shells to calibrate thermoluminescence (PYE and JOHNSON, 1988) and amino acid racemization dating techniques (CLARK et al., 1989). Many of these studies were conducted prior to the advent of accelerator mass spectrometry (AMS) in the mid-1980’s. The conventional ^{14}C dating techniques that were used typically required relatively large sample sizes and, therefore, numerous shells of different taxa were often lumped together. In addition, many of these studies did not identify the specific taxa used for ^{14}C measurements. The net effect is that it is not possible to determine if specific gastropod taxa are suitable for ^{14}C dating based on these early studies.

INITIAL RESULTS

Live gastropods

In 2001, PI Pigati measured the ^{14}C content of a suite of gastropods living in alluvium dominated by Paleozoic carbonates in the American Southwest. The ^{14}C activities of *Pupilla blandi* and *Euconulus fulvus* were indistinguishable from the ^{14}C value of live plants (Table 1), which suggests that these taxa do not incorporate limestone or other sources of old carbon during shell formation. Other small gastropods collected in 2001 appeared to incorporate at least some limestone-derived carbon in their shells. The ^{14}C activity of *Cochlicopa lubrica* was slightly lower than the atmospheric ^{14}C activity, which suggests that ~2% of the shell carbon was derived from limestone. The ^{14}C activity of *Discus whitneyi* and *Vallonia cyclophorella* indicated that ~6-8% of the shell carbon for each of these taxa was derived from limestone. Finally, the measured ^{14}C activity of *Oreohelix concentrata* deviated significantly from the measured atmospheric value, by ~28%. This is similar to the upper limit of the percentage of limestone-derived carbon observed by Goodfriend and Stipp (1983).

Table 1 ^{14}C activities of live terrestrial gastropods

Locality*	Taxa	Date collected	^{14}C activity	^{14}C Atmosphere	% C from Limestone
DC	*Pupilla blandi*	6/23/2001	1.0893 ± 0.0064	1.0919 ± 0.0039	0.2±0.7
DC	*Euconulus fulvus*	6/23/2001	1.0864 ± 0.0044	1.0919 ± 0.0039	0.5±0.5
GC	*Cochlicopa lubrica*	8/04/2001	1.0719 ± 0.0047	1.0919 ± 0.0039	1.8±0.6
WC	*Vitrina alaskana*	5/26/1976	1.3444 ± 0.0060	1.37 ± 0.01	1.9±0.8
DC	*Discus whitneyi*	6/23/2001	1.0223 ± 0.0047	1.0919 ± 0.0039	6.4±0.5
DC	*Vallonia cyclophorella*	6/23/2001	1.0075 ± 0.0076	1.0919 ± 0.0039	7.7±0.8
CM	*Vallonia perspectiva*	6/09/1971	1.3093 ± 0.0075	1.55 ± 0.01	15.5±0.7
GC	*Orehelix concentrata*	8/04/2001	0.7826 ± 0.0039	1.0919 ± 0.0039	28.3±0.4
CM	*Gastrocopta pellucida*	6/09/1971	0.9591 ± 0.0049	1.55 ± 0.01	38.1±0.5

* CM = Chisos Mountains, TX; DC = Deer Creek, NV; GC = Garden Canyon, AZ; WC = Willow Creek, NV

PI Pigati also measured the ^{14}C activities of three taxa collected in the 1970's by Will Pratt of the Marjorie Barrick Museum of Natural History at the University of Nevada at Las Vegas. The ^{14}C activity of *Vitrina alaskana* collected live from Willow Creek in southern Nevada in 1976 was slightly lower than the atmospheric ^{14}C activity during the year of collection, which suggests that ~2% of the shell carbon was derived from limestone. Specimens of *Vallonia perspectiva* and *Gastrocopta pellucida* collected live in 1971 from the Chisos Mountains in Texas were significantly lower than the atmospheric ^{14}C activity during the time of shell formation. The results suggested that *V. perspectiva* and *G. pellucida* incorporate ~15 and 38% of their shell carbon from limestone, respectively.

