

## THE USE OF LAND SNAIL SHELLS IN PALEOENVIRONMENTAL RECONSTRUCTION\*

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Fossil land snail shells constitute a valuable source of paleoenvironmental information for the Quaternary. They can be dated by a variety of methods, including radiocarbon, amino acid racemization and epimerization, and perhaps also Th/U and ESR. The vast majority of paleoenvironmental studies based on land snail shells have examined the faunal composition of fossil assemblages, from which a variety of paleoenvironmental characteristics such as biome, temperature, and moisture conditions have been reconstructed. Still, there are a number of problems involved in using this approach and these are discussed. Shell morphology has occasionally been used to reconstruct such factors as rainfall and temperature. Stable isotope studies on Quaternary land snails include: analysis of  $\delta^{13}\text{C}$  values of organic matter in the shells, to reconstruct  $\text{C}_4$  plant distributions from which rainfall amounts can be inferred, and analysis of  $\delta^{18}\text{O}$  values of shell carbonate, from which trends in the oxygen isotope composition of rainfall can be reconstructed. Stable carbon isotopes of shell carbonate have also been studied but their interpretation is not clear. Amino acid epimerization analysis (D-alloisoleucine/L-isoleucine ratios) of land snail shells has been used for estimation of paleotemperatures. Some potential uses of land snail shells for paleoenvironmental reconstruction include the study of stable isotopes of H and N, periodic growth lines, and deposits of pedogenic carbonates on the shells.

### INTRODUCTION

Land snail shells are commonly preserved in the fossil record in many regions. They constitute a record of the species that lived in a particular place in the past, and of the form, structure, and chemistry of the shells that the snails deposited there. Since each of these is influenced by the nature of the environment that the snails lived in, we may learn something about the past environments of the snails by studying their shell remains. Most species of land snails present in the Quaternary fossil record are extant, so it is usually possible to establish the relationship of environmental factors to the distribution of species and to the morphological and chemical characteristics of their shells by studying modern populations.

A variety of paleoenvironmental information has been obtained from Quaternary land snails, e.g. vegetation types,  $\text{C}_4$  plant distributions, soil moisture conditions, temperature and the amount and isotopic composition of rainfall. Here I review the properties of land snail shells that have been used, or have the potential for use, for paleoenvironmental reconstructions and the type of information obtained from them. The method of application and the strengths and weaknesses of each of these approaches are critically evaluated. This review of approaches to paleoenvironmental reconstruction is preceded by consideration of some of the general methodology common to all types of analysis of land snails — sampling procedures and dating methods.

### SAMPLING PROCEDURES

The means of procuring and processing land snail

samples for study is constrained by the types of analyses to be performed. For faunal analysis, quantitative samples are preferred. This requires sampling of sediments and processing to ensure complete collection of all individuals, since picking individual shells out of exposures may bias the sampling toward larger species. Sieving through a graded series of sieves (either wet or dry) ensures the most complete collection of specimens; but from some types of deposits, a large amount of debris or sediments may remain in the sieves and require picking. Flotation methods (e.g. Barber, 1983) require less work but do not ensure complete recovery of individuals. Dispersive agents such as hydrogen peroxide or sodium hydroxide may be needed to separate shells in clayey or organic-rich sediments. But these may render the material useless for amino acid racemization/epimerization analyses and for isotopic analysis of shell organics. Drying material at too high a temperature (above ca. 50–60°C) will also render the material useless for amino acid racemization/epimerization analysis, since it will cause conversion of L amino acids to D amino acids. Further details on sorting and enumeration procedures can be found in Evans (1972).

### DATING OF LAND SNAIL SHELLS

Radiocarbon ( $^{14}\text{C}$ ) analysis is by far the most important and widely applicable method for dating of land snails, although it covers only the last 40–50 ka (about the last 2% of the Quaternary). Radiocarbon dating of land snail shells is not straightforward because the shell carbonate typically has a  $^{14}\text{C}$  age anomaly — the apparent age is greater than the true age. This is the result of ingestion of old carbonates (limestone or soil carbonates) by the snails (Goodfriend and Stipp, 1983) which generates  $^{14}\text{C}$ -deficient  $\text{CO}_2$  in the stomach. This dissolves in the bicarbonate pool in the hemolymph

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(blood and body fluids), from which the shell carbonate is precipitated (Goodfriend and Hood, 1983), with the result that the shell carbonate is deficient in  $^{14}\text{C}$  relative to modern levels. Consequently, it is necessary to correct radiocarbon ages of fossil land snails for this anomaly. The correction factor can be estimated by comparison of the  $^{14}\text{C}$  activity of shell carbonate of modern snails of the same species (preferably from the same region as the fossils) with contemporary  $^{14}\text{C}$  activity of the atmospheric  $\text{CO}_2$  (or as recorded in plant carbon). To estimate contemporary  $^{14}\text{C}$  activity, the year when the shell carbonate was deposited must be known, as atmospheric  $^{14}\text{C}$  levels are changing rapidly since the thermonuclear bomb tests at the end of the 1950s (see, e.g. Segl *et al.*, 1983). This would generally be the year preceding collection for annual snails. But for longer-lived snails the situation is not so simple and it is much more preferable to analyze snails collected before the end of the 1950s (as obtained from museum collections, for example). Atmospheric levels were then much more stable, so several years of uncertainty as to the time (or duration) of deposition of shell carbonate does not matter. Age anomalies have been estimated for a number of species in various regions (Tamers, 1970; Evin *et al.*, 1980; Burleigh and Kerney, 1982; Goodfriend and Stipp, 1983; Goodfriend, 1987c). They show a maximum of about 3 ka and in some cases show reasonable consistency among samples from different sites ( $\pm$  ca. 200 years) (Goodfriend, 1990). This uncertainty contributes to the overall error of the corrected age (see Goodfriend (1987c) for calculation procedures and correction for fractionation).

Conventional radiocarbon analysis typically utilizes 20–25 g of shell material but for younger samples, mini-counters requiring 1 g or less may be used. Accelerator mass spectrometry (AMS) measurements require far smaller samples, some 10–30 mg. It is also possible to analyze the  $^{14}\text{C}$  activity of shell organic matter by AMS (Haynes and Mead, 1987). This should not be subject to age anomalies, since it is derived from the plant diet of the snails. However, this has not yet been investigated in known-age shells. Thorough cleaning of shells is critical for radiocarbon analysis (see Goodfriend (1987a) for procedures), since they often have secondary (pedogenic) carbonates deposited on them. In some cases, recrystallization of shells might occur, leading to anomalously young ages. In general, X-ray diffraction analysis should suffice to determine this, since original land snail shells are always aragonitic, whereas secondary carbonate is usually calcitic; but additional methods are also available (Yates, 1986).

Amino acid epimerization analysis (D-alloisoleucine/L-isoleucine, or A/I ratio) has been used for dating of land snail shells, primarily beyond the range of radiocarbon (Harmon *et al.*, 1983; Nelson and Van-Arsdale, 1986; Miller, B.B., *et al.*, 1987; Hearty, 1987; Bowen *et al.*, 1989; Clark *et al.*, 1989). The method depends on an alternative method for dating (e.g. Th/U) of one or more samples which allows the rate of epimerization to be estimated. From this estimate, ages

can be calculated from the A/I ratios. Alternatively, the method can be used simply for correlation purposes, without any assumptions concerning ages. Within the range of radiocarbon, land snail epimer ratios show good age-predictive ability (Goodfriend, 1987d, 1990b; Clark *et al.*, 1989). But since there are no studies where epimer ratios can be compared with a series of independently-derived preradiocarbon ages, the reliability of the method for such older material is not known. Problems of diagenesis of organic matter in older shells could lead to incorrect conclusions regarding ages. Amino acid epimerization analyses have also been used to look at variation among individual shells within a deposit in order to identify age mixtures resulting from redeposition of shells (Goodfriend, 1987a, 1989b). Sets of uniform-age shells for paleo-environmental analysis have been picked out of mixed-age deposits by the same approach (Goodfriend, 1989b). Analysis of individual shells is made possible by the fact that only small amounts of shell material (5–100 mg) are needed for analysis of epimer ratios.

Very little work has been done on the Th/U dating of land snail shells (Holyoak and Preece, 1985). In general, mollusk shells cannot be considered reliable materials for Th/U dating; they do not always behave as closed systems with respect to these elements (Kaufman *et al.*, 1971 and many subsequent studies). However, recent studies on Th/U dating of fossil land snails from the Negev Desert indicate that this method may be reliable under some circumstances (Kaufman and Goodfriend, unpublished data).

