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Research Paper

Radiocarbon dating of small terrestrial gastropod shells in North America

Jeffrey S. Pigati [a,*], Jason A. Rech [b], Jeffrey C. Nekola [c]

[a] U.S. Geological Survey, Denver Federal Center, Box 25046, MS-980, Denver CO 80225, USA
[b] Department of Geology, Miami University, Oxford, OH 45056, USA
[c] Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA

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ABSTRACT

Fossil shells of small terrestrial gastropods are commonly preserved in wetland, alluvial, loess, and glacial deposits, as well as in sediments at many archeological sites. These shells are composed largely of aragonite ($CaCO_3$) and potentially could be used for radiocarbon dating, but they must meet two criteria before their ^{14}C ages can be considered to be reliable: (1) when gastropods are alive, the ^{14}C activity of their shells must be in equilibrium with the ^{14}C activity of the atmosphere, and (2) after burial, their shells must behave as closed systems with respect to carbon. To evaluate the first criterion, we conducted a comprehensive examination of the ^{14}C content of the most common small terrestrial gastropods in North America, including 247 AMS measurements of modern shell material (3749 individual shells) from 46 different species. The modern gastropods that we analyzed were all collected from habitats on carbonate terrain and, therefore, the data presented here represent worst-case scenarios. In sum, ~78% of the shell aliquots that we analyzed did not contain dead carbon from limestone or other carbonate rocks even though it was readily available at all sites, 12% of the aliquots contained between 5 and 10% dead carbon, and a few (3% of the total) contained more than 10%. These results are significantly lower than the 20–30% dead carbon that has been reported previously for larger taxa living in carbonate terrain. For the second criterion, we report a case study from the American Midwest in which we analyzed fossil shells of small terrestrial gastropods (7 taxa; 18 AMS measurements; 173 individual shells) recovered from late-Pleistocene sediments. The fossil shells yielded ^{14}C ages that were statistically indistinguishable from ^{14}C ages of well-preserved plant macrofossils from the same stratum. Although just one site, these results suggest that small terrestrial gastropod shells may behave as closed systems with respect to carbon over geologic timescales. More work on this subject is needed, but if our case study site is representative of other sites, then fossil shells of some small terrestrial gastropods, including at least five common genera, *Catinella*, *Columella*, *Discus*, *Gastrocopta*, and *Succinea*, should yield reliable ^{14}C ages, regardless of the local geologic substrate.

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1. Introduction

Gastropods are one of the most successful animal groups on Earth, with at least 70,000 extant species occupying terrestrial, marine, and freshwater habitats. Globally, terrestrial gastropods encompass at least 35,000 species (Barker, 2001), span 4–5 orders of magnitude in shell volume, and represent a variety of trophic levels, including polyphagous detritivores, herbivores, omnivores, and carnivores (Kerney and Cameron, 1979; Burch and Pearce, 1990). They 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). It is clear, however, that the preference for terrestrial habitats of North American gastropods developed independently in three of six basal clades (Neritomorpha, Caenogastropoda, and Heterobranchia), with the informal group Pulmonata representing more than 99% of the continental fauna. Of the Pulmonata, the most common size class[1] in both modern and fossil assemblages are individuals with adult shells that are <10 mm in maximum dimension (Nekola, 2005) (Fig. 1).

[1] Size classes of gastropods are categorized by the maximum shell 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 in this study range from small to micro, for simplicity, we refer to them collectively as "small".

* Corresponding author. Tel.: +1 303 236 7870; fax: +1 303 236 5349.
E-mail address: jpigati@usgs.gov (J.S. Pigati).

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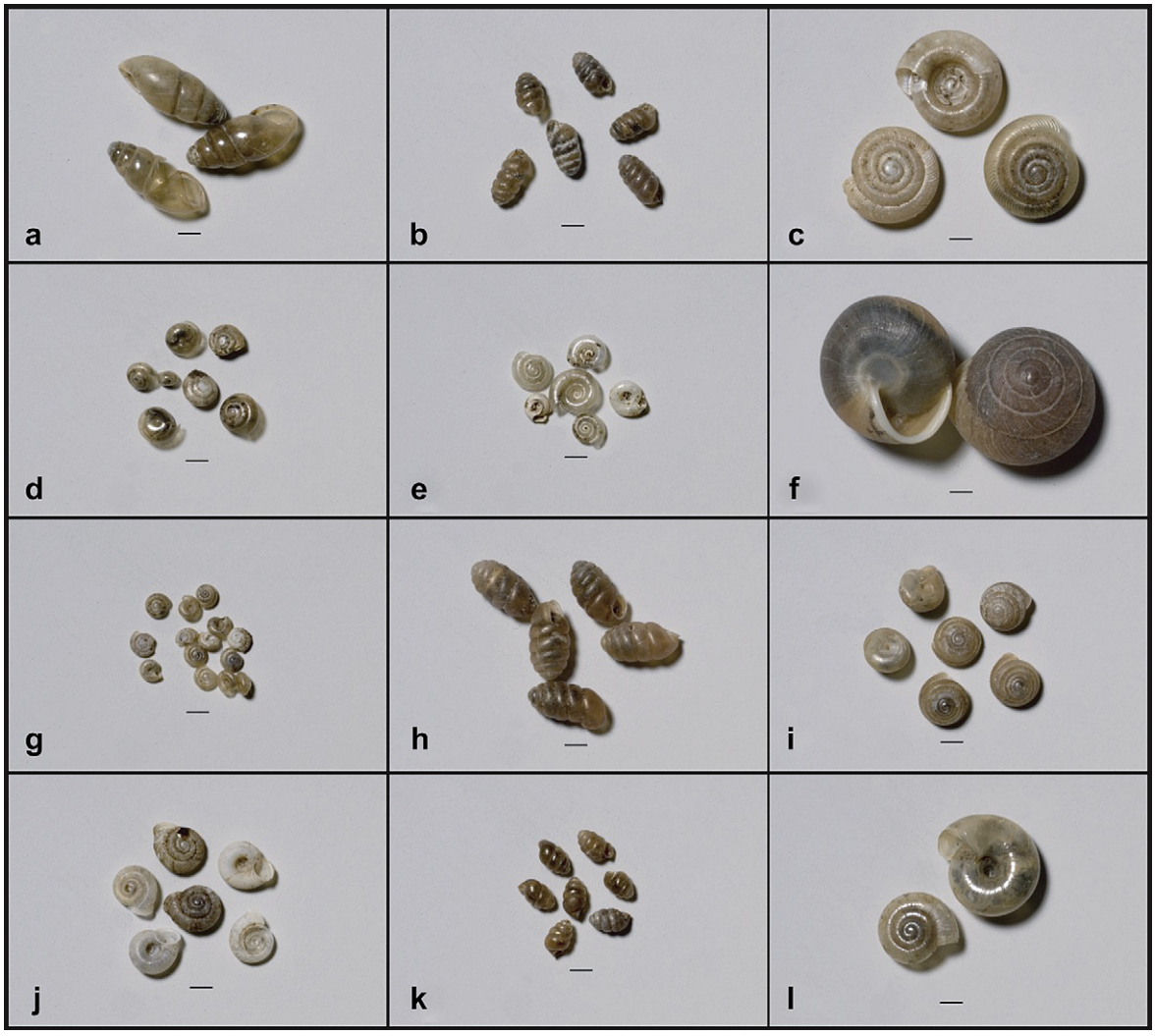

Fig. 1. Photographs of select small terrestrial gastropods included in this study (1 mm bar in each panel for scale). (a) *Cochlicopa lubricella*, (b) *Columella columella alticola*, (c) *Discus macclintockii*, (d) *Euconulus fulvus*, (e) *Hawaiia miniscula*, (f) *Hendersonia occulta*, (g) *Punctum minutissimum*, (h) *Pupilla muscorum*, (i) *Strobilops labyrinthica*, (j) *Vallonia gracilicosta*, (k) *Vertigo elatior*, and (l) *Zonitoides arboreus*.

Today, small terrestrial gastropods occupy and thrive in incredibly diverse habitats, from marshes, wet meadows, and grasslands to upland forests and tundra. Species are known from all continents, save Antarctica, and occupy almost all climate regimes except hyperarid deserts and the high Arctic. Their distribution in the fossil record is equally diverse. Gastropod shells are commonly preserved in wetland, alluvial, loess, and glacial deposits, as well as within sediments at archeological sites worldwide (e.g., Evans, 1972). But even though their distribution is widespread and their aragonitic shells contain ~12% by weight carbon, terrestrial gastropods are often avoided for ^{14}C dating because many taxa incorporate ^{14}C-deficient (or "dead") carbon from limestone and other carbonate rocks 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 ~3000 yrs too old.

Despite the Limestone Problem, geochronologists have continued to investigate the possibility of using terrestrial gastropod shells for ^{14}C dating because of their widespread occurrence and potential for dating Quaternary sediments. Most ^{14}C studies of gastropod shells have found that gastropods consistently incorporate dead carbon from limestone in their shells when it is available (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; Zhou et al., 1999; Quarta et al., 2007; Romaniello et al., 2008). These studies, however, were generally limited to a few individual gastropods collected from a small number of sites, and were biased toward large taxa and warm climates. Brennan and Quade (1997) analyzed a number of small terrestrial gastropod taxa and found that small shells generally yielded reliable ^{14}C ages for late-Pleistocene paleowetland deposits in the American Southwest. Pigati et al. (2004) followed by measuring the ^{14}C activities of a suite of small gastropods living in alluvium dominated by Paleozoic carbonate rocks in Arizona and Nevada and found that while some of the small gastropods did incorporate dead carbon from limestone when building their shells, others did not.