Finally, PI Pigati measured the ^{14}C activity of the wetland land snail *Catinella* sp. (*Succineidae*) to determine the amount of water-derived carbon incorporated during shell formation. Specimens of *Catinella* sp. were collected live from grassy areas adjacent to ^{14}C-deficient surface waters at Cold Creek in southern Nevada and Montezuma's Well in central Arizona. Although the ^{14}C activity of these waters differ by an order of magnitude (DAMON et al., 1964; THOMAS et al., 1991), the fraction of ^{14}C-deficient carbon incorporated in *Catinella* shell carbonate was remarkably similar, 10.9±1.8% at Cold Creek and 9.1±0.6% at Montezuma's Well. Pigati et al. (2004) concluded that *Catinella* can provide reliable ^{14}C ages if local water bodies are at or near equilibrium with atmospheric CO_2. If ^{14}C-deficient water is present at the surface, a correction of ~10% of the local carbon-reservoir effect must be applied.

Fossil gastropods

American Southwest

PI Pigati also measured the ^{14}C ages of small gastropod shells recovered from the Coro Marl, a ground-water discharge deposit at the Murray Springs Paleoindian Site in the San Pedro Valley of southern Arizona. The ^{14}C ages of fossil shells of *Succineidae*, *Euconulus fulvus,* and *Pupilla muscorum* (a close relative to *P. blandi*) recovered from 10 cm blocks from two sections maintained stratigraphic order (Table 2; Fig. 4). Moreover, the gastropod ^{14}C ages fell within the permissible bounds imposed by ^{14}C ages for the overlying (12,820±390 ^{14}C years B.P.) and underlying (29,000±200 ^{14}C years B..P) units (PIGATI et al., 2004), which suggests that their shells remained closed with respect to carbon after burial.

Table 2 ^{14}C ages of fossil gastropods, southern Arizona

Section	Depth (cm)	Gastropod taxa*	^{14}C Age
2	0-12	*Euconulus fulvus*	13,140 ± 60
2	0-12	*Succinea* sp. (*Succineidae*)	13,680 ± 80
2	37-49	*Succinea* sp. (*Succineidae*)	19,780 ± 120
2	73-85	*Succinea* sp. (*Succineidae*)	23,020 ± 200
1	0-10	*Succinea* sp. (*Succineidae*)	17,860 ± 80
1	0-10	*Succinea* sp. (*Succineidae*)	18,160 ± 80
1	10-20	*Succinea* sp. (*Succineidae*)	19,380 ± 110
1	20-30	*Succinea* sp. (*Succineidae*)	21,030 ± 100
1	30-40	*Succinea* sp. (*Succineidae*)	21,600 ± 120
1	40-50	*Succinea* sp. (*Succineidae*)	23,570 ± 120
1	50-60	*Succinea* sp. (*Succineidae*)	23,690 ± 130
1	60-70	*Succinea* sp. (*Succineidae*)	24,420 ± 140
1	70-80	*Succinea* sp. (*Succineidae*)	24,980 ± 140
1	80-90	*Euconulus fulvus*	24,740 ± 200
1	80-90	*Pupilla muscorum*	25,700 ± 210
1	80-90	*Succinea* sp. (*Succineidae*)	24,470 ± 120
1	90-100	*Succinea* sp. (*Succineidae*)	24,620 ± 140
1	100-110	*Succinea* sp. (*Succineidae*)	24,310 ± 180
1	100-110	*Succinea* sp. (*Succineidae*)	24,860 ± 170

Figure 4 Section 1 of the Coro Marl (white unit) in the San Pedro Valley of southern Arizona.