Electron spin resonance (ESR) dating could be used for land snail shell carbonate but there are as yet no published studies. Although the method has been used extensively for marine mollusks, it is by no means without problems. A related method, thermoluminescence (TL) dating, cannot be used for carbonates but can be used for dating of some types of quartz- or feldspar-containing sediments in which land snail shells may occur. This provides a valuable means of dating preradiocarbon samples.

## FAUNAL ANALYSIS

### *The Study of Modern Faunas*

The basis for paleoenvironmental reconstruction from the species composition or abundance of species in fossil assemblages depends ultimately on knowledge of the ecological factors that control the distribution and abundance of modern land snail species.

### *Establishing the controlling factors — general considerations*

Two types of studies have been used to establish these controls: geographic surveys of the occurrence or abundance of land snail species in relation to environmental characteristics and experimental studies of land snail survival, reproduction, or growth rate in relation to controlled environmental conditions. By far the largest number of studies have utilized the survey

approach (Table 1). A major problem with this method of study is the difficulty in establishing which of a series of factors is controlling the distributional limits or abundance of a species in a region — there are a large number of potentially important environmental variables and many of these are correlated. Multivariate analyses have been used to sort out this complex of factors into sets of correlated environmental variables which account for the occurrence or abundance of land snail species (e.g. Riggle, 1976; Bishop, 1977; Dillon, 1980; André, 1984). However, within these sets it is usually not possible to determine which of the factors has a dominant role. For example, various measures of temperature (e.g. annual and monthly means, maxima and minima) are likely to be highly correlated with each other within the limits of a survey region, so that their independent effects cannot be assessed.

Results of correlation studies can be misleading when historical events cause species distributions to be unstable. Climatic change or habitat alteration can occur rapidly, such that species have not yet had enough time to readjust their distributional limits. Alternatively there may be barriers to dispersal which cause retardation of the response of the distribution to climatic change (Thomas, 1985). Alteration of the environment by humans can cause species to occur where they cannot survive on a long-term basis or can cause extinctions of populations of species in areas having environments to which they are well suited. Another complication in trying to understand the environmental controls of distributions or abundance through survey methods is that the importance of various environmental variables will vary geographically. Thus local surveys provide information only on local controls which may not be applicable to other regions, whereas broad surveys will require different explanations for different parts of the species range.

Experimental studies in the laboratory offer an advantage over the survey approach in that they allow one to control particular environmental factors independently of others and thus isolate their specific effects. However, interactions between various environmental factors may be important (e.g. humidity tolerance may depend on temperature). Consequently, it is problematic to extrapolate experimental results to situations in nature where other environmental conditions are different from those in the laboratory. Further difficulties come from the fact that the occurrence or abundance of a species at a site depends on a combination of survival and reproduction, both of which would need to be evaluated in the lab. These life history properties depend in turn on environmental effects on a variety of other snail properties such as growth rate, feeding, activity, water balance, etc., which interact in a complex way. These problems can be circumvented to a large extent through the use of field experiments. These offer the best of both worlds: the controlled conditions provided by experimental methodology and a relatively natural context for the studies. However, they must be carried out for long

periods of time in order to evaluate the effects of environmental differences on survival and reproductive success of the populations. Also it cannot be considered that such studies represent truly natural conditions, since normally the animals must be caged in order to ensure adequate recovery of individuals and to restrict the populations to the areas where the desired environmental conditions pertain. This then affects their movements as well as their food supply and perhaps also predation on the populations.

#### *Environmental associations of modern land snails*

By far the largest number of surveys of land snail distributions or abundances in relation to the environment have been carried out in Europe and North America. Little information is available for other regions, especially the tropics (Table 1). In most studies only one or a very limited number of environmental variables have been considered, but more comprehensive studies have been carried out in a few areas, such as the British Isles (Bishop, 1977, 1981), France (André, 1975), British Columbia (Cameron, 1986), and the southeastern United States (Branson and Batch, 1970; Coney *et al.*, 1982). Vegetation characteristics (biome, species composition, density) stand out as the most widely documented environmental correlates; but land snail distributions or abundance have been found to be related also to various measures of rainfall and temperature, and to soil characteristics such as pH and moisture content. These relationships are observed both on a broad geographic scale in relation to climatic variation (e.g. Agócsy, 1962; Heller, 1988) as well as on a very local scale in relation to habitat heterogeneity (e.g. Harvey, 1974; Murray *et al.*, 1982). Competition among snail species has traditionally been viewed as a relatively unimportant factor (Boycott, 1934). Although some recent studies have revealed that there may indeed be important competitive interactions between snail species (Rollo and Wellington, 1979; Heller, 1988), it would seem that these are generally less important controls than in, for example, plants. For this reason, land snail distributions or abundance may reflect more the influence of the physical or chemical environment, rather than the biotic environment, and therefore may be especially useful in paleoenvironmental reconstruction.

Experimental studies on land snails have generally not contributed very much to the understanding of the controls of snail distributions or abundances. Environmental factors such as moisture, temperature, and light have been shown to have direct effects on life history properties such as mortality, growth, and reproduction, as well as indirect effects, through their influence on snail activity or water balance (Table 2). However, the significance of these environmental influences in natural populations is not clear from these studies. For example, in a carefully designed series of field experiments in which levels of humidity, temperature, and light were varied, it was found that *Mesodon roemeri*, a forest species, was more sensitive to moisture condi-

TABLE 1. Some surveys of the distribution, abundance, and frequency of the land snail species in relation to various environmental factors