Based in part on these initial positive results, small terrestrial gastropod shells have been used recently to date Quaternary wetland and lacustrine deposits in the Americas (e.g., Pedone and Rivera, 2003; Placzek et al., 2006; Pigati et al., 2009). However, it is unclear if the results obtained from modern gastropods collected from a limited number of sites in the American Southwest can be extrapolated to all geologic, ecologic, and climatic environments. Moreover, it is not known if results for one taxonomic level (family, genus, or species) can be extrapolated to other members of the

same level living elsewhere, or even between individuals living within the same population.

Here we report the results of a comprehensive analysis of the Limestone Problem for small terrestrial gastropods from 163 localities in North America (Fig. 2). All samples that we analyzed were collected from habitats on carbonate terrain and, therefore, the data reported here represent worst-case scenarios. In addition, we measured the ^{14}C activities of a number of fossil shells recovered from well-dated sediments at a late-Pleistocene site in the American Midwest as a case study to determine if the shells remain closed systems with respect to carbon over geologic timescales. Positive results for both tests for a particular taxon would allow us to consider ^{14}C ages derived from fossil shells of that taxon to be reliable, regardless of the local geologic substrate.

2. Shell carbonate and ^{14}C dating

All materials (organic and 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 yrs ago was the same as the ^{14}C activity of the atmosphere T yrs ago (after accounting for isotopic fractionation). Second, after death, the material behaved as a closed system; carbon was neither added to nor removed from the sample material. If both of these criteria are met, then the measured ^{14}C activity is a function of only two parameters: the initial ^{14}C activity of the atmosphere and the amount of time elapsed since the death of the organism.

The measured ^{14}C activity and the ^{14}C age of the material are related by the familiar decay equation

$$A = A_o e^{-\lambda t} \quad (1)$$

where A and A_o are the measured and initial ^{14}C activities of the material, respectively, λ is the decay constant, and t is the time elapsed since the death of the organism. Conventional radiocarbon ages assume that the atmospheric ^{14}C activity is invariant through time (i.e., $A_o = 1$). Radiocarbon ages can be converted to calendar year ages to account for temporal variations in the ^{14}C activity of the atmosphere (Reimer et al., 2009).

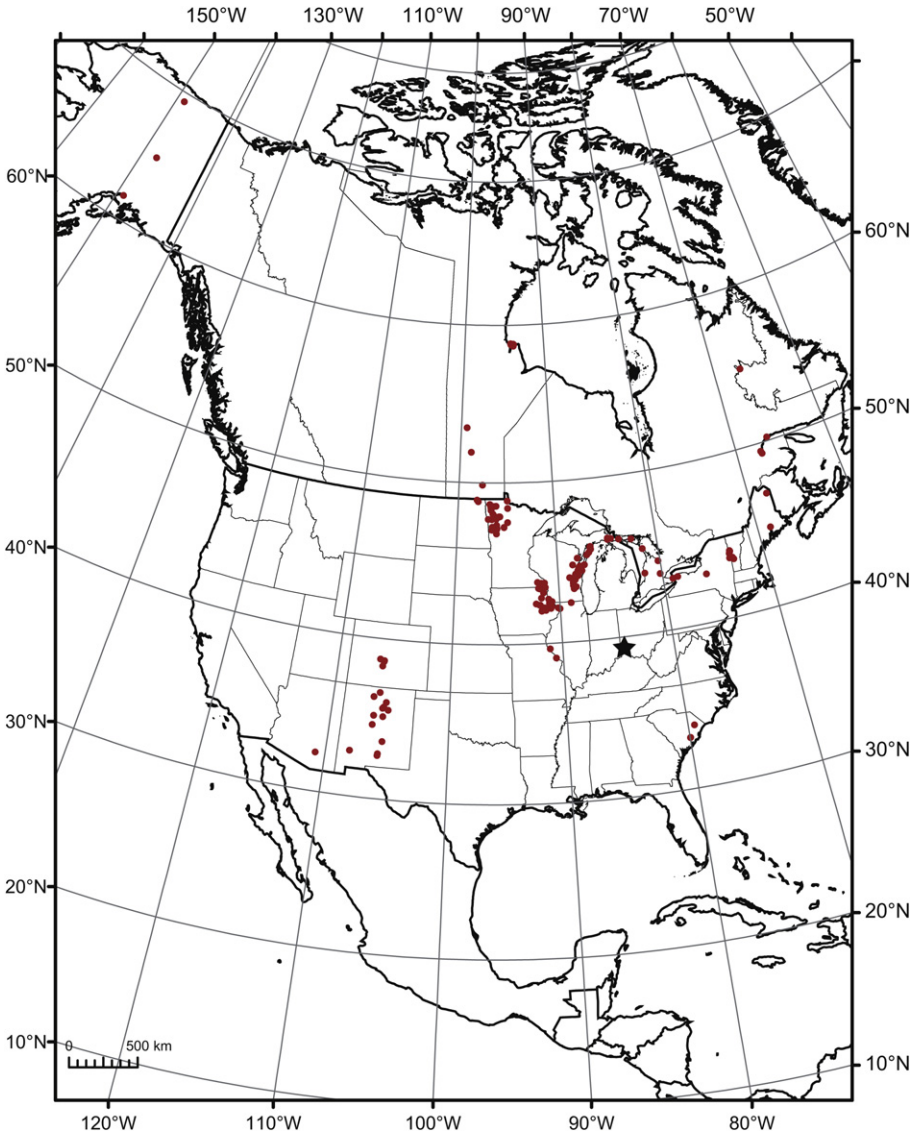

Fig. 2. Locations of modern localities (red dots) and the fossil locality at the Oxford East outcrops in southwestern Ohio (star). Modern localities and collection information are listed in Tables S1 and S2, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

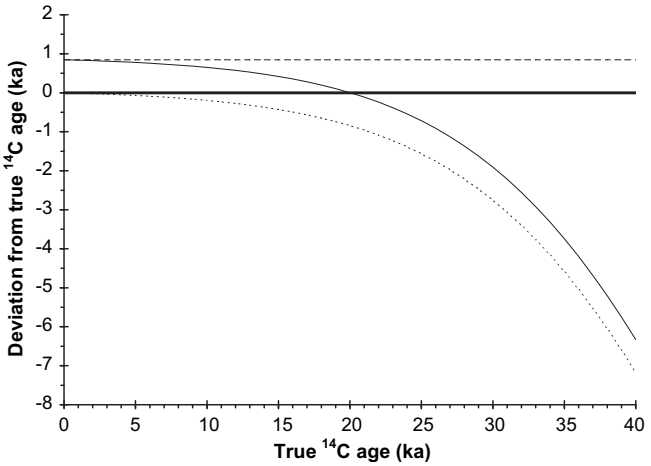

Fig. 3. Modeled deviation from the true ^{14}C age for four scenarios: (1) closed-system behavior and no dead carbon (thick solid line), (2) closed-system behavior and 10% dead carbon (dashed line), (3) open-system behavior equivalent to 1% modern carbon contamination and 10% dead carbon (thin solid line), and (4) open-system behavior equivalent to 1% modern carbon contamination and no dead carbon (dotted line).

2.1. Sources of shell carbon

In order to evaluate the validity of a ^{14}C age of a given sample, the ^{14}C contents of the original sources of the carbon and their contribution to the total carbon content must be known. Carbon in gastropod shell carbonate originates from as many as four different sources: atmospheric CO_2, food, water, and carbonate rocks.

Gastropods incorporate atmospheric CO_2 in their shell carbonate via respiration. Respired CO_2 is introduced to the bicarbonate pool in the gastropod's hemolymph and passed along to the extrapallial fluid, from which the shell carbonate is ultimately precipitated (Wilbur, 1972). Estimates of the contribution of atmospheric CO_2 to gastropod shell carbonate vary between negligible (Stott, 2002), 16–48% (Romaniello et al., 2008), and 30–60% (Goodfriend and Hood, 1983).

Carbon from food sources (e.g., living plants, fungi, organic detritus) 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 (Wilbur, 1972). 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 into the shell carbonate. Estimates of the amount of carbon derived from plants, either directly or indirectly through urea, vary between 25 and 40% (Goodfriend and Hood, 1983), 36–73% (Romaniello et al., 2008), and ~100% (Stott, 2002).

Terrestrial gastropods ingest water from multiple sources, including dew, soil moisture, standing water, and precipitation, 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. Pigati et al. (2004) found that aqueous carbon sources account for ~10% of the shell carbon for one species of *Catinella*, but it is not known if this value is constant across the entire Succineidae family. To our knowledge, data for other terrestrial taxa do not exist.

Finally, some terrestrial gastropods are able to scrape carbonate rocks (limestone, dolomite, soil carbonate), and ingest the powder or granules which then dissolve in their stomach acid to produce CO_2. As before, the dead carbon from the rocks is introduced to the hemolymph, passed on to the extrapallial fluid, and ultimately incorporated in the shell carbonate. Dead carbon from limestone can account for up to ~30% of the total carbon in shells of large terrestrial gastropods. (Goodfriend and Stipp, 1983).