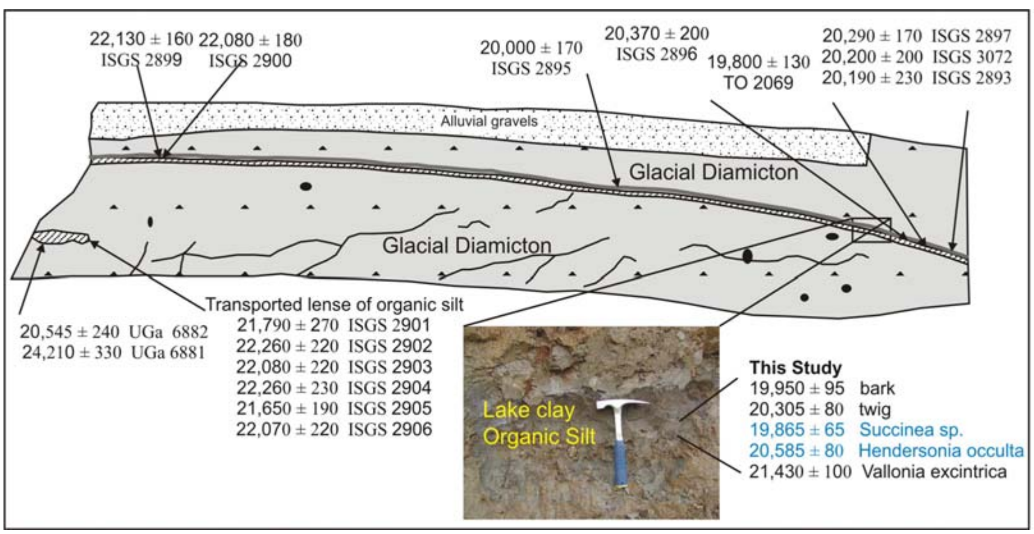

Figure 5 Radiocarbon ages from Laurentide glacial deposits, Oxford OH (modified from Lowell *et al*. (1995)) .

<u>American Midwest</u>

In 2004, PIs Pigati and Rech collected gastropods and plant macrofossils from an organic silt interstadial unit at the Oxford, OH glacial outcrops (Fig. 5). The Oxford outcrops contain a series of glacial diamictons from the Miami Lobe of the Laurentide Ice Sheet that are separated by thin (3-5 cm) units of calcareous organic silt that contain gastropods, plant macrofossils, and occasional tree stumps (ECKBERG et al., 1993; LOWELL, 1995). We obtained ^{14}C ages of 19,950±95 and 20,305±80 ^{14}C yrs B.P. from a piece of bark and a small twig recovered from the organic silt unit. We also obtained ^{14}C ages of 20,585±80, 19,865±65, and 21,430±100 ^{14}C yrs B.P. for shells from three different gastropod taxa, *Succinea* sp. (*Succineidae*), *Hendersonia occulta*, and *Vallonia gracilicosta*. The ^{14}C ages of the *Succinea* sp. and *H. occulta* shells are within one standard deviation (1σ) of the ^{14}C ages of the plant macrofossils, whereas the ^{14}C age of the *V. gracilicosta* shell is ~1000 ^{14}C years older (Fig. 5). These results suggest that the *Succineidae* and *Hendersonia occulta* incorporated no or minimal amounts of limestone and remained a closed system with respect to carbon over the last ~24,000 calendar years in humid environments. The older ^{14}C age for *Vallonia gracilicosta* suggests that it obtains ~7% of its shell carbon from limestone. This is in agreement with previous results for *Vallonia* in the American Southwest that suggested between 7-15% of its shell carbon was derived from limestone (Table 1).

PROPOSED RESEARCH

<u>The overall goal of the proposed project is to clearly identify small gastropod taxa that are capable of consistently yielding reliable ^{14}C ages, regardless of local lithology, environmental conditions, climate, or ecological habitat</u>. To that end, we propose to address the following research questions:

1. Can we extrapolate the positive ^{14}C results for select taxa from a few localities in the American Southwest to other localities, particularly those in more humid environments?