Environmental factor	Data*	Scale of survey (km)	Area	Reference
<b>Eurasia</b>				
Biome, veg. density, soil chem.	abund.	10 <sup>1</sup>	Ireland	Bishop, 1977
Biome, soil chem.	abund.	10 <sup>1</sup>	England	Baker, 1968
Veg. density, soil pH	p/a	10 <sup>1</sup>	England	Cameron, 1973
Biome, soil pH	p/a	10 <sup>0</sup>	England	Cameron and Redfern, 1972
Veg., as indicator of grazing	abund.	10 <sup>-1</sup>	England	Cameron <i>et al.</i> , 1977
Veg. density	abund.	10 <sup>0</sup>	England	Tattersfield, 1981
Biome	p/a	10 <sup>-1</sup>	England	Paul, 1978
Biome, veg. density	freq.	10 <sup>0</sup>	England	Harvey, 1974
Biome	abund.	10 <sup>0</sup>	England	Humphreys, 1980
Biome	freq.	10 <sup>1</sup>	England	Cameron and Letanka, 1976
Biome	freq.	10 <sup>1</sup>	England	Cameron and Palles-Clark, 1971
Plant species	freq.	10 <sup>-1</sup>	England	Grime and Blythe, 1969
Biome	p/a	10 <sup>0</sup>	England	Berry, 1973
Calcium	p/a	10 <sup>2</sup>	Gr. Britain	Kerney, 1972
Biome, veg. density, soil moisture and pH	abund.	10 <sup>1</sup>	Gr. Britain	Bishop, 1981
Biome	freq.	10 <sup>1</sup>	Faroe Is.	Solhøy, 1981
Elevation	abund.	10 <sup>1</sup>	Norway	Solhøy, 1976
Biome, soil pH	abund.	10 <sup>2</sup>	Sweden	Waldén, 1981
Biome	abund.	?	Sweden	Wäreborn, 1970
Soil chem. and moisture, biome	abund., freq.	10 <sup>1</sup>	Sweden	Wäreborn, 1969
Soil pH	abund.	10 <sup>1</sup>	Finland	Valovirta, 1968
Biome	abund.	10 <sup>2</sup>	Spain	Larraz and Jordana, 1984
Veg. density, soil pH	abund.	10 <sup>1</sup>	France	André, 1982
Rainfall, temperature, biome	abund.	10 <sup>2</sup>	France	André, 1975
Veg. density	abund.	10 <sup>-1</sup>	France	Lazaridou-Dimitriadou, 1978
Biome, veg. density	abund.	? 10 <sup>0</sup>	France	André, 1981
Soil moisture	abund.	? 10 <sup>0</sup>	France	Badie and Rondelaud, 1979
Biome	freq.	10 <sup>1</sup>	France	Sacchi, 1954
Temperature, biome	p/a	10 <sup>3</sup>	France	Magnin, 1989
Biome	abund.	10 <sup>1</sup>	Netherlands	Reinink, 1979
Elevation, biome	p/a	10 <sup>1</sup>	Switzerland	Meier, 1987
Biome	abund., freq.	10 <sup>2</sup>	W. Germany	Ant, 1969
Calcium carbonate	p/a	10 <sup>2</sup>	W. Germany	Lais, 1943
Biome	freq.	10 <sup>1</sup>	E. Germany	Körnig, 1986
Biome	freq.	10 <sup>1</sup>	E. Germany	Körnig, 1985
Biome	p/a	10 <sup>1</sup>	Czechoslovakia	Körnig, 1983
Biome (succession)	p/a	10 <sup>2</sup>	Hungary	Bába, 1986
Temperature, moisture	p/a	10 <sup>2</sup>	Hungary	Agócsy, 1962
Rainfall, competition	p/a	10 <sup>2</sup>	Israel	Heller, 1988
Rainfall	p/a	10 <sup>2</sup>	Israel	Heller, 1984
Rainfall	p/a	10 <sup>2</sup>	Iraq	Harris, 1978
<b>North America</b>				
Biome, litter type, soil moisture	abund., freq.	10 <sup>2</sup>	Br. Columbia	Cameron, 1986
Biome	p/a	? 10 <sup>2</sup>	Alberta	Harris, 1978
Biome	abund.	10 <sup>0</sup>	Alberta	Locasciulli and Boag, 1987
Veg. density	abund.	? 10 <sup>0</sup>	Arizona	Dillon, 1980
Biome	abund.	10 <sup>2</sup>	western U.S.	Karlin, 1961
Moisture, vegetation	p/a	10 <sup>2</sup>	Texas	Neck, 1990
Elevation	p/a	10 <sup>1</sup>	New Mexico	Metcalf, 1984
Biome	abund.	10 <sup>0</sup>	Kansas	Fitch and Lokke, 1956
Calcium	abund.	10 <sup>2</sup>	midwestern U.S.	Atkins, 1966
Biome	abund.	? 10 <sup>-1</sup>	Minnesota	Coulter <i>et al.</i> , 1983
Soil chem., pH	abund.	10 <sup>-2</sup>	Illinois	Riggie, 1976
Biome	abund.	10 <sup>-1</sup>	New York	Beyer and Saari, 1977
Soil chem.	abund.	10 <sup>1</sup>	Virginia	Burch, 1955
Biome	freq.	10 <sup>1</sup>	Virginia	Burch, 1956
Temperature, biome, soil pH	abund.	10 <sup>0</sup>	Kentucky	Branson and Batch, 1970
Biome, soil moisture and pH	abund.	10 <sup>1</sup>	Tennessee	Coney <i>et al.</i> , 1982
<b>Other Regions</b>				
Rainfall	p/a	10 <sup>1</sup>	Jamaica	Goodfriend, 1986a
Biome	p/a	10 <sup>0</sup>	Bahamas	Maly and Doolittle, 1977
Plant species	abund.	10 <sup>-2</sup>	Moorea	Murray <i>et al.</i> , 1982

\*abund. = abundance, p/a = presence or absence, freq. = frequency.

TABLE 2. Some experimental studies of environmental effects on survival, reproduction, growth and other ecological properties of land snails

Environmental factor	Ecological property	Taxon	Reference
<b>Laboratory Studies</b>			
Moisture	egg hatchability	<i>Limax flavus</i>	Carmichael and Rivers, 1932
Moisture	reproduction	<i>Cepaea nemoralis</i>	Wolda, 1965
Temperature, humidity	water loss	misc.	Warburg, 1965
Temperature	survival, reproduction	<i>Cepaea nemoralis</i>	Wolda, 1967
Humidity	survival and hatching of eggs	<i>Deroceras reticulatus</i>	Bayne, 1969
Humidity	activity	helicid spp.	Cameron, 1970a
Temperature	activity	helicid spp.	Cameron, 1970b
Calcium salts	reproduction	<i>Cochlicopa lubrica</i> , <i>Discus rotundatus</i>	Wärebörn, 1970
Low temperature	survival	<i>Arianta arbustorum</i>	Stöver, 1973
Temperature, humidity	survival, growth	<i>Mesodon roemerii</i> , <i>Bulimulus dealbatus</i>	Randolph, 1973
Temperature, humidity	survival	zonitid spp.	Mordan, 1977
Temperature, moisture, light	growth rate, mortality	<i>Cepaea nemoralis</i>	Oosterhoff, 1977
Presence of other snail species	activity, growth	helicid spp.	Cameron and Carter, 1979
Light	growth	<i>Arion</i> sp.	Chevallier, 1982
Photoperiod	egg production	<i>Helix aspersa</i>	Guemene and Daguzan, 1982
Temperature	survival	<i>Theba pisana</i>	Cowie, 1985
Ca, Mg	growth	<i>Helix aspersa</i>	Gomot, A. <i>et al.</i> , 1989
Temperature, light	reproduction	<i>Helix aspersa</i>	Gomot, P. <i>et al.</i> , 1989
Desiccation	survival	<i>Sphincterochila</i> spp.	Arad <i>et al.</i> , 1989
<b>Field Studies</b>			
Moisture, temperature, light	survival, growth	<i>Mesodon roemerii</i> , <i>Bulimulus dealbatus</i>	Randolph, 1973
Plant density	abundance	misc.	Paul, 1978
Presence of other snail species	activity, growth	misc. slug spp.	Rollo, 1983

tions than the more catholic *Bulimulus dealbatus*, showing both increased mortality and decreased growth at lower humidity (Randolf, 1973). But these results do not necessarily indicate that these conditions are limiting to *M. roemerii*; e.g. it is possible that this species is limited to forests because of food preferences, in which case it would not evolve a tolerance for dry conditions to which it was not subjected.

What we know based on these survey and experimental studies is the empirical correlation between snail distributions or abundance and environmental factors — we do not know the actual causes for these correlations. These empirical relations are known, however, for only a few species in a few regions.

### Interpretation of Fossil Land Snail Assemblages

#### The relation of faunal change to environmental change

Our understanding of the distribution and abundance of modern land snails forms the basis for paleoenvironmental interpretation of fossil land snail assemblages. This uniformitarian approach is taken not because it must be correct but simply because there is not a better alternative. It can be criticized on several grounds (e.g. Scott, 1963; Taylor, 1965). The most obvious problem is the assumption of no evolutionary change, i.e. that the environmental requirements of each species remain constant over time. Species are seen as responding to climatic change by becoming extinct or rarer in areas where the climate has become less favorable and by

colonizing or increasing abundance in areas where the climate has become more favorable. However, the fact that changing environmental conditions causes increases or decreases in abundance implies that natural selection is likely to be acting on the populations. Long-term evolutionary trends, not necessarily related to climatic change, may also occur. If these evolutionary changes are only minor, then at least the general trend of environmental change, if not precise quantitative changes, can still be assessed from fossil faunas.

Another problem of this approach of basing interpretations of fossils on modern analogs is that in the past, the relationships between environmental variables may have been different from the present. We can imagine modern environments as occupying a multidimensional space within a series of axes representing a variety of environmental variables. However, not all environments of the past will be included within this space, that is to say, they may not have modern analogs. For example, with changes in seasonality as a result of changes in the Earth's orbital parameters (Milankovich cycles), the relationship of mean annual temperature and seasonal mean temperature will change. Thus the early Holocene environment, which had an enhanced seasonality in the northern hemisphere (Kutzbach, 1981) may have no analogous modern environment. As another example, it has been suggested that the eastern Mediterranean region, which now receives rains only in the cooler part of the year, may have once also experienced summer rainfall (Horowitz and Gat,

1984). Consequently, modern faunas and their environmental associations may not establish a basis for interpretation of fossil assemblages but rather an extrapolation to nonextant conditions may need to be made. The existence of paleoenvironments with no modern analogs is probably one important reason for the occurrence of fossil assemblages that have no modern analogs. Such assemblages, composed of species whose modern ranges are nonoverlapping, are common among Quaternary land snail deposits in a wide range of regions (Goodfriend, 1989) and occur equally commonly in other groups of animals and plants.

Paleoenvironmental interpretation of fossil assemblages is also subject to some of the same problems as those encountered in establishing the relations of modern snails to their environments, namely those causing the assemblages to be out of equilibrium with the environment. As discussed above, these may result from climatic change that outpaces faunal response or from human disturbance (Evans, 1968; Kerney *et al.*, 1980; Christensen and Kirch, 1981; Preece *et al.*, 1986).