2.2. Effects of carbon sources on ^{14}C ages of shell carbonate

In most environments, the ^{14}C activities of live plants are in equilibrium with atmospheric carbon. Gastropods that obtain their shell carbon from live plants and the air, therefore, should yield reliable ^{14}C ages, assuming they behave as closed systems after burial (Fig. 3). Gastropods that consume organic detritus (i.e., decaying plant litter) typically do not pose a significant problem for ^{14}C dating because the time between plant death, its incorporation into decomposition products, and consumption by gastropods is usually quite short, on the order of a few yrs.

The ^{14}C activity of water that is available for consumption by terrestrial gastropods (e.g., dew, standing water, precipitation) is at or near equilibrium with atmospheric ^{14}C and, therefore, water is unlikely to introduce a significant error to ^{14}C ages of terrestrial gastropod shells. Exceptions include gastropods living directly adjacent to springs that discharge waters from deeply-circulating carbonate aquifers, lakes or rivers with significant hard water effects, or in active volcanic areas where ^{14}C-deficient CO_2 in surface waters may be abundant (e.g., Riggs, 1984; Grosjean, 1994). ^{14}C ages of gastropods living in such areas should be evaluated carefully.

The incorporation of ^{14}C from limestone and other carbonate rocks can present a significant problem for ^{14}C dating of terrestrial gastropod shells. The ^{14}C activity of atmospheric carbon, plants, and water consumed by gastropods is essentially the same, ~100% modern carbon (pMC). In contrast, because most carbonate rocks are of pre-Quaternary age, their ^{14}C activity is typically 0 pMC. Thus, for ^{14}C dating, the magnitude of the potential error introduced by carbonate rocks is a direct function of the amount of carbon from rocks that is incorporated in the gastropod shell (Fig. 3). Unfortunately, a simple correction that accounts for the incorporation of ^{14}C-deficient carbon in gastropod shells 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 derived from terrestrial gastropod shells, it is imperative that we identify and avoid taxa that incorporate dead carbon from rocks altogether.

2.3. Open-system behavior

Even if some terrestrial gastropods consistently manage to avoid the Limestone Problem regardless of the local geologic substrate or environmental conditions, there is another hurdle that must be overcome before we can confidently use their shells for ^{14}C dating. That is, gastropod shells must remain closed systems with respect to carbon after burial. For reliable ^{14}C dating, 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, shells must resist the addition or exchange of ^{14}C atoms with the local environment. Shells that exhibit open-system behavior typically yield ^{14}C ages that are too young, and the magnitude of the error depends upon the degree of such behavior (Fig. 3).

Previous work has suggested that ^{14}C ages from small terrestrial gastropod shells recovered from fossil deposits in arid environments may be reliable back to at least ~30,000 ^{14}C yrs B.P., but a small degree of open-system behavior appears to compromise ^{14}C dates obtained from shells older than this (Pigati et al., 2009). In

Fig. 4. Photographs of the three genera of the Succineidae family: *Catinella* (left panels), *Oxyloma* (middle panels), and *Succinea* (right panels); all are ~10 mm in length. The simple shells of the three genera contain few diagnostic characteristics and, therefore, species-level identification is based on soft-body reproductive organ morphology, which is rarely preserved in the fossil record.

this study, we analyzed fossil shells from the American Midwest because of their abundance in Quaternary deposits in the region, the presence of multiple calcareous substrates (Paleozoic limestone, calcareous till, and loess), and the humid climate (annual precipitation in southwestern Ohio is ~100 cm yr^{-1}). If fossil shells exhibit even a small degree of open-system behavior in arid environments, it may be exacerbated and, therefore, more easily detected in humid environments where interaction between shells and DIC in ground water is more prevalent.

3. Methods

3.1. Live gastropods

Previous ecological sampling by one of us (JCN) has resulted in an extensive collection of modern terrestrial gastropods from North America, constituting ~250 taxa and over 470,000 individuals from more than 1000 modern environments. Gastropods were collected at each site from a representative 100–1000 m^2 area by hand collection of larger taxa and litter sampling of smaller taxa, which provides the most complete assessment of site faunas (Oggier et al., 1998; Cameron and Pokryszko, 2005). Collections were made at places of high mollusc density, such as loosely compacted leaf litter lying on top of highly compacted damp soil or humus (Emberton et al., 1996). Litter was removed by hand and sieved by shaking, tapping, or other agitation in the field using a shallow sieve (ASTME #10; 2.0 mm mesh) nested inside a second sieve (ASTME #30; 0.6 mm mesh). The process was continued for 15–60 min during which time 50–500 mg of material was collected and retained.

Gastropods and detritus were dried at room temperature in the laboratory and then hand-picked against a neutral background. All shells, shell fragments, and slug plates were removed and identifiable material was assigned to species using JCN's reference collection. Nomenclature generally follows that of Hubricht (1985) with updates and corrections by Nekola (2004).

We selected 247 aliquots of shell material (3749 individual shells) from 163 sites across the United States and southern Canada for ^{14}C analysis. Nearly all of the specimens that we chose for analysis were collected live, but at a few sites, only recently-dead gastropods were available, which were identified by a translucent appearance or the retention of color in the shells. Shells of small gastropods that are dead for more than a year or so become increasingly white and opaque with time (J. Nekola, unpublished data), and were excluded from our study.

In the fossil record, species-level identification of fossil shells is possible for most small terrestrial gastropods and, therefore, the results of our investigation of modern gastropods can be applied directly to the fossil record. An exception is the Succineidae family, which is composed of three genera (*Catinella*, *Oxyloma*, and *Succinea*) that are difficult to differentiate in modern faunas, let alone the geologic record (Fig. 4). Their simple shells exhibit few diagnostic characteristics and, therefore, species-level identification is based on soft-body reproductive organ morphology, which is rarely preserved in the fossil record. This presents a significant problem for geochronologists; that is, can we be confident in ^{14}C ages derived from shells from any taxon within the Succineidae family, or do we need to target a specific genus or species? To address this issue, we measured the ^{14}C activity of 100 aliquots of gastropod shell material (802 individual shells) for twelve species of the Succineidae family to determine the level of identification (i.e., family, genus, or species) required to apply our results to the fossil record.

We prepared aliquots of modern shell material for ^{14}C analysis at the University of Arizona Desert Laboratory (JSP) and Miami University (JAR). We selected multiple shells at random for X-ray diffraction (XRD) analysis using a Siemens Model D-500 diffractometer to verify that only shell aragonite remained prior to preparation for ^{14}C analysis. There was no evidence of primary or secondary calcite in any of the shells that we analyzed. When possible, shells were broken, the adhering soft parts were removed using forceps, and the shells were treated with 6% NaOCl for 18–24 h at room temperature to remove all remnants of organic matter. Shells were not powdered during pretreatment to minimize the potential for adsorption of atmospheric ^{14}C (Samos, 1949). We selectively dissolved some of the shells by briefly introducing dilute HCl to remove secondary carbonate (dust) from primary shell material. Shells were washed repeatedly in ASTM Type 1, 18.2 MΩ (hereafter "ultrapure") water, sonicated for a few seconds to remove adhered solution, washed again with ultrapure water, and dried in a vacuum oven overnight at ~70 °C.

Shell aragonite was converted to CO_2 using 100% H_3PO_4 under vacuum at either 50 or 75 °C until the reaction was visibly complete (~1 h). Water, SO_x, NO_x, and halide species were removed using passive Cu and Ag traps held at ~600 °C and the resulting CO_2 was split into two aliquots. One aliquot was converted to graphite by catalytic reduction of CO (modified after Slota et al., 1987) and submitted to the Arizona-NSF Accelerator Mass Spectrometry (AMS) facility for ^{14}C analysis. The second aliquot was submitted for $\delta^{13}C$ analysis in order to correct the measured ^{14}C activity of the shell carbonate for isotopic fractionation.

^{14}C data for modern gastropods are presented as $\Delta^{14}C$ values in per mil (Stuiver and Polach, 1977; Reimer et al., 2004) and analytical uncertainties are reported at the 2σ (95%) confidence level. $\delta^{13}C$ values are given in the usual delta (δ) notation as the per mil deviation from the VPDB standard. Analytical uncertainties for $\delta^{13}C$ measurements are less than 0.1‰ based on repeated measurements of standards.

We also measured the ^{14}C content of several gastropod bodies for comparison to their corresponding shells. The bodies were treated with 10% HCl for 15–30 min to remove any remnants of the carbonate shell, rinsed repeatedly, and dried in a vacuum oven at

~70 °C. The dried bodies were placed in 6 mm quartz tubes along with ~100 mg of cupric oxide (CuO) and a small piece (1 mm × 5 mm) of silver foil, all of which were pre-combusted at 900 °C for 4–6 h. The tube was evacuated, sealed with a glass-blower's torch, and combusted offline at 900 °C. The resulting CO_2 gas was isolated and converted to graphite as above.

3.2. Modeling of ^{14}C values of gastropod diets

To quantify the amount of carbon in a gastropod shell that was derived from limestone or other carbonate rocks, it is necessary to compare the measured $\Delta^{14}C$ values of shells with $\Delta^{14}C$ values of the gastropod diet. $\Delta^{14}C$ values of live plants consumed by gastropods are identical to $\Delta^{14}C$ values of the atmosphere (Fig. 5a), which were calculated using ^{14}C data averaged over the Northern Hemisphere (Hua, 2004). We assigned a 5‰ uncertainty to the atmospheric values to account for short-term, regional variations (Hsueh et al., 2007) and small changes in atmospheric ^{14}C values that occur at a given site during the short (usually annual) lifespan of the small gastropods (Manning et al., 1990; Meijer et al., 1995).