In the American Southwest, Pigati *et al*. (2004) identified three gastropod taxa, *Euconulus fulvus, Pupilla blandi*, and *Succineidae* that do not appear to incorporate limestone-derived carbon in their shells. We propose to determine if these taxa also avoid limestone and other carbonate rocks when living in other localities and environments across North America. PI Nekola has collected live specimens of *Euconulus fulvus* from at least 41 different localities with carbonate substrates, and *Pupilla blandi* from at least 3 different localities with carbonate substrates (Table 3). Here, we propose to measure the ^{14}C content of three aliquots of shell material[3] for each of these taxa from three different localities (a total of 18 AMS ^{14}C measurements).

For *Succineidae*, a similar evaluation is more complicated. *Succineidae* are, by far, the most common gastropod taxon in the Quaternary deposits of North America. It is the most common taxon in ground-water discharge deposits in the American Southwest, the most common taxon in Midwestern loess deposits, and it is common in numerous other Quaternary deposits across North America. Part of the reason for their *perceived* abundance is that the *Succineidae* family is composed of multiple genera (*Succinea*, *Oxyloma*, and *Catinella*) that are very difficult to differentiate in modern faunas, let alone the geologic record. Because of their simple shells with few diagnostic identifying characteristics, species-level identification in the *Succineidae* is based on soft-body reproductive organ morphology, which is rarely preserved in the fossil record. This poses a significant problem for geochronologists - can we be confident in ^{14}C ages derived from shells from any species or genera within the *Succineidae*, or do we need to target specific members within the family? To answer this question, a comprehensive analysis of the ^{14}C inventory of the *Succineidae* is required. We propose to measure the ^{14}C activity of three aliquots of shell material for the most common species within each of the three main genera: 3 species of the genus *Catinella*, 2 species of the genus Oxyloma, and 6 species of the genus *Succinea* from three different localities in North America (a total of 99 AMS ^{14}C measurements). While the amount of time and effort required for this part of the proposed work is relatively high, the potential payoff (that is, an extremely common and easily identifiable shell that may yield reliable ^{14}C ages) is correspondingly high.

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[3] Each AMS ^{14}C measurement requires ~1 mg of carbon or ~12 mg of shell material. Depending on the size of the individual shells, this will require ~4-8 shells per measurement.