#### *Taphonomic problems*

Some taphonomic problems that can complicate interpretation of fossils include the relationship between death assemblages and living assemblages, differential preservation of species, and the occurrence of mixed-habitat and mixed-age assemblages. Little quantitative work comparing living and death assemblages of land snails has been carried out. Briggs *et al.* (1990) found that samples of surface accumulations of dead land snail shells along a flood plain reflected the local living snail communities. However, these surface accumulations apparently do not represent samples that become preserved in the fossil record, as no snail assemblages were found within the floodplain sediments. Biasing of species abundances may occur as a result of the accumulation of shell middens or by differential destruction of certain species by predatory animals such as birds (Carter, 1990). Differential preservation of snail shells has only recently been studied (Carter, 1990), although it is often alluded to in the literature (e.g. Evans, 1972). This problem is a difficult one to analyze directly, since the original composition of a fossil assemblage cannot be known. However, Carter (1990) demonstrated that there was differential survival of the lip of *Pupilla muscorum* shells relative to the more fragile apex in a soil under a humid, temperate climate. This implies that differential survival of the shells of different species of snails can also be expected to occur under these conditions.

The shells of snails are not always deposited exactly where the snail lived. Particularly in fluvial sediments, shells are likely to have been transported from some distance away. Thus individuals living in a variety of different habitats may end up being deposited together (Tuthill *et al.*, 1965; French, 1982). A particularly wide range of vegetation types and associated snail communities occurs along rivers and this makes fossil

assemblages in fluvial sediments particularly difficult to interpret. In contrast, other types of deposits such as soils, loess deposits, and some animal middens (e.g. rodent middens; Goodfriend, 1987a) will be likely to contain only shells of snails living in the immediate area. Transport of shells by humans or by predators such as birds can result in the occurrence of mixed-habitat assemblages in archeological sites (for an extreme case, see Murphy, 1973).

The problem of redeposition of fossils, resulting in mixed-age assemblages, has received increasingly greater attention recently. Before the availability of AMS measurements of radiocarbon, it was generally not possible to radiocarbon-date individual specimens since these usually are not large enough. Consequently, dates were run on bulk samples or on other associated materials such as wood, charcoal, or soil organics, so age mixtures could not be detected. Other criteria, such as differences in degree of wear of specimens, were taken to indicate different depositional histories and therefore possibly different ages for the individual fossils (e.g. Paul, 1984). Recent intrusions of shells might be indicated by their 'fresh' appearance (Plug, 1990) or the presence of periostracum (Carter, 1990). However, these various criteria do not provide quantitative estimates of age differences among specimens within an assemblage and the validity of this last criterion is questionable (Bobrowsky, 1984). AMS radiocarbon studies have shown recently that age mixtures are a common feature of many different types of deposits (see Goodfriend (1989b) for brief review). Amino acid epimerization analysis of individual shells within an assemblage has also been used recently to identify mixed-age land snail assemblages (see section on dating, above). These have been shown to occur in cave sediments (Goodfriend and Mitterer, 1987, 1988) as well as fluvial and colluvial sediments (Goodfriend, 1987a, 1989b). These mixed-age assemblages are most likely to be another major cause for the occurrence of fossil assemblages lacking modern analogs. A recent AMS study on insect assemblages from an archeological site has shown this to be the case — specimens representing different climatic regimes give different ages (Elias and Toolin, 1990). The recent discovery of the high frequency of mixed-age assemblages calls back into question the interpretation of nonanalogous assemblages: are such fossil assemblages truly non-analogous, i.e. containing species with presently non-overlapping ranges which lived together at the same place and time; or are most such assemblages actually the result of age mixtures?

#### *Methodology*

Two main procedures have been used in paleoenvironmental analysis of fossil land snail assemblages. The first is a qualitative approach which looks at the species composition of the assemblage and compares this to the present fauna of the region. Interpretation is based mainly on the species which occur outside their present ranges or which are associated with biomes not

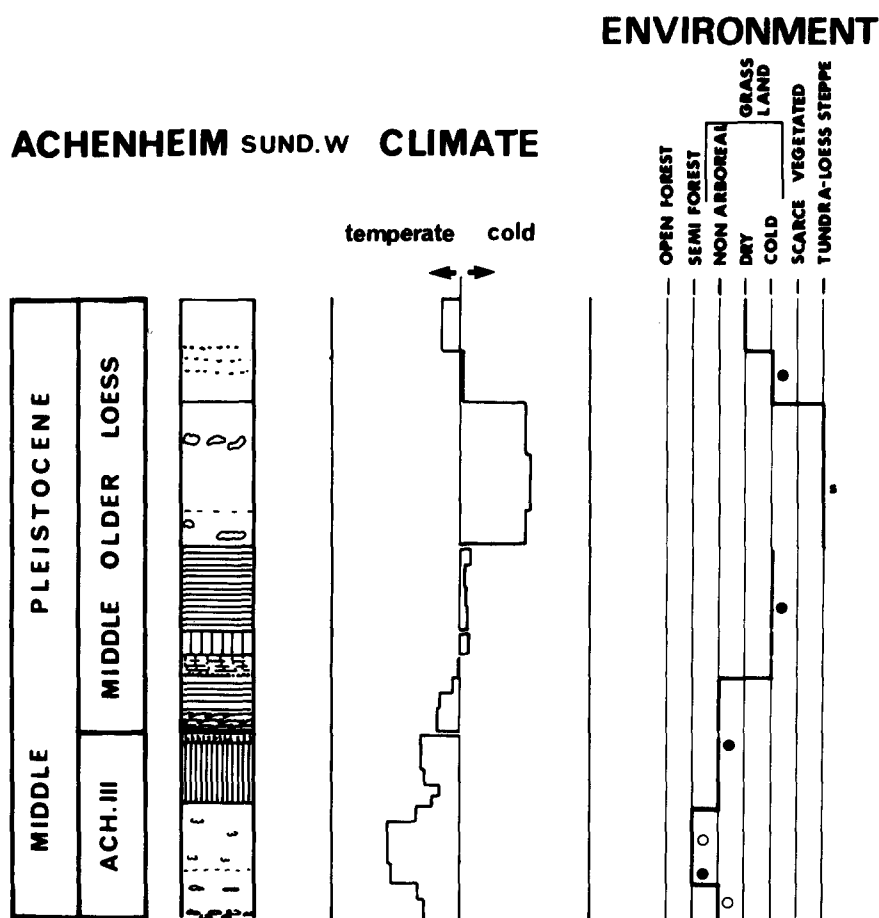


FIG. 1. Paleoenvironmental interpretation of land snail faunas from the Middle Older Loess sequence of Achenheim, Alsace, France. The loadings of the assemblages on the first factor axis of a correspondence analysis are interpreted in terms of paleotemperature variations and plotted here on a temperate-cold axis. Interpretations of the biomes represented by the faunas is given under "environment", along with indications of drier (filled circles) or wetter (open circles) conditions (from Rousseau, 1987b).

presently existing in the area of the fossil site. Based on the present environmental associations of these extralimital species, the direction of difference from the present environment (e.g. colder, drier, etc.) is inferred (e.g. Leonard, 1950; Burchell, 1961). The second approach is a quantitative one that looks at the relative abundance of ecological groups of species within the fossil assemblage. These ecological groups are generally based on the biomes occupied by the species but may also take into account different moisture or temperature facies of these biomes. In one approach (Sparks, 1961; Ložek, 1964), the proportions of the various ecological groups, weighed by the number of individuals, is considered as the basis for paleoenvironmental interpretation. Alternatively, multivariate analysis of species abundances in a series of fossil assemblages from a site can be performed (Rousseau, 1990). The resulting loadings of the assemblages on the various factor axes serve as a basis for interpretation, where the axes are assumed to represent various ecological factors controlling the snail abundances (Fig. 1) (Laurin and Rousseau, 1985; Rousseau, 1987b). This latter method is appropriate only for following temporal trends in a series of samples from a single area. Recently a third approach — that employing transfer functions — has been applied to the

estimation of paleotemperatures from fossil land snail assemblages (Rousseau, 1989, 1991). This method involves the development of multiple regression equations relating environmental factors (here, temperature and rainfall) to the abundances of a series of species, based on analysis of modern faunas and their association with known values of the environmental factor. Data on abundances of species in fossil assemblages are then plugged into the equation to estimate the value of the environmental factor in the past. Although this method provides quantitative estimates of paleoenvironmental variables, these can be taken only as estimates, not calculations. They are still based on unproven assumptions concerning nonevolution of species, etc. as discussed above. Application of this method to foraminiferal assemblages, for example, has yielded results that are not consistent with a variety of other indicators (Rind and Peteet, 1985).