Plant detritus from previous years' primary production has a higher ^{14}C activity than live plants because of the ^{14}C "bomb-spike" (Hua, 2004). Simply comparing the $\Delta^{14}C$ values of shells with the $\Delta^{14}C$ of the atmosphere or live plants during the year that the gastropod was alive, therefore, would ignore the potential impact of detritus in the gastropod diet. We estimated the amount of detritus from a given year that was available for consumption using a wide range of carbon turnover rates (0.2–0.002 yr^{-1}; Fig. 5b), which are applicable to O horizons and the upper few centimeters of A horizons in which small terrestrial gastropods typically live (Guadinski et al., 2000; Torn et al., 2005; Brovkin et al., 2008). We intentionally chose a wide range of carbon turnover rates, which are equivalent to mean residence times for carbon of 5–500 yrs, to encompass the potentially wide range of detritus ages at the 163 localities included in our study. We then used Monte Carlo simulation to generate 10,000 values for the $\Delta^{14}C$ of the gastropod diets for each of the past 13 yrs (the time span of our collections), which allowed two factors to vary randomly: the carbon turnover rate (0.2–0.002 yr^{-1}) and the age of the detritus fraction included in the diet (range of 0–1000 yrs). We also ran simulations in which we let the age of the detritus vary up to 10,000 yrs, but the results did not change significantly.

We took the average and standard deviation of the 10,000 generated values as the gastropod diet $\Delta^{14}C$ value for each year of collection between 1996 and 2008 (Fig. 5c). All uncertainties are reported at the 2σ (95%) confidence level. As expected, the modeled $\Delta^{14}C$ value of the gastropod diet for a given year is slightly higher than the atmospheric $\Delta^{14}C$ value for the same year. Uncertainties associated with the modeled values are relatively large, on the order of ~35%, because of the large range of detritus $\Delta^{14}C$ values that could be present at a given site.

Shells with $\Delta^{14}C$ values that are lower than the modeled $\Delta^{14}C$ value of the gastropod diet during the year in which the gastropod was alive indicate the presence of dead carbon from limestone or other carbonate rocks. When applicable, the difference between the $\Delta^{14}C$ values was converted into ^{14}C yrs to estimate the "limestone effect", which represents the potential error introduced by the incorporation of dead carbon in the shells. The magnitude of the limestone effect should be considered a maximum value because the calculation assumes that all of the dead carbon came from carbonate rocks, rather than older (but not infinitely-aged) organic matter. Because of the uncertainties associated with modeling the $\Delta^{14}C$ of the gastropod diet, we are unable to discern limestone effects smaller than ~300 ^{14}C yrs.

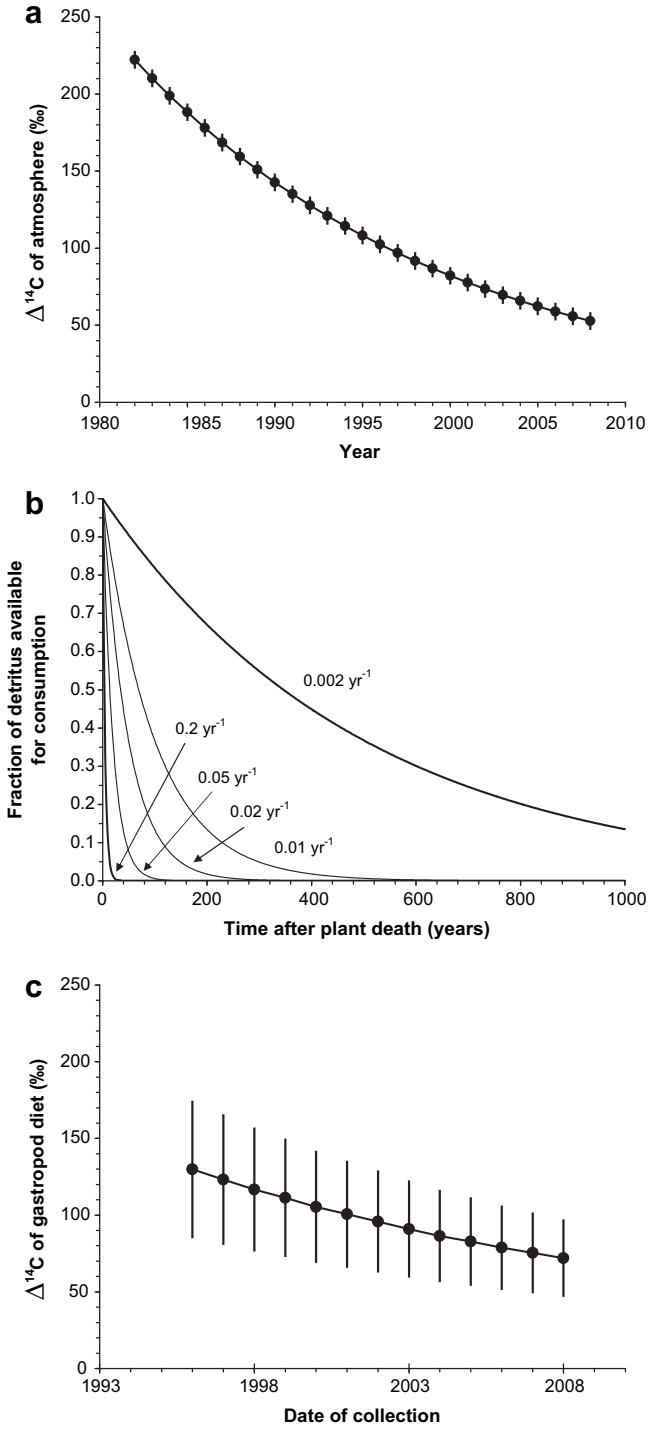

Fig. 5. Modeling results for (a) the ^{14}C activity of the gastropod diet using measured atmospheric values for the northern hemisphere (after Hua, 2004), (b) carbon turnover rates (CTRs) ranging from 0.2 to 0.002 yr^{-1}, and (c) Monte Carlo simulation to generate estimates of the $\Delta^{14}C$ values of gastropod diets for each of the past 13 yrs.

3.3. Fossil gastropods

Fossil gastropod shells were collected from glacial deposits at the Oxford East glacial outcrops in southwestern Ohio as a case study to determine if the shells remain closed systems with respect to carbon over geologic timescales. These 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-rich silt that contain gastropods, plant macrofossils, and rooted tree stumps. AMS ^{14}C dating of plant macrofossils and *in situ* tree stumps has shown that the age of this unit is between ~20,100 and 21,400 ^{14}C yrs B.P. (Eckberg et al., 1993; Lowell, 1995). Gastropod taxa identified previously from this unit include *Columella columella*, *Discus cronkhitei*, *Euconulus fulvus*, *Hendersonia occulta*, *Pupilla muscorum*, *Vertigo elatior*, and multiple Succineidae taxa (Dell, 1991).

Gastropod-bearing sediment was collected and placed in deionized water with a deflocculant for several days to soften the sediment enough to pass through a 0.5 mm sieve. A few samples were placed in an ultrasonic bath for ~1 h to further disaggregate the sediment. Fossil shells were hand-picked from the retained fraction, placed in a beaker of ultrapure water, subjected to an ultrasonic bath for a few seconds, and then repeatedly dunked in a second beaker of ultrapure water to remove sediment that adhered to the shell surface or was lodged within the shell itself. The recovered shells were broken and examined under a dissecting microscope to ensure that the interior whorls were free of secondary carbonate and detritus. Fossil shells that were free of detritus were then processed for ^{14}C in the same manner as the modern specimens, including random selection of shells for XRD analysis. None of the fossil shells that we analyzed contained measurable quantities of either primary or secondary calcite.

Organic samples, which included bark, charcoal, plant fragments, and wood, were subjected to a standard acid–base–acid (ABA) chemical pretreatment with 1N HCl (1 h at 60 °C), 1N NaOH (18–24 h at 60 °C), and 1N HCl again (2–4 h at 60 °C) before combustion at 900 °C in the presence of cupric oxide and silver foil. The resulting CO_2 was purified and converted to graphite in the same manner as above.

Conventional radiocarbon ages are reported in ^{14}C yrs and, after calibration, in calendar yrs. For calibration, we used the IntCal09.14C dataset (CALIB 6.0.0, Stuiver and Reimer, 1993; Reimer et al., 2009).

4. Results

4.1. Modern shells

A few aliquots (11 of 247, or 4.5% of the total) yielded Δ^{14}C values that were higher than the modeled dietary Δ^{14}C values of the corresponding year of collection, which indicates these individuals consumed unusually high amounts of bomb-spike carbon (Table S1, Fig. 6). Data from these shells were excluded from further analysis. For the remaining 236 aliquots of gastropod shells from the 46 different species that we analyzed, ~78% did not contain any dead carbon from limestone or other carbonate rocks even though it was readily available at all sites, ~12% contained between 5 and 10% dead carbon, and a few (3% of the total) contained more than 10% (Table S1, Fig. 6). Δ^{14}C values for all taxa ranged from −97.5 to 158.4‰, and limestone effects averaged only ~180 ^{14}C yrs.