Table 3: Targeted modern gastropods

Family	Genus	Species	Physical habitat	Total sites	$CaCO_3$ sites
Cochlicopidae	*Cochlicopa*	*lubrica*	clay-rich soils	138	26
Cochlicopidae	*Cochlicopa*	*lubricella*	aspen parkland, prairies	169	15
Cochlicopidae	*Cochlicopa*	*morseana*	mesix woodlands	43	8
Discidae	*Discus*	*catskillensis*	woodland	394	98
Discidae	*Discus*	*macclintocki*	ls talus, cliffs	10	8
Discidae	*Discus*	*shimeki*	montane forest	ca. 10	1
Discidae	*Discus*	*whitneyi*	wet prairies to mesic woods	182	21
Helicarionidae	*Euconulus*	*alderi*	wetland	175	23
Helicarionidae	*Euconulus*	*dentatus*	calc. forest	5	2
Helicarionidae	*Euconulus*	*fulvus*	upland forest	405	41
Helicarionidae	*Euconulus*	*polygyratus*	upland forest	132	23
Helicinidae	*Hendersonia*	*occulta*	ls cliffs, talus	94	46
Punctidae	*Punctum*	*minutissimum*	upland forest	450	55
Pupillidae	*Columella*	*columella*	willow scrub	10	3
Pupillidae	*Gastrocopta*	*pentodon*	upland forest, prairie	319	93
Pupillidae	*Gastrocopta*	*tappaniana*	lowland forest, grassland	265	29
Pupillidae	*Pupilla*	*blandi*	montane forest	ca. 30	2
Pupillidae	*Pupilla*	*muscorum -* E	disturbed calc. sites	14	7
Pupillidae	*Pupilla*	*muscorum -* NA	generalist, arctic	4	1
Pupillidae	*Vertigo*	*elatior*	wetland	181	33
Pupillidae	*Vertigo*	*hannai*	calc tundra	15	5
Pupillidae	*Vertigo*	*hubrichti*	wooded ls cliffs	136	51
Pupillidae	*Vertigo*	*modesta*	willow-birch thicket	31	9
Pupillidae	*Vertigo*	*paradoxa*	wooded ls cliffs	85	19
Strobilopsidae	*Strobilops*	*affinis*	marl flats; calc clays	41	12
Strobilopsidae	*Strobilops*	*labyrinthica*	generalist	473	105
Succineidae	*Catinella*	*"exile"*	wetland	29	11
Succineidae	*Catinella*	*"gelida"*	mesic	31	14
Succineidae	*Catinella*	*"vermita"*	xeric	13	5
Succineidae	*Oxyloma*	*"retusa"*	temperate, wetland	71	15
Succineidae	*Oxyloma*	*"verrilli"*	arctic, wetland	9	4
Succineidae	*Succinea*	*"bakeri"*	mesic	ca. 40	10
Succineidae	*Succinea*	*"grosvernori"*	xeric	3	1
Succineidae	*Succinea*	*"indiana"*	xeric	3	1
Succineidae	*Succinea*	*"Minnesota* n.sp.*"*	mesic	ca. 40	10
Succineidae	*Succinea*	*"ovalis"*	wetland	ca. 90	9
Succineidae	*Succinea*	*"strigata"*	wetland	ca. 90	9
Valloniiidae	*Vallonia*	*cyclophorella*	montane forest	ca.20	2
Valloniiidae	*Vallonia*	*gracilicosta*	aspen, plains, ls cliffs	154	33
Valloniiidae	*Vallonia*	*perspectiva*	xeric, ls cliffs	83	47
Zonitidae	*Hawaiia*	*minuscula*	generalist	287	110
Zonitidae	*Nesovitrea*	*binneyanna*	mesic forest	83	22
Zonitidae	*Nesovitrea*	*electrina*	wetland	352	34
Zonitidae	*Zonitoides*	*arboreus*	general forest	596	72

Notes:

(1) Species names for the *Succineidae* reflect known ecological morphs, rather than true taxonomic entities. The taxonomic name most closely allied to a given ecophenotype is provided, but these do not necessarily represent biological entities.

(2) Total sites represents the number of extant populations represented in PI Nekola's collection.

(3) $CaCO_3$ sites represents the number of stations with exposed carbonate substrates (e.g. limestone, dolomite, marl) and at least 10 observed individuals in PI Nekola's collection.

(4) *Pupilla muscorum* is assumed here to represent two entities, one a native North American arctic taxon (NA), and another which is a European invasive (E) that is found south of the Great Lakes and limited to anthropogenic habitats.

2. Are there other small gastropod taxa in North America that are suitable for ^{14}C dating?

Based on the three criteria listed in the Proposed Work and Significance section (see above), we have identified 31 additional species of small gastropods in North America that may be suitable for ^{14}C dating (Table 3). PI Nekola's collection currently contains sufficient material for 26 of these species. Specimens of the remaining five species will be obtained by PI Nekola via additional field sampling in New England, the Carolina coastal plain, arctic Quebec, and/or arctic Alaska. For each of the 31 species, we will first measure 3 aliquots of shell material collected at a single locality (humid environment, carbonate substrate) as an initial screening test (a total of 93 AMS ^{14}C measurements). Based on the results of Pigati *et al*. (2004), we anticipate that approximately one-fourth of the 31 species (likely ~8 species in all) will not incorporate bedrock-derived carbon in their shells. For each of these 8 species, we propose to measure the ^{14}C content of three aliquots of shell material from two additional localities (a total of 48 AMS ^{14}C measurements) to determine if they will be suitable for ^{14}C dating, regardless of local conditions. To ensure that old carbon from surficial organic deposits does not significantly alter ^{14}C concentrations in tundra or peatland target taxa, these additional sites will be sampled across the full extent of the North American arctic.