A major limitation of the application of all these methods of interpretation of fossil faunas is that they depend on a very limited and generally nonquantitative database of modern land snail ecology. Although there have been some advances in quantifying the environmental associations of land snails (André, 1975; Coney *et al.*, 1982), the geographic coverage of these studies is very limited. Whereas with studies on pollen or

foraminifera, there are extensive, quantitative data on environmental associations of modern species, the same is not yet true for land snails. It is quite symptomatic of the state of land snail paleoecological research that only very recently have there been applications of methods of analysis like transfer functions, which were developed at the end of the 1960s (Imbrie and Kipp, 1971).

#### *Discussion of paleoenvironmental studies*

Numerous studies using land snail faunas to reconstruct paleoenvironments have been carried out, some examples of which are cited in Table 3. The aspects of the paleoenvironments that were reconstructed are classified here necessarily somewhat arbitrarily, since it is often the case that inferences about the biomes represented by the fossils will lead to conclusions also about climatic features, such as temperature or rainfall, or local paleoenvironmental features such as soil moisture. In fact the reconstruction of biomes is the predominant piece of paleoenvironmental information that has been obtained from fossil snail assemblages. These reconstructions are usually of a general nature, such as grassland, steppe, deciduous forest, or marsh environments. In some cases somewhat more specific information has been obtained (e.g. Preece (1979), mesic forest). However, reconstructions of the plant species composition have not been made. Such information is potentially obtainable since some land snail species are fairly specific in their occurrence with respect to vegetation composition (Grime and Blythe, 1969).

Paleoenvironmental information has also been obtained on temperature (average and seasonal average), an example of which is shown in Fig. 1. Various aspects of moisture amounts and seasonality (rainfall, humidity, soil moisture) have been studied but their interpretation is problematic. In general it has not been possible to sort out the various factors which may affect moisture conditions — rainfall, humidity, temperature (as it affects evapotranspiration), vegetation (also affecting evapotranspiration), and groundwater. The latter factor may, in some cases, not even be indicative of local environmental conditions, since recharge can occur some distance away.

Given the various problems of paleoenvironmental reconstruction from land snail faunas, the results obtained are probably only broadly correct, but not in detail. The use of a quantitative approach, based on a well-quantified study of environmental associations of modern land snails, is certainly to be preferred; but even here, the results cannot be taken too literally. The best results are probably obtained for cases where there is extreme environmental change, such as was seen in northern Europe and the northern United States during glaciation and deglaciation periods. Here the possibilities of changes in environmental associations of the snails, resulting from evolutionary changes or changes in the covariance patterns of environmental factors, are

small relative to the magnitude of environmental change.

### **SHELL MORPHOLOGY**

Variation in morphological features of land snail shells (e.g. diameter, height, thickness, color) is often related to environmental variation. Consequently it is possible to infer paleoclimatic conditions from the morphology of fossil land snails. The state of our knowledge concerning these relationships between land snail shell form and environment was reviewed recently (Goodfriend, 1986b) and therefore I will mention here only the major conclusions of that survey. There are no general patterns of correlation between shell morphology and environment — different patterns are seen in different species. However, one correlation that is commonly seen is between shell size and rainfall. In many species, shells tend to be larger in areas with higher rainfall, but the opposite pattern is often seen along elevational gradients, where shells tend to become smaller with an increase of rainfall (and decrease of temperature) at higher elevations. Variation in size results from variation in the number and/or width of the whorls of the shell. Another common pattern seen is these shells tend to be thicker in areas with calcium carbonate present; but this is also not a general pattern. Because there are no general patterns of correlation, it is necessary to study variation in modern populations of each species of interest in order to establish a basis for interpretation of their morphology in the fossil record.

Observed variations may be due either to genetic variations among populations, resulting from differences in natural selection in different environments; or the variations may be directly environmentally induced (ecophenotypic). Breeding studies on land snails indicate that variations among populations with respect to morphological characteristics, such as size, often have a genetic basis — they are not environmentally induced. Whether the variation has a genetic basis or not, it can still be used as a basis for interpreting paleoenvironments from the morphology of fossil shells. However, it should be kept in mind that these different bases of variation will show different rates of response to environmental change. Whereas environmentally-induced characters will respond to environmental change within the next generation, genetically-based features will take many generations to reflect changes in the selective regime resulting from environmental change. Thus environmentally-induced characters can be used to study very short term climatic changes ( $10^0$ – $10^1$  years) which would not be reflected in genetically-based characters. Environmentally-induced characters will also show no lag time between the onset of environmental change and morphological response.

Many land snail species reach a final adult size, marked by expansion of the lip of the shell and/or by formation of denticles (tooth-like projections) in the aperture of the shell, and then grow no more. Such species are ideal for morphometric studies, since



TABLE 3. Some studies of Quaternary land snail assemblages and their paleoenvironmental interpretations

Environmental factor	Location of Deposit		
	Europe	North America	Other regions
Biome (forest, grassland, meadow, marsh, etc.)	Sparks, 1957 Kerney, 1968 Ložek, 1969 Kerney, 1971a Clair <i>et al.</i> , 1972 Girod, 1973 Krolopp, 1977 Fink and Kukla, 1977 Puissegur, 1978b Barrett and Chatfield, 1978 Ložek, 1978 Preece, 1979 Kerney <i>et al.</i> , 1980 Preece, 1980 Gilbertson, 1980 Esu, 1981b Alexandrowicz, 1984 Dubar, 1984 Holyoak and Seddon, 1984 Ellis, 1985 Preece <i>et al.</i> , 1986 Geissert, 1986 Rousseau, 1986 Rousseau, 1987a Preece, 1990 Preece, 1991	Leonard, 1957 Leonard and Frye, 1960 Tuthill <i>et al.</i> , 1965 Metcalf, 1967 Browne and Bruder, 1968 Metcalf, 1970 Pauken, 1971 Cheatum, 1976 French, 1982 Baker <i>et al.</i> , 1986 Neck, 1987a Neck, 1987b	
Temperature (average)	Burchell, 1961 Sparks, 1961 Settepassi and Verdel, 1965 Kerney, 1968 Ložek, 1969 Kerney, 1971b Girod, 1973 Krolopp, 1977 Puissegur, 1978a Wagner, 1979a,b Giusti and Mantovani, 1979 Paul, 1984 Hertelendi <i>et al.</i> , in press	Leonard, 1952 Hubricht, 1964 Taylor, 1967 Browne and Bruder, 1968 Harris and Pip, 1973	Gould, 1969a (Bermuda)
Temperature (seasonal average)	Esu, 1981a Laurin and Rousseau, 1985 Schütt <i>et al.</i> , 1985 Rousseau, 1989 Rousseau, 1991	Taylor, 1960 Getz and Hibbard, 1965 Miller, 1975 Kolb <i>et al.</i> , 1975 Miller and Kay, 1981 Miller and Eshelman, 1985	
Moisture (rainfall, humidity, etc.)	Rotarides, 1932 Krolopp, 1977 Brunnacker <i>et al.</i> , 1980 Laurin and Rousseau, 1985 Rousseau <i>et al.</i> , 1990	Browne and McDonald, 1960 Getz and Hibbard, 1965 Frye <i>et al.</i> , 1978 Miller, 1978 Baerreis, 1980 Neck, 1987b	Solem, 1972 (Afganistan) Gould, 1969a (Bermuda) Haynes and Mead, 1987 (Sudan) Haynes and Mead, 1987
Rainfall seasonality		Leonard, 1950 Miller, 1975 Miller and Eschelman, 1985 Neck, 1987b	
Soil moisture		Cheatum and Allen, 1965 Frye <i>et al.</i> , 1974 Baker <i>et al.</i> , 1986 Neck, 1987b	

populations can be compared at a standard life history stage. However, it is also possible to study the morphology of populations of species showing continual growth by comparing morphologies at standard whorl numbers (Gould, 1969b; Goodfriend, 1983).

The use of shell morphology as a paleoenvironmental indicator suffers from most of the same problems as faunal analysis, since both involve assessment of environmental effects on complex biological systems. As with faunal analysis, the causes of the environmental correlations with shell morphology are usually not known. Rather, empirical correlations form the basis for interpretation of the fossils.