Dead carbon was not detected in the shells of at least 23 different species, including (number of shells in parentheses) *Catinella avara* (99), *Catinella gelida* (66), *Catinella vermeta* (39), *Cochlicopa lubricella* (17), *Cochlicopa morseana* (16), *Columella columella* (94), *Discus catskillensis* (40), *Discus cronkhitei* (47), *Discus macclintockii* (5), *Euconulus alderi* (71), *Euconulus polygyratus* (57), *Gastrocopta pentodon* (131), *Nesovitrea binneyana* (46), *Punctum minutissimum* (542), *Pupilla hebes* (7), *Strobilops affinis* (36), *Succinea bakeri* (27), *Succinea grosvernori* (1), *Succinea* n. sp. 'Minnesota A' (1), *Succinea ovalis* (50), *Succinea strigata* (14), *Vertigo hubrichti* (144), and *Vertigo modesta* (73).

Δ^{14}C values were most negative (i.e., contained the most dead carbon) for shells from the *Pupilla* and *Vallonia* genera. Maximum limestone effects for these genera ranged from 780 ± 310 ^{14}C yrs for *P. muscorum* to 1590 ± 280 ^{14}C yrs for *P. sonorana*, and from 1010 ± 380 ^{14}C yrs for *Vallonia perspectiva* to 1500 ± 270 ^{14}C yrs for *V. cyclophorella*, respectively (Table 1). The only other species that exhibited a limestone effect that was greater than 1000 ^{14}C yrs was *H. occulta* (1210 ± 250 ^{14}C yrs).

These results can be applied directly to the fossil record if it is possible to identify the taxa to the species-level based on shell morphology. For the Succineidae family, the data must be evaluated at the family or genus level to be applicable. Taking the Succineidae family as a whole, 85% of the shell aliquots that we analyzed did not contain measurable amounts of dead carbon; the remaining aliquots contained an average of 5.2% dead carbon. Within the family, Δ^{14}C values for the genus *Catinella* ranged from 63.7 to 147.0‰, *Oxyloma* values ranged from −0.8 to 135.0‰, and *Succinea* values ranged from 16.1 to 147.8‰. Members of the *Catinella* genus incorporate little, if any, dead carbon from limestone or other carbonate rocks in their shells; 32 of 33 aliquots (97%) of *Catinella* shells did not contain measurable amounts of dead carbon. The remaining sample (DL-170) contained only a very small amount of dead carbon, equivalent to a limestone effect of 320 ± 310 ^{14}C yrs. Similarly, 36 of 39 aliquots (92%) of *Succinea* shells did not contain dead carbon. The remaining three aliquots were all *Succinea indiana*; limestone effects for these shells ranged from 430 ± 370 to 610 ± 380 ^{14}C yrs. For *Oxyloma*, 15 of 24 aliquots (63%) did not contain measurable amounts of dead carbon. Limestone effects for the remaining samples ranged between 250 ± 210 and 670 ± 240 ^{14}C yrs.

4.2. Modern gastropod bodies

We also measured the ^{14}C activity of the bodies of eight gastropods to determine the magnitude of the offset between the body carbon and shell carbonate (Table 2). Ideally, we would have preferred to measure the ^{14}C content of the extrapallial fluid to compare with the shell carbonate to determine if carbon isotopes are fractionated when the shells are formed, but this was not feasible because the gastropod bodies were simply too small. Regardless, the measured Δ^{14}C values of gastropod body carbon ranged from 42 to 101‰, similar to the Δ^{14}C values of shell carbonate from the same sites, which ranged from 43 to 133‰. However, we did not observe a clear relation between the ^{14}C activity of gastropod body carbon and shell carbonate. Δ^{14}C values of bodies of *Oxyloma retusa* collected from Maquokata River Mounds, Iowa were indistinguishable from the Δ^{14}C values of their corresponding shells ($\Delta^{14}C_{body}$ = 42 ± 6‰, $\Delta^{14}C_{shell}$ = 43 ± 10‰), as were values for *S. ovalis* from Dave Pepin Homestead, Minnesota ($\Delta^{14}C_{body}$ = 101 ± 8‰, $\Delta^{14}C_{shell}$ = 110 ± 8‰). In contrast, Δ^{14}C values for bodies of *S. ovalis* were significantly lower than their shells from Brewer Boat Ramp, Maine ($\Delta^{14}C_{body}$ = 55 ± 6‰, $\Delta^{14}C_{shell}$ = 82 ± 5‰) and Zippel Bay State Park, Minnesota ($\Delta^{14}C_{body}$ = 84 ± 6‰, $\Delta^{14}C_{shell}$ = 133 ± 12‰). The reason(s) for this difference is unclear.

4.3. Fossil shells

Well-preserved fossil organic material (bark, plant macrofossils, and wood) recovered from sediments at the Oxford East outcrops yielded calibrated ages that ranged from 24.60 ± 0.40 to 25.28 ± 0.55 ka, with an average of 24.93 ± 0.30 ka (n = 5; Table 3, Fig. 7). Gastropod shells recovered from the same stratigraphic unit yielded ages that ranged from 23.92 ± 0.66 to 25.81 ± 0.94 ka, and averaged 24.73 ± 0.44 ka (n = 18). Average ages of six of the seven fossil taxa were indistinguishable from the average age of the organic matter: *Discus shimeki* (24.80 ± 0.17 ka; n = 3), *P. muscorum* (24.34 ± 0.32 ka; n = 3), *Vallonia gracilicosta* (24.20 ± 0.40 ka; n = 2), *Vertigo hannai* (24.90 ± 0.77 ka; n = 1), *V. modesta*

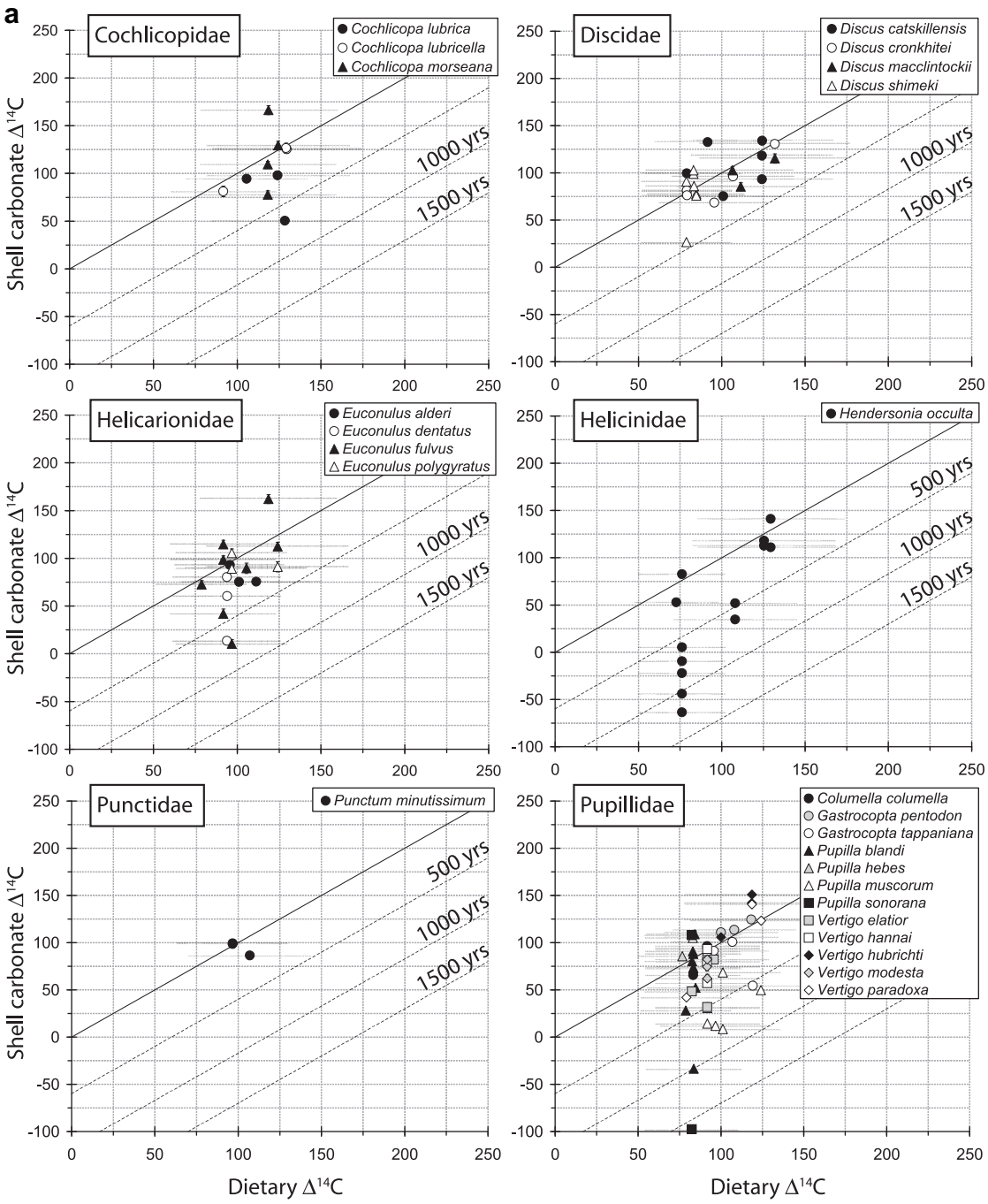

Fig. 6. Shell carbonate $\Delta^{14}C$ values compared to modeled dietary $\Delta^{14}C$ values for modern gastropods. Data points that fall on the solid black line in each panel represent gastropods that obtained their carbon from live plants and the atmosphere. Data points that fall below the solid line indicate that dead carbon from limestone or other carbonate rocks was incorporated during shell construction. The magnitude of this phenomenon, called the "limestone effect", depends upon the amount of shell carbon that was derived from rocks as shown by the dashed lines.