Thus, in sum, for any given species that appears to be suitable for ^{14}C dating, we propose to measure the ^{14}C inventory of three aliquots of shell material (again, each consisting of 4-8 shells) from three different localities, for a total of 9 measurements. In essence, these 9 measurements will represent an amalgamation of the ^{14}C inventory of 35-70 individual shells, which allows for meaningful statistical power (using student's t and χ^2 tests) to calculate how much or how little dead carbon is used for shell building by each species as a whole.

3. Do small gastropod shells remain closed systems with respect to carbon over geologic timescales in humid environments?

Numerous materials may be in equilibrium with the ^{14}C content of the atmosphere when an organism is alive, but do not yield reliable ^{14}C ages because they do not behave as closed systems with respect to carbon over geologic time (e.g., bone). If small gastropod shells are to be used for ^{14}C dating, we must establish that they remain chemically and isotopically closed systems after death. To that end, we propose to measure the ^{14}C activity of 3 aliquots of shell material from at least 5 taxa recovered from three sites in the American Midwest - the Oxford Organic Silt Bed, the Two Creeks Forest Bed, and the Conklin Quarry site (a total of 45 AMS ^{14}C measurements). These sites were chosen because they are very well dated, represent brief snapshots of geologic time, are located in humid environments, and contain abundant small gastropod shells.

<u>Oxford Organic Silt Bed</u> (22,000 ^{14}C yrs BP) - The Oxford glacial outcrops contain a series of glacial diamictons that are separated by thin (3-5 cm) units of calcareous organic silt that contain abundant gastropods, plant macrofossils, and occasional tree stumps (ECKBERG et al., 1993; LOWELL, 1995). AMS ^{14}C dating of plant macrofossils and *in situ* tree stumps has shown that the age of this unit is ~22,100 ^{14}C yrs BP. Gastropod taxa from this unit were described by Dell (1991), and include seven different small gastropod taxa from our target list, including *Columella columella*, *Discus cronkhitei*, *Euconulus fulvus*, *Hendersonia occulta*, *Pupilla muscorum*, *Succineidae*, and *Vertigo elatior*.

Two-Creeks Forest Bed (12,050 to 11,750 ^{14}C years) - The Two Creekian interstadial deposit from the Upper Peninsula of Michigan is composed of a forest bed that was buried by the advancing Laurentide Ice Sheet during the Older Dryas chronozone (Broecker and Farrand, 1963; Kaiser, 1994). The deposit spans ~252 years (tree ring chronology from *in situ* tree stumps) and dates to between 12,050 and 11,750 ^{14}C years (Kaiser, 1994). Gastropods identified in the Two Creeks Bed that we have targeted include *Columella columella*, *Pupilla muscorum*, *Catinella avara*, and *Vertigo elatior* (Black, 1970, Nekola unpublished data).

Conklin Quarry Site (18,100 to 16,700 ^{14}C yrs) – The Conklin Quarry site consists of full-glacial silts that fill an exposed swale in southeastern Iowa (Baker et al., 1986). The sediments contain an unusually diverse biota that includes pollen, bryophytes, plant macrofossils, mammals, molluscs, and insects. Radiocarbon ages from wood range between 16,710±270 and 18,090±190 ^{14}C yrs B.P. The collection of gastropods recovered from the deposits includes no less than sixteen of our targeted taxa!

4. Can species that avoid use of bedrock-derived carbon for shell construction be predicted based on their phylogeny, physical characteristics, or ecological range?