Fossil land snail morphology has only infrequently been used for paleoenvironmental reconstruction (Table 4). This is somewhat surprising given the good correlations of morphology and environment seen in modern snails and the availability of morphological information from the fossil record. One limitation is that although only small samples may be required for qualitative analysis of faunal composition, larger series of shells of particular species are needed for morphometric studies. Information on environmental correlations of shell morphology are available in the literature only for very few species and areas, so studies of the modern snails usually need to be carried out alongside study of the fossils. Where these environmental relations have been well studied in modern snails, very useful paleoenvironmental information has been obtained from the fossils, especially in studying past variations in rainfall (Table 4). An example of the use of shell size in reconstructing rainfall conditions is given in Fig. 2.

Roth (1991) has used shell morphology in a different way, analyzing the distribution of height/width ( $H/W$ ) ratios of the species comprising the total fauna and comparing this to the patterns for faunas from various regions. This approach is based on the studies of Cain (e.g. 1977), which showed that most faunas display a bimodal distribution of  $H/W$ , with mostly elongate ( $H/W > 1$ ) and depressed ( $H/W < 1$ ) forms, and few globose forms ( $H/W \approx 1$ ). However, some wet tropical assemblages are an exception to this general pattern, with globose forms relatively common. Roth inter-

preted the predominance of globose forms in an Eocene fauna from California as indicating the possible occurrence of wet tropical conditions, by analogy with extant faunas. It is not clear whether this 'faunal physiognomy' approach might be applicable to Quaternary faunas; gradients in physiognomy in relation to climate have not been analyzed in modern faunas.

### STABLE ISOTOPE COMPOSITION OF SHELL ORGANIC MATTER

Recent studies on the stable carbon isotope composi-

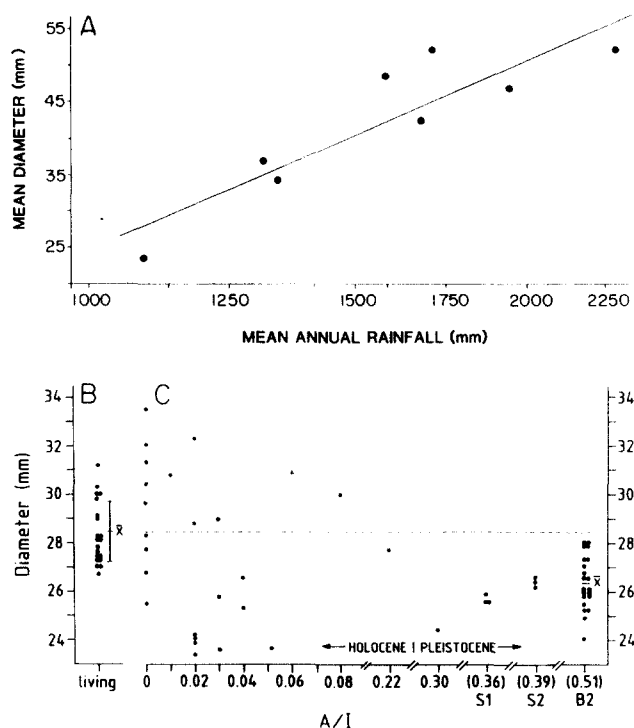


FIG. 2. (A) The correlation between mean shell diameter and mean annual rainfall in modern populations of the Jamaican land snail *Pleurodonte lucerna* (from Goodfriend, 1987b). (B) Shell diameter of modern *Pleurodonte lucerna* collected from the forest at Green Grotto Cave on the north coast of Jamaica. (C) Shell diameter of fossil *Pleurodonte lucerna* from deposits at Green Grotto Cave in relation to age, as represented by the D-alloisoleucine/L-isoleucine ( $A/I$ ) ratios of the shells. The trend points to drier-than-present conditions in the late Pleistocene and again in the late Holocene (from Goodfriend and Mitterer, 1988).

TABLE 4. Some studies of the morphological variation in Quaternary land snail shells and its paleoenvironmental interpretation

Environmental factor	Morphological characteristic	Area	Reference
Rainfall	size	Afghanistan	Solem, 1972
Calcium	thickness	Bermuda	Gould, 1969a
Temperature	size	Italy	Giusti and Mantovani, 1979
Moisture	size	Utah, U.S.A.	Baerreis, 1980
Rainfall	size	Israel	Magaritz and Heller, 1980
Temperature, moisture	size	France	Rousseau and Laurin, 1984
Rainfall	size	Jamaica	Goodfriend, 1987b
Rainfall	size	Jamaica	Goodfriend and Mitterer, 1988
Temperature	frequency of color bands	England	Currey and Cain, 1968
Temperature	shell color	England	Cain, 1971
Rainfall	lip color	England	Cain, 1971

tion ( $^{13}\text{C}/^{12}\text{C}$  ratio) of organic matter in land snail shells have shown that it can be used for reconstruction of the past distribution of plants with a  $\text{C}_4$  photosynthetic pathway, which in turn provides paleoclimatic information (Goodfriend, 1988, 1990). Land snail shells contain a small amount of organic matter, on the order of 0.02–0.03% by weight (excluding the outer organic periostracum layer which is present in many modern snail shells but is lost quickly in fossil snail shells). This consists predominantly of proteins (Hare and Abelson, 1965) with some polysaccharides (Poulicek, 1982). As is the usual with animals, these organic compounds are derived from the diet, which is generally plant material in the case of land snails. Since  $\text{C}_4$  plants are highly enriched in  $^{13}\text{C}$  as compared to plants having the common  $\text{C}_3$  photosynthetic pathway, it would be expected that the organic matter in shells of snails that consume  $\text{C}_4$  plants would be enriched in  $^{13}\text{C}$ . This has been confirmed from studies of the isotopic composition of organic matter in populations of a species of land snail collected from different types of plant communities in the Negev Desert (Goodfriend, 1988).  $\text{C}_4$  plants often show distinct ecological distributions (they are characteristic of drier and/or hotter areas) and therefore reconstruction of their past distributions is informative about paleoclimate. In the Negev, for example, they are generally limited to areas receiving less than 290 mm mean annual rainfall (Goodfriend, 1990). Analysis of fossil land snails from the Negev have permitted detailed reconstruction of the range limit of plant communities with  $\text{C}_4$  species. During the middle Holocene, the boundary between pure  $\text{C}_3$

communities and those containing  $\text{C}_4$  species was shifted ca. 20 km south of its present position, implying a comparable shift in the locations of the rainfall isohyets at that time (Fig. 3; Goodfriend, 1990).

This method of paleoenvironmental reconstruction has the advantage that it provides fine geographical detail. The snails are strictly local paleoenvironmental indicators, as long as post-mortem transport does not carry them some distance away from where they lived. This level of detail cannot be achieved from the more direct method of palynology, since wind transportation of pollen will blur the boundaries of distributions. On the other hand, the use of stable isotopes of land snail organic matter has the disadvantages that it requires relatively large samples (in the order of grams), due to the low concentration of organics in the shells. Thus, only larger species are practical to work with and then only when sufficient quantities are available. The method also requires a calibration study for any species used; there is no guarantee that the species used will be sufficiently nonspecialized in its feeding habits to eat  $\text{C}_4$  species wherever they are present. Diagenesis of the shell organic matter is a potential problem. Over time the shell proteins undergo partial hydrolysis to free amino acids (Kriaušakul and Mitterer, 1980). Loss of certain organic components from the shell could lead to isotopic changes in the remaining organics, since the organic compounds are not uniform in their isotopic composition. Thus it is important to determine the state of preservation of organic matter in the shells. In Holocene land snails from the Negev, the state of preservation is excellent (Goodfriend, 1990), but it is