(24.86 ± 0.32 ka; $n = 3$), and Succineidae (25.29 ± 0.54 ka; $n = 3$). The average age of *H. occulta* (24.34 ± 0.15 ka; $n = 3$) was slightly younger than the organic ages.

5. Discussion

5.1. Small terrestrial gastropods and the limestone problem

Approximately 78% of the modern shells that we analyzed did not contain any dead carbon from limestone or other carbonate rocks even though it was readily available at all sites, ~12% of the aliquots contained between 5 and 10% dead carbon, and a few (3% of the total) contained more than 10%. Even at the high end, the amount of dead carbon in the small shells is significantly less than the 20–30% dead carbon that has been previously reported for larger taxa (e.g., Goodfriend and Stipp, 1983).

If we extrapolate our results to the fossil record and assume that the shells behave as closed systems with respect to carbon over geologic timescales, then small terrestrial gastropod shells should provide accurate ^{14}C ages ~78% of the time and ages that are

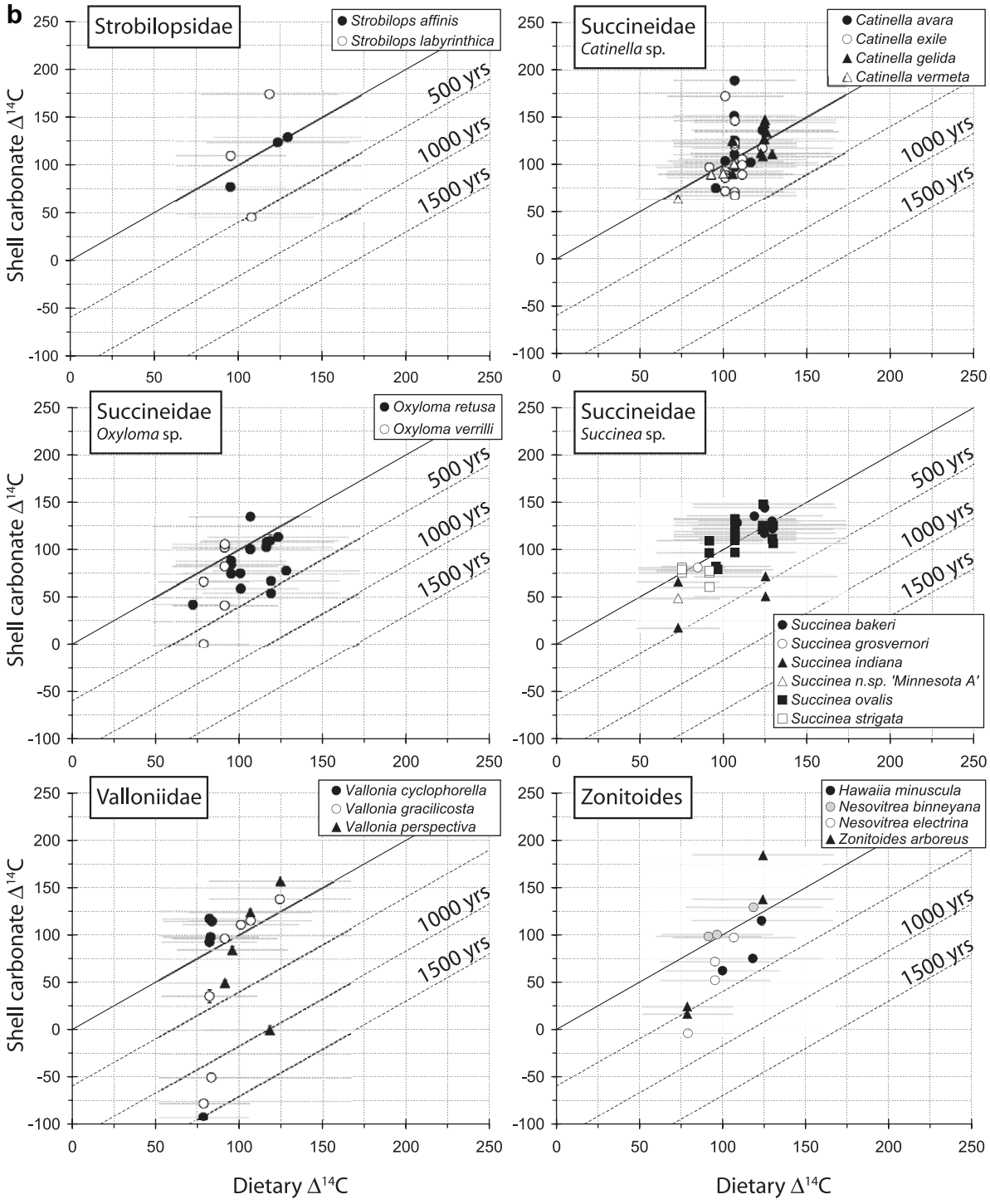

Fig. 6. (*continued*).

within ~1000 ^{14}C yrs of the true age ~97% of the time. Shells from at least 23 different species did not contain dead carbon, and therefore should yield reliable ^{14}C ages if the modern shell data can be applied directly to the fossil record.

For the Succineidae family as a whole, 85% of the shell aliquots that we analyzed did not contain measurable amounts of dead carbon; the remaining aliquots contained an average of 5.2% dead carbon, equivalent to a limestone effect of 425 ^{14}C yrs. At the genus level, shells of the genus *Catinella* should yield reliable ^{14}C ages ~97% of the time, again assuming closed-system behavior, and ages that are within ~300 ^{14}C yrs of the true age every time. Similarly, *Succinea* shells should yield reliable ^{14}C ages ~92% of the time and ages that are within ~600 ^{14}C yrs of the true age every time. Results for the genus *Oxyloma* suggest that some caution should be used when evaluating ^{14}C ages derived from these shells. AMS results for the *Oxyloma* shells show that nearly 1 in 3 aliquots contained at least some dead carbon. Although the amount was relatively minor, <7% of the total, dead carbon was present in *Oxyloma* shells more frequently than in either *Catinella* or *Succinea* shells.

Table 1
Summary of ^{14}C results for modern gastropod shells.

Family	Genus	Species	Aliquots	Shells	Limestone effect[a] (^{14}C yrs)	
					Negligible[b]	Maximum[c]
Cochlicopidae	*Cochlicopa*	*Cochlicopa lubrica*	3	17	53%	650 ± 390
		Cochlicopa lubricella	3	17	100%	–
		Cochlicopa morseana	4	16	100%	–
Discidae	*Discus*	*Discus catskillensis*	6	40	100%	–
		Discus cronkhitei	6	47	100%	–
		Discus macclintockii	3	5	100%	–
		Discus shimeki	7	33	97%	430 ± 240
Helicarionidae	*Euconulus*	*Euconulus alderi*	3	71	100%	–
		Euconulus dentatus	3	34	68%	670 ± 290
		Euconulus fulvus	8	107	57%	730 ± 300
		Euconulus polygyratus	3	57	100%	–
Helicinidae	*Hendersonia*	*Hendersonia occulta*	13	13	46%	1210 ± 250
Punctidae	*Punctum*	*Punctum minutissimum*	3	542	100%	–
Pupillidae	*Columella*	*Columella columella*	3	94	100%	–
	Gastrocopta	*Gastrocopta pentodon*	3	131	100%	–
		Gastrocopta tappaniana	3	105	92%	540 ± 360
	Pupilla	*Pupilla blandi*	9	90	67%	1000 ± 270
		Pupilla hebes	1	7	100%	–
		Pupilla muscorum	8	80	38%	780 ± 310
		Pupilla sonorana	2	29	66%	1590 ± 280
	Vertigo	*Vertigo elatior*	3	113	38%	500 ± 280
		Vertigo hannai	3	123	65%	280 ± 270
		Vertigo hubrichti	3	144	100%	–
		Vertigo modesta	3	73	100%	–
		Vertigo paradoxa	3	124	74%	380 ± 240
Strobilopsidae	*Strobilops*	*Strobilops affinis*	3	36	100%	–
		Strobilops labyrinthica	3	43	65%	520 ± 320
Succineidae	*Catinella*	*Catinella avara*	9	99	100%	–
		Catinella exile	15	316	97%	320 ± 310
		Catinella gelida	9	66	100%	–
		Catinella vermeta	4	39	100%	–
	Oxyloma	*Oxyloma retusa*	17	136	65%	540 ± 360
		Oxyloma verrilli	7	47	57%	670 ± 240
	Succinea	*Succinea bakeri*	8	27	100%	–
		Succinea grosvernori	1	1	100%	–
		Succinea indiana	4	6	17%	610 ± 380
		Succinea n.sp. 'Minnesota A'	1	1	100%	–
		Succinea ovalis	19	50	100%	–
		Succinea strigata	6	14	100%	–
Valloniidae	*Vallonia*	*Vallonia cyclophorella*	6	129	95%	1500 ± 270
		Vallonia gracilicosta	7	155	60%	1370 ± 270
		Vallonia perspectiva	5	221	68%	1010 ± 380
Zonitidae	*Hawaiia*	*Hawaiia minuscula*	3	152	29%	340 ± 270
	Nesovitrea	*Nesovitrea binneyana*	3	46	100%	–
		Nesovitrea electrina	4	33	73%	710 ± 240
	Zonitoides	*Zonitoides arboreus*	4	20	85%	530 ± 240

[a] Defined as the theoretical difference between the measured and true ^{14}C ages for gastropods that incorporate the same amount of dead carbon in their shells as the aliquots measured here. These values are based on the difference between the modeled diet and shell carbonate $\Delta^{14}C$ values and converted into ^{14}C yrs.
[b] Percent of shells measured by AMS that did not contain dead carbon from limestone or other carbonate rocks (i.e., the $\Delta^{14}C$ values for the shells were statistically indistinguishable from the modeled diet $\Delta^{14}C$ value).
[c] Maximum limestone effect for a given taxon (given in ^{14}C yrs). Uncertainties are given at the 2σ (95%) confidence level.