The 44 taxa targeted for ^{14}C measurements represent a wide cross-section of small North American land snails. Because these taxa span a wide range of phylogenies (representing most extant superfamilies) and habitats (ranging from moist tundra to humid subtropical forests to desert parkland) we propose to determine if levels of bedrock-sourced carbon incorporated during shell construction can be predicted based on these factors. The analyses proposed here will not only provide an important first-step in understanding land snail shell bioenergetics across a wide evolutionary and ecological range, but may also help identify factors that will help locate other candidate taxa for use in ^{14}C dating within and beyond North America. This will enable our findings to be made applicable to the global community of geochronologists and ecologists.

METHODS AND PROCEDURES

Field Collection

Although the great majority of modern shell material required for the above analyses currently resides in the collection of PI Nekola currently housed at the University of New Mexico, a few taxa have not been sampled adequately to allow for the planned analyses. For these, additional field sampling will be necessary in New England, the southeastern Coastal Plain, arctic Quebec, and/or arctic Alaska. Sampling of target populations across the extent of the North American arctic will also allow us to document the role of carbon from ancient organic sediments in shell construction. Additional material will be gathered by either collecting material from previously documented populations, or by locating new sites based upon previously noted ecological distribution patterns. In all cases, additional shells will be gathered via sieving soil detritus through a 3 mm mesh into a 0.75 mm mesh in the field, using methods outlined in Nekola (2005).

Modern gastropod shells

Gastropod shells will be broken, all adhering soft parts will be removed, and the shells will be treated with 6% NaOCl for 48-72 h to remove all remnants of organic matter. Shells will not be powdered during pretreatment to minimize the potential for adsorption of atmospheric ^{14}C

(SAMOS, 1949). We will selectively dissolve the shell carbonate by introducing it to dilute HCl for a few seconds to a few minutes, depending on the resistivity of the shell material, to remove secondary carbonate from primary shell material. Shell aragonite will then be converted to CO_2 using 100% H_3PO_4 under vacuum at 50°C. CO_2 will be extracted and purified using standard cryogenic techniques. CO_2 will be converted to graphite by catalytic reduction of CO (SLOTA et al., 1987) and submitted to the Arizona-NSF AMS facility for ^{14}C analysis.

Fossil gastropod shells

Gastropod shells will be collected in the field by excavation of the interstadial beds and wet sieving to ensure collection of suitable quantities of gastropod taxa for ^{14}C dating. Shells will be broken and examined under a dissecting microscope to ensure that the interior whorls are free of secondary carbonate and/or detritus. Fossil shell carbonate will then be processed in the same manner as the modern specimens.

PERSONNEL, QUALIFICATIONS, AND RESPONSIBILITIES

Jeffrey S. Pigati (PI). Pigati's research is focused primarily in ^{14}C geochronology (*in situ* cosmogenic ^{14}C and standard ^{14}C dating) and applying these techniques to construct records of Quaternary climate change. Pigati will direct the project and oversee the ^{14}C measurements of modern gastropods at the University of Arizona's Desert Laboratory.

Jason A. Rech (Co-PI). Rech's research is generally focused on Quaternary sediments and soils, and reconstructing Quaternary climate change. Rech also has a laboratory dedicated to ^{14}C dating and extensive experience with ^{14}C dating of organic material. Rech will co-direct the project with Pigati, and will oversee the collection and ^{14}C dating of fossil gastropod shells at his laboratory at Miami University.

Jeffrey C. Nekola (Co-PI). Nekola is a community and landscape ecologist specializing in North American terrestrial gastropods. Nekola will oversee the identification of modern and fossil gastropod taxa, as well as provide expertise on terrestrial gastropod ecology, taxonomy, and physiology that is essential for advancing our understanding of why some gastropods may be suitable for ^{14}C dating and others are not.

Graduate Student (Miami University). The primary roles of an unnamed graduate student will be to assist in field collection, sample preparation, and ^{14}C analysis of fossil gastropod shells.

Undergraduate Student (University of Arizona). The primary roles of an unnamed undergraduate student will be to assist in sample preparation and ^{14}C analysis of modern gastropod shells.