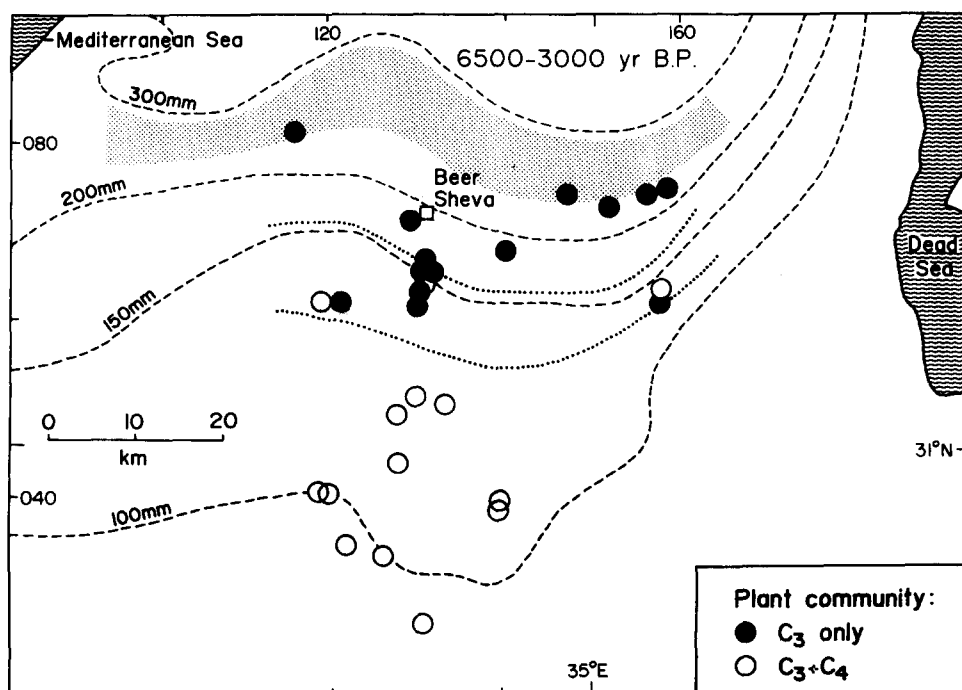


FIG. 3. The distribution of pure  $\text{C}_3$  and mixed  $\text{C}_3 + \text{C}_4$  plant communities in the northern Negev Desert during the middle Holocene (6500–3000 BP), based on analysis of the stable carbon isotope composition ( $^{13}\text{C}/^{12}\text{C}$  ratio) of organic matter in the shells of the land snail *Trochoidea seetzeni*. The dotted lines outline the position of the transition zone between pure  $\text{C}_3$  and mixed  $\text{C}_3 + \text{C}_4$  plant communities during the middle Holocene and the shaded area indicates the position of this zone at present (from Goodfriend, 1990).

not clear how general this pattern is in other regions or in older material.

Studies on the stable isotope composition of other elements in land snail shell organic matter, such as N, H, or O, have not been carried out.

### STABLE ISOTOPE COMPOSITION OF SHELL CARBONATE

#### *Carbon Isotopes*

The carbon of land snail shell carbonate is derived ultimately from three sources: organic carbon in the diet (released as respiratory  $\text{CO}_2$ ), ingested carbonates which react with acid in the stomach to produce  $\text{CO}_2$ , and atmospheric  $\text{CO}_2$  (by isotopic exchange) (Goodfriend and Hood, 1983). Consequently, interpretation of variations in the stable carbon isotope composition of shell carbonate is not a straightforward matter. Increased contributions of plant-derived  $\text{CO}_2$  will tend to deplete the shell carbonate in  $^{13}\text{C}$  relative to atmospheric or carbonate carbon sources. In areas with higher rainfall, carbonate  $\delta^{13}\text{C}$  values tend to be more depleted (Goodfriend and Magaritz, 1987). This may be the result of greater plant or soil  $\text{CO}_2$  production, causing the atmospheric  $\text{CO}_2$  at ground level to become isotopically lighter; or to increased activity of the snails in wetter areas, which would result in higher feeding rates and respiration rates. A seasonal depletion in  $^{13}\text{C}$ , during the wetter part of the year, has also been observed in one species of land snail (Magaritz and Heller, 1983). Snails living in plant communities containing  $\text{C}_4$  species tend to be slightly enriched in  $^{13}\text{C}$  as compared to those in pure  $\text{C}_3$  communities (Goodfriend and Magaritz, 1987). This is because the respiratory  $\text{CO}_2$  produced from consumption of  $\text{C}_4$  plants is enriched in  $^{13}\text{C}$ . The  $\delta^{13}\text{C}$  value of various species of land snails also shows a correlation with size, with larger species generally depleted in  $^{13}\text{C}$  (Goodfriend and Hood, 1983). This may be due to allometric surface area-volume relationships: larger snails have a lower surface area/volume ratio and therefore will be expected to undergo slower exchange with atmospheric  $\text{CO}_2$ . Consequently, respiratory  $\text{CO}_2$  will tend to dominate the  $\text{CO}_2$ -bicarbonate pool of the snail.

Variation of  $\delta^{13}\text{C}$  values of the shell carbonate of fossil land snails has received very little study. Yapp (1979) observed  $^{13}\text{C}$  variations in some species of land snails from a site in the southwestern U.S. but did not propose an explanation for this. Studies of modern snails suggest that the  $^{13}\text{C}$  of fossil shell carbonate may be a useful indicator of trends in moisture conditions or other factors that might affect plant productivity and snail activity, such as temperature. But further study of the basis for environmental correlations of shell carbonate  $^{13}\text{C}$  are needed. Analysis of shell carbonate  $^{13}\text{C}$  can also be used as a  $\text{C}_4$  plant indicator but the results will be much less precise than those obtained by analysis of the shell organic matter. Nevertheless it may be a useful method in older fossil samples where preservation of organics may be poor.

#### *Oxygen Isotopes*

The  $\delta^{18}\text{O}$  value of land snail shell carbonate relates to the  $\delta^{18}\text{O}$  value of rains, which are of paleoclimatic interest because they provide information on patterns of atmospheric circulation (source areas and trajectories of rain-bearing systems) and perhaps also temperature. The patterns of variation in the stable oxygen isotope composition ( $^{18}\text{O}/^{16}\text{O}$  ratio) of the shell carbonate of modern land snails has been the subject of a number of studies. These studies have included geographic surveys in relation to various environmental factors (Yapp, 1979; Magaritz and Heller, 1980; Lécolle, 1985; Goodfriend and Magaritz, 1987) as well as studies of temporal variations on time scales of months (Magaritz *et al.*, 1981; Magaritz and Heller, 1983) and days (Goodfriend *et al.*, 1989). The relationship between shell  $\delta^{18}\text{O}$  values and precipitation  $\delta^{18}\text{O}$  values can be thought of as involving two control steps: that determining the isotopic composition of snail body water and that involving isotopic fractionation between the body water and the shell carbonate precipitated from it. Studies of day-to-day variations in the  $\delta^{18}\text{O}$  and  $\delta D$  values of body water in a natural population of land snails living on the coastal plain of the eastern Mediterranean point to the isotopic composition of atmospheric water vapor as being the dominant control of body water isotopic composition (Goodfriend *et al.*, 1989), as originally suggested by Magaritz and Heller (1983). Since the isotopic composition of atmospheric water vapor is controlled mainly by the isotopic composition of rain, shell carbonate  $\delta^{18}\text{O}$  values can be used as indicators of rain  $\delta^{18}\text{O}$  values. Indeed, a very strong correlation between snail body water  $^{18}\text{O}$  (not measured directly but calculated from shell carbonate  $^{18}\text{O}$  by assuming equilibrium fractionation between water and carbonate) and rain  $^{18}\text{O}$  was shown for European land snails by Lécolle (1985), who suggested its use in estimating rain isotope values. However, humidity isotope values will depart from rain values where there is an influence of evaporation from a large body of water, i.e. near the shores of seas or lakes, and thus an influence on snail isotope values would be expected. Land snail body water  $\delta^{18}\text{O}$  values are enriched relative to equilibrium with rainwater (Goodfriend *et al.*, 1989; and as calculated from shell carbonate values by Lécolle (1985)). This enrichment is not fully understood but it appears to be due to enrichment in  $^{18}\text{O}$  of body water as a result of metabolic effects (metabolic water and  $\text{CO}_2$  released from respiration and therefore ultimately of plant origin); evaporation from the snail does not seem to play a significant role (Lécolle, 1985; Goodfriend *et al.*, 1989). Differences of 1–2‰ in  $\delta^{18}\text{O}$  values are found among species living together at the same location (Goodfriend and Magaritz, 1987). This is most likely to reflect differences in body water  $\delta^{18}\text{O}$  values at the time of shell deposition. It has been suggested that this could result from differences among species with respect to the time during their activity cycles (within-day or day-to-day cycles) when they deposit shell

carbonate (Goodfriend *et al.*, 1989). Within a region, a given species of snail shows relatively uniform  $\delta^{18}\text{O}$  values from population to population (Lécolle, 1985; Goodfriend and Magaritz, 1987), which implies that the offset between rainfall  $\delta^{18}\text{O}$  values and body water  $\delta^{18}\text{O}$  values is relatively uniform spatially. It is likely, therefore, that this offset will also be relatively constant over time, so that temporal changes in body water  $\delta^{18}\text{O}$  values, as indicated by measurements of shell carbonate  $\delta^{18}\text{O}$  values, will reflect changes in rainwater oxygen isotope composition, rather than changes in rainwater-body water fractionation. However, a more thorough understanding of this latter fractionation would be desirable.