5.2. Ca-limiting hypothesis

Large gastropod shells (>20 mm in maximum dimension) routinely contain 20–30% dead carbon when living in habitats on carbonate terrain (e.g., Evin et al., 1980; Goodfriend and Stipp, 1983), whereas the small shells measured in this study rarely contained more than ~10%. We speculate that calcium may hold the clues to determining the reasons for the difference. Gastropod shell carbonate (aragonite) is composed of three elements – calcium, carbon, and oxygen. The latter two elements are readily available in the environments in which gastropods live and, therefore, cannot be considered as possible limiting factors for shell construction. In most settings, however, calcium is present in plants and water in low concentrations (typically parts per million). If small terrestrial gastropods can acquire enough calcium from their "normal" diet (plants, detritus, and water), then they may not have to consume carbonate rocks to supplement their calcium intake when building their shells. Larger taxa may find it more difficult to obtain enough calcium from these sources without turning to carbonate rocks when they are available.

Our results support this hypothesis, but only on a gross scale. There is clearly a significant difference in the amount of dead carbon incorporated in the shells of large taxa previously studied and the small taxa studied here. However, shell size alone is not the only factor to consider when evaluating the results within the small body size class. For example, in the present study, we did not observe a significant correlation between shell size and measured $\Delta^{14}C$ values ($R^2 = 0.015$). The largest taxon that we included in our analysis, *H. occulta*, averaged 15.6 mg per shell and contained approximately the same amount of dead carbon as *P. muscorum* and *Vallonia* shells, which averaged only 1.4 and 0.7 mg per shell, respectively. Similarly, we did not find a clear correlation between shell size and measured $\Delta^{14}C$ values even within a single family. For Succineidae, *Catinella* shells were generally the smallest, averaging 1.1 mg per shell and contained the least amount of dead carbon, and

Table 2
^{14}C results for modern gastropod bodies and corresponding shells.

Lab #	AA #	Taxon	Site[a]	Lat (°N)	Long (°W)	Mass (mg)	δ^{13}C (vpdb)	$F^{14}C$[b]	Shell Δ^{14}C	Atmos Δ^{14}C	Diet Δ^{14}C	Limestone Effect[c] (^{14}C yrs)
Bodies												
MU-109	80177	*Succinea ovalis*	1	44.819	68.723	4.22	−24.9	1.0547 ± 0.0064	55 ± 6	70 ± 5	96 ± 33	330 ± 280
MU-114	80181	*Succinea ovalis*	2	48.410	94.819	8.64	−24.8	1.0996 ± 0.0082	101 ± 8	80 ± 5	107 ± 36	50 ± 300
MU-108	80176	*Succinea ovalis*	3	48.906	96.027	3.79	−25.1	1.0946 ± 0.0062	96 ± 6	80 ± 5	107 ± 36	90 ± 300
MU-111	80178	*Succinea ovalis*	4	47.874	96.422	11.05	−26.0	1.0877 ± 0.0062	89 ± 6	80 ± 5	107 ± 36	150 ± 300
MU-117	80183	*Oxyloma retusa*	5	42.559	90.713	9.04	−26.1	1.0419 ± 0.0064	42 ± 6	52 ± 5	73 ± 25	250 ± 210
MU-115	80182	*Succinea ovalis*	6	50.264	66.411	12.88	−25.0	1.0485 ± 0.0072	49 ± 7	57 ± 5	79 ± 27	250 ± 230
MU-112	80179	*Succinea strigata*	7	64.858	147.862	4.01	−24.2	1.0740 ± 0.0060	74 ± 6	54 ± 5	75 ± 26	0 ± 210
MU-113	80180	*Succinea ovalis*	8	48.866	94.843	6.88	−23.5	1.0833 ± 0.0060	84 ± 6	80 ± 5	107 ± 36	180 ± 300
Shells												
MU-162	80928	*Succinea ovalis*	1	44.819	68.723	8.80	−10.0	1.0817 ± 0.0048	82 ± 5	70 ± 5	96 ± 33	110 ± 270
MU-128	80194	*Succinea ovalis*	2	48.410	94.819	11.72	−9.8	1.1090 ± 0.0084	110 ± 8	80 ± 5	107 ± 36	0 ± 300
MU-179	80942	*Oxyloma retusa*	5	42.559	90.713	13.08	−11.0	1.0425 ± 0.0100	43 ± 10	52 ± 5	73 ± 25	250 ± 220
MU-141	80910	*Succinea ovalis*	8	48.866	94.843	8.91	−9.6	1.1316 ± 0.0116	133 ± 12	80 ± 5	107 ± 36	0 ± 300

Uncertainties are given at the 2σ (95%) confidence level.
[a] Key to sites: 1 = Brewer Boat Ramp, Maine; 2 = Dave Pepin Homestead, Minnesota; 3 = Duxby, Minnesota; 4 = Huot Forest WMA, Minnesota; 5 = Maquokata River Mounds, Iowa; 6 = September Islands, Quebec; 7 = University of Alaska – Fairbanks; 8 = Zippel Bay State Park, Minnesota.
[b] F^{14} C values are derived from the measured ^{14}C activity, corrected for fractionation, and account for decay that occurred between the time of collection and the AMS measurement.
[c] Defined in Table 1.

Oxyloma shells averaged 2.1 mg per shell and contained the most dead carbon. *Succinea* shells were the largest, averaging 5.8 mg per shell, but were between *Catinella* and *Oxyloma* in terms of the amount of dead carbon in their shells (Table S1).

The results presented here suggest that the Limestone Problem for small terrestrial gastropods is often negligible and always much less than the 20–30% dead carbon for larger taxa. However, there are additional factors that apparently influence the dietary intake of carbonate rocks of small terrestrial gastropods living side by side, which may include opportunistic behavior, variations in microhabitats, and the dietary needs or wants of individual gastropods.

Table 3
^{14}C results for the Oxford East outcrops.

Lab #	AA #	Taxon	N[a]	Mass (mg)	δ^{13}C (vpdb)	$F^{14}C$	^{14}C age (ka)	Calendar age (ka)[b]	*P*[c]
Organics									
MU-212	82584	bark	–	4.47	−24.6	0.0731 ± 0.0026	21.02 ± 0.28	25.15 ± 0.34	1.00
MU-213	82585	bark	–	3.28	−25.1	0.0767 ± 0.0025	20.62 ± 0.27	24.64 ± 0.37	1.00
MU-214	82586	twig	–	3.80	−24.9	0.0721 ± 0.0028	21.13 ± 0.32	25.28 ± 0.55	1.00
MU-211	82583	wood	–	3.82	−22.6	0.0743 ± 0.0042	20.88 ± 0.45	24.97 ± 0.63	1.00
MU-210	82582	wood chip	–	4.29	−23.6	0.0772 ± 0.0025	20.58 ± 0.26	24.60 ± 0.40	1.00
		Average						**24.93 ± 0.30**	
Gastropod shells									
MU-194	82567	*Discus shimeki*	2	9.20	−6.4	0.0758 ± 0.0052	20.72 ± 0.55	24.73 ± 0.75	1.00
MU-195	82568	*Discus shimeki*	2	10.94	−6.9	0.0762 ± 0.0052	20.68 ± 0.54	24.67 ± 0.74	1.00
MU-196	82569	*Discus shimeki*	2	14.99	−6.4	0.0745 ± 0.0053	20.87 ± 0.57	25.00 ± 0.79	1.00
		Average						**24.80 ± 0.17**	
MU-188	82561	*Hendersonia occulta*	1	12.41	−6.4	0.0805 ± 0.0051	20.24 ± 0.51	24.18 ± 0.67	1.00
MU-189	82562	*Hendersonia occulta*	1	10.29	−6.1	0.0787 ± 0.0055	20.42 ± 0.56	24.37 ± 0.68	1.00
MU-190	82563	*Hendersonia occulta*	1	18.42	−7.1	0.0777 ± 0.0055	20.52 ± 0.57	24.47 ± 0.70	1.00
		Average						**24.34 ± 0.15**	
MU-199	82572	*Pupilla muscorum*	8	10.86	−6.5	0.0760 ± 0.0052	20.71 ± 0.55	24.71 ± 0.74	1.00
MU-200	82573	*Pupilla muscorum*	9	11.88	−6.4	0.0805 ± 0.0052	20.24 ± 0.52	24.18 ± 0.68	1.00
MU-201	82574	*Pupilla muscorum*	10	14.13	−6.4	0.0809 ± 0.0051	20.20 ± 0.51	24.13 ± 0.67	1.00
		Average						**24.34 ± 0.32**	
MU-191	82564	Succineidae	8	10.58	−5.3	0.0712 ± 0.0052	21.23 ± 0.59	25.33 ± 0.80	1.00
MU-192	82565	Succineidae	4	9.32	−5.5	0.0689 ± 0.0056	21.49 ± 0.65	25.81 ± 0.94	1.00
MU-193	82566	Succineidae	15	9.53	−5.8	0.0759 ± 0.0055	20.71 ± 0.58	24.73 ± 0.78	1.00
		Average						**25.29 ± 0.54**	
MU-202	82575	*Vallonia gracilicosta*	15	10.72	−6.0	0.0776 ± 0.0058	20.53 ± 0.60	24.49 ± 0.76	1.00
MU-203	82576	*Vallonia gracilicosta*	15	11.08	−6.2	0.0824 ± 0.0058	20.05 ± 0.56	23.92 ± 0.66	0.98
		Average						**24.20 ± 0.40**	
MU-205	82577	*Vertigo hannai*	30	10.46	−6.5	0.0750 ± 0.0052	20.81 ± 0.55	24.90 ± 0.77	1.00
MU-206	82578	*Vertigo modesta*	15	11.47	−6.7	0.0751 ± 0.0052	20.80 ± 0.55	24.88 ± 0.77	1.00
MU-207	82579	*Vertigo modesta*	15	14.14	−7.0	0.0771 ± 0.0053	20.59 ± 0.55	24.54 ± 0.71	1.00
MU-208	82580	*Vertigo modesta*	20	15.28	−6.7	0.0729 ± 0.0053	21.04 ± 0.58	25.18 ± 0.77	1.00
		Average						**24.86 ± 0.32**	