TIMELINE FOR PROPOSED WORK

Summer 2006	- Meet at the University of New Mexico to select specimens for ^{14}C dating from Nekola's collection of modern gastropods (Pigati, Rech, Nekola, graduate student). - Collect fossil shells from Oxford and Two Creeks beds (Rech, Pigati, graduate student). - Obtain shells from the Conklin Quarry site in the University of Iowa repository (Nekola). - Conduct additional field sampling of modern material to allow for adequate initial surveys for all target species via field work in the southeastern Coastal Plain, New England, and arctic Quebec at the Schefferville field station, operated by McGill University (Nekola). - Prepare modern gastropod shells for ^{14}C analysis (Pigati, undergraduate student).

(cont'd)	- Prepare fossil gastropod shells for ^{14}C analysis (Rech, graduate student).
Fall 2006	- Begin ^{14}C analyses of modern gastropods (Pigati, undergraduate student).
Spring 2007	- Begin ^{14}C analyses of fossil gastropods (Rech, graduate student).
Summer 2007	- Conduct field sampling in arctic Alaska at the Toolik Field Station, operated by the University of Alaska – Fairbanks to collect target tundra species (Nekola).
Fall 2007	- Second round of ^{14}C analyses of modern shells (Pigati, undergraduate student). - Second round of ^{14}C analysis of fossil shells (Rech, graduate student).
Spring 2008	- Prepare final results for publication and dissemination to the public .

INTELLECTUAL MERIT

Sound geochronology forms the basis of all research that relies on the interpretation and correlation of the fossil record. Radiocarbon dating of charcoal and well-preserved plant macrofossils has been used in countless studies to establish the chronology of deposits that are within the range of ^{14}C dating (<50 ka). When this material is absent, however, researchers generally rely on less reliable materials for ^{14}C dating, such as bulk organic sediments or soil organic matter. The quality of chronologies based on ^{14}C dating of these materials are often poor and preclude or confound correlation with other paleoenvironmental or paleoclimatic proxy records. The identification of a new material (small terrestrial gastropod shells) that yield ^{14}C ages that are as accurate as plant macrofossils and charcoal will be an extremely important addition to the relatively small list of materials that consistently yield robust ^{14}C ages. Among many potential applications in Quaternary research, ^{14}C dating of small terrestrial gastropod shells could be used to revolutionize our understanding of paleohydrologic conditions in the American Southwest, the Middle East, North and East Africa, Central and South America, and Australia since the last glacial maximum. Spring discharge deposits, which demarcate the position of past water tables on the landscape and are therefore sensitive to climate change, often contain fossil gastropod shells. Radiocarbon dating of these shells could be used to improve chronologic constraints for changes in water table elevations through time, which, in turn, would allow researchers to determine how hydrologic systems around the world responded to high-frequency climate variations, such as the Younger Dryas cold event and Dansgaard-Oeschger cycles. Similarly, improved temporal control of loess, alluvial, and glacial deposits would allow researchers to better understand the response these and other geomorphic systems to past climate change. Precise and accurate chronologic control is absolutely essential for such evaluations.
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BROADER IMPACTS

Broader impacts of the proposed research include the training (field collection, sample preparation, and laboratory techniques) of undergraduate and graduate students in geology, and the interdisciplinary collaboration between geologists and ecologists. Working with this broad array of scientists will expose the students to diverse scientific fields that could utilize the results from this study for different applications, including Quaternary geochronology, paleoclimatology, paleobiology, and paleoecology. Results will be disseminated to the scientific community through presentations at scientific meetings and through publication in both technical and non-technical journals. We will also produce a web-based guide that will lead geologists through the identification of gastropod shells that are suitable for ^{14}C dating. Results will be disseminated to the lay public via collaboration with the Education Division of the New Mexico Museum of Natural History and Science. Potential outreach materials include teaching guides regarding radioisotope dating, isotope measurement techniques, and the importance of geochronology in interpreting past and present biodiversity, climate, and landscapes.

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