Uncertainties for the raw and calibrated ^{14}C ages are given at the 2σ (95%) confidence level.
[a] Number of shells per aliquot.
[b] Calibrated ages were calculated using CALIB v. 6.0.0, IntCal09.14C dataset; limit 50.0 calendar ka B P. Calibrated ages are reported as the midpoint of the calibrated range. Uncertainties are reported as the difference between the midpoint and either the upper or lower limit of the calibrated age range, whichever is greater. Multiple ages are reported when the probability of a calibrated age range exceeds 0.05.
[c] *P* = probability of the calibrated age falling within the reported range as calculated by CALIB.

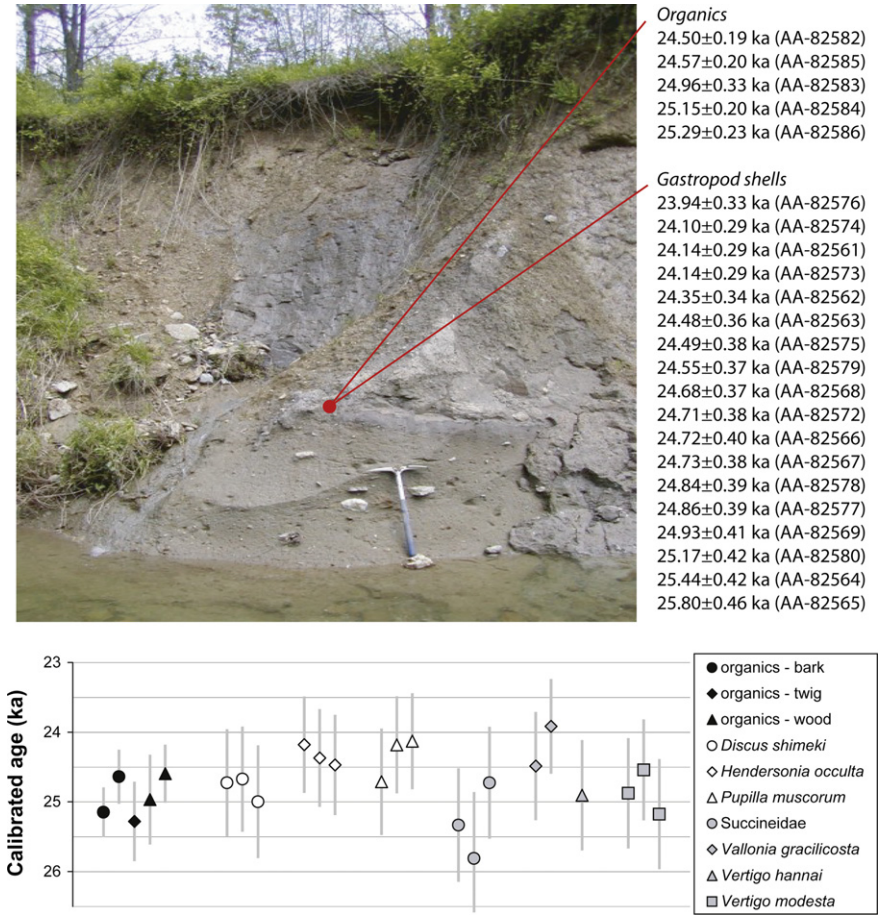

Fig. 7. Photograph of the section at the Oxford East outcrops and the calibrated ages obtained from the organic material and fossil gastropod shells.

5.3. Small terrestrial gastropods and open-system behavior

The present study includes only a single fossil locality, the Oxford East outcrops of southwestern Ohio, which we present here as a case study. Average ages of organic materials and fossil gastropod shells from the Oxford East outcrops were statistically indistinguishable; 24.93 ± 0.30 ka for the organics and 24.73 ± 0.44 ka for the shells. Six of the seven taxa that we analyzed (*D. shimeki*, *P. muscorum*, Succineidae, *V. gracilicosta*, *V. hannai*, and *V. modesta*) yielded average ^{14}C ages that are indistinguishable from the organic ages; the seventh (*H. occulta*) yielded ages that were slightly younger than the organic ages. The range of ages of the shell material, 1.8 ka, is significantly larger than the range of ages of the organics, 0.8 ka. If the dispersion of shell ages was related to open-system behavior, then we would expect the ages to be systematically younger than the organic matter ages, which they are not. It may be that the small number of organic samples fails to adequately capture the full range of time represented by the sampled stratum. More work needs to be done on this subject, including additional comparisons of shell and organic ages from other sites, but the results from the Oxford East outcrops suggest that small terrestrial gastropod shells may behave as closed systems with respect to carbon in the American Midwest for at least the past ~25 ka.

6. Summary and conclusions

Fossil shells of small terrestrial gastropods are commonly preserved in Quaternary sediment across North America, including loess, wetland, glacial, and alluvial deposits, as well as in sediments at many archeological sites. Their aragonitic shells contain ~12% by weight carbon, and therefore contain sufficient carbon for ^{14}C dating. However, terrestrial gastropod shells in carbonate terrains are often avoided for ^{14}C dating because large taxa are known to incorporate dead carbon from limestone or other carbonate rocks when building their shells, which can cause their ^{14}C ages to be up to 3000 yrs too old. Previous studies suggested that small terrestrial gastropod shells may yield reliable ^{14}C ages in arid environments, but a systematic and comprehensive analysis was needed before ages derived from their shells could be considered reliable outside of the Desert Southwest.

To this end, we measured the ^{14}C activity of 247 aliquots of modern shell material (3749 individual shells) from 163 localities across North America. Approximately 78% of the aliquots did not contain measurable amounts of dead carbon even though limestone or other carbonate rocks were readily available at all sites, ~12 of the aliquots contained between 5 and 10% dead carbon, and the remaining few (3% of the total) contained more than 10%. The average Limestone Effect for these samples was only ~180 ^{14}C yrs, which is significantly less than the 2000–3000 ^{14}C yrs that previous researchers found for larger taxa. Assuming that the small gastropod shells behave as closed systems with respect to carbon after burial, they should yield reliable ^{14}C ages ~78% of the time, and ages that are within ~1000 yrs of the true age ~97% of the time, regardless of the taxon analyzed, local bedrock type, climate, or environmental conditions. If fossil shells can be identified to the species level, then at least 23 different species should yield reliable ^{14}C ages if the modern shell data can be applied directly to the fossil record.

The terrestrial gastropod family Succineidae is one of the most common gastropod taxa in North America. Unlike the other

gastropods studied here, our ^{14}C data for Succineidae must be evaluated at the genus or even family level because species-level identification is based on soft-part morphology, which is rarely preserved in the fossil record. Based on the data from modern shells, the Succineidae family as a whole should yield reliable ^{14}C ages ~85% of the time, and ages that are within ~700 ^{14}C yrs every time. At the genus level, *Catinella* should yield reliable ^{14}C ages ~97% of the time, again assuming closed-system behavior, and ages that are within ~300 ^{14}C yrs of the true age every time. Similarly, *Succinea* shells should yield reliable ^{14}C ages ~92% of the time and ages that are within ~600 ^{14}C yrs of the true age every time. Caution should be used when evaluating shells of the genus *Oxyloma*, however, as nearly 1 in 3 aliquots contained dead carbon, equivalent to a limestone effect of up to ~700 ^{14}C yrs.

Fossil shells of small terrestrial gastropods recovered from well-dated, late-Pleistocene sediments in the Midwest yielded ages that were statistically indistinguishable from ages obtained from well-preserved plant macrofossils (wood, bark, plant remains). Although just one site, these results suggest that small terrestrial gastropod shells may behave as closed systems with respect to carbon over geologic timescales. More work on this subject is needed, but if our case study site is representative of other sites, then fossil shells of some small terrestrial gastropods, including at least five common genera, *Catinella*, *Columella*, *Discus*, *Gastrocopta*, and *Succinea*, should yield reliable ^{14}C ages, regardless of the local geologic substrate. Fossil shells of these and other small terrestrial gastropods are common in a wide range of Quaternary deposits in North America and, therefore, our results may have broad chronologic applications to Quaternary geology and New World archeology.

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Appendix. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.quageo.2010.01.001.

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