The shell carbonate is precipitated from dissolved bicarbonate in the body fluids of the snail. The bicarbonate oxygen undergoes rapid isotopic exchange with the oxygen of the body water and thus its isotopic composition is set by that of the body water. Equilibrium isotopic fractionation in the water-bicarbonate-carbonate system is generally assumed for biogenic carbonates (e.g. Fritz and Poplawski, 1974). However, there is also some evidence to support a small (1–2‰) nonequilibrium fractionation between body water and shell carbonate in land snails (Goodfriend *et al.*, 1989). The equilibrium fractionation is temperature-dependent, increasing about 1‰ per 4°C decrease (Epstein *et al.*, 1953). On a broad geographic scale, precipitation  $\delta^{18}\text{O}$  values are positively correlated with temperature (Yurtsever and Gat, 1981). Within Europe, for example, precipitation  $\delta^{18}\text{O}$  values increase 1‰ per 1.2°C increase (Lécolle, 1985). Although these two temperature dependencies are opposite in direction, their net effect is dominated by the stronger relationship of precipitation oxygen isotope composition to temperature. In some areas, there is also a close relationship between variation in precipitation  $\delta^{18}\text{O}$  values and temperature over time, on a seasonal or year-to-year time scale (Siegenthaler and Matter, 1983). In other areas, variations in the source areas of rain-bearing air masses is the dominant control of temporal variations in rainwater  $\delta^{18}\text{O}$  (Rindsberger *et al.*, 1983). Thus interpretations of the paleoclimatic significance of changes in precipitation  $\delta^{18}\text{O}$  values over time will vary for different regions.

The oxygen isotope composition of land snail shell carbonate does not necessarily reflect the annual mean  $\delta^{18}\text{O}$  value of precipitation. Most land snails are seasonal in their activity, becoming dormant during dry or cold seasons. Since shell growth will occur only during periods of activity, the isotopic value of the shell carbonate will represent only those rains which occurred within the activity season of the snails. In some areas this presents no special problem. For example, around the Mediterranean, rains occur only during the cooler half of the year; but temperatures are then warm enough so that activity can generally occur after each rain event (except in high mountains), with the result that the snails will sample the whole year's precipitation. On the other hand, in more temperate areas,

activity will be inhibited by low temperatures during seasons when rains may occur.

There have been relatively few studies of  $^{18}\text{O}$  variation in fossil land snails. Yapp (1979) studied a series of Holocene land snails from an archeological site in the southwestern U.S. and attributed the observed trend to changes in moisture or temperature. Magaritz and Heller (1980) studied samples from several archeological sites in the southern Levant and interpreted isotopic changes as relating to changes in moisture conditions. Subsequent studies of modern land snails suggest changes in rain  $\delta^{18}\text{O}$  values would be a more likely explanation in both these cases. In Europe, small differences in the oxygen isotope composition of land snail shell carbonate between modern and apparently Holocene samples have been suggested to reflect small temperature changes (Lécolle and Létolle, 1990). Recently, an  $^{18}\text{O}$  curve for the Holocene of the Negev Desert in southern Israel has been derived from shell carbonate of fossil land snails (Goodfriend, 1991a). This shows a distinct trend (Fig. 4), with a minimum centered around ca. 6 ka BP and points to temporal changes in atmospheric circulation, which brought rains from different source areas into the region.

Although not without problems, land snail shell carbonate would seem to provide one of the better sources of information on the isotopic composition of rains in the past. Many materials are subject to large evaporative enrichment effects (plant cellulose, freshwater carbonates) whereas others may be strongly modified by metabolic effects (bone phosphate). Even direct measurements of paleogroundwaters are subject to problems, e.g. they cannot usually be well dated and samples are available only for wetter periods when recharge occurred.

#### PALEOTEMPERATURE ESTIMATES FROM AMINO ACID EPIMERIZATION/RACEMIZATION RATES

Rates of racemization (referring to D/L enantiomer ratios of various amino acids) and epimerization (referring to D/L epimer ratios, usually D-alloisoleucine/L-isoleucine) are highly temperature dependent, approximately doubling with every 4–5°C increase. While absolute temperature estimates from the racemization/epimerization rates are not very precise (McCoy, 1987), the average difference in temperature between two periods of time can be estimated with reasonable precision from two known-age samples, based on the following equation (Goodfriend and Mitterer, 1988, as modified from Schroeder and Bada, 1973):

$$T_2 - T_1 = \Delta T = \frac{RT_1 T_2}{E_a} \ln(k_2/k_1), \quad (1)$$

where  $T$  is the average sample temperature (in K),  $R$  is the gas constant ( $=1.987 \times 10^{-3}$  kcal/deg mol),  $E_a$  is the Arrhenius activation energy, and subscripts 1 and 2

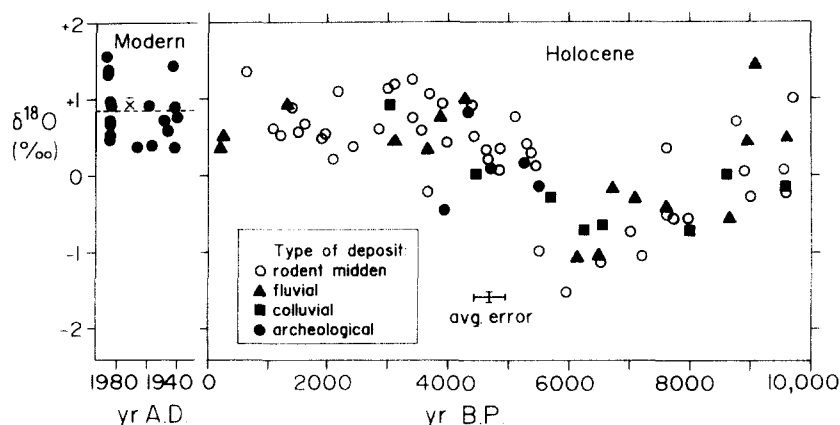


FIG. 4.  $\delta^{18}\text{O}$  values of shell carbonate of the land snail *Trochoidea seetzeni* from the northern Negev Desert. Values of modern snails are shown on the left and fossil snail values are plotted (right) in relation to radiocarbon ages. Fossil samples were collected from several different types of deposits (from Goodfriend, 1991a).

refer to the two samples of different ages. This equation can be solved by iteration (Goodfriend and Mitterer, 1988). The value for the activation energy ( $E_a$ ), which reflects the sensitivity of the epimerization or racemization rate to temperature changes, can be estimated from measurement of the rate at a range of different temperatures (e.g. Bada *et al.*, 1973; Mitterer, 1975; Miller, 1985). Since the older of the two fossil samples used for paleotemperature analysis will have experienced, during the later part of its existence, the same temperature history as the younger sample, this part of the racemization or epimerization of the older sample (which occurred during the duration of existence of the younger sample) can be 'subtracted out', to determine the net racemization or epimerization which occurred during the earlier part of its existence. Comparison of rates for these earlier and later periods then yields an estimate of the temperature difference between these periods. The rate constant ( $k$ ) for epimerization can be calculated from the age and D-alloisoleucine/L-isoleucine ratios of the samples, according to the following equation (Goodfriend and Mitterer (1988):

$$k = 0.565 \left[ \ln \left( \frac{0.565}{0.565 - A_{t_2}} \right) - \ln \left( \frac{0.565}{0.565 - A_{t_1}} \right) \right] / (t_2 - t_1), \quad (2)$$

where  $A_t = R/(1+R)$  of the sample of age  $t$  ( $R$  is the D-alloisoleucine/L-isoleucine ratio). For enantiomers, the racemization rate constant can be calculated from:

$$k = \left( \ln \left[ \frac{1+D/L}{1-D/L} \right]_{t_2} - \ln \left[ \frac{1+D/L}{1-D/L} \right]_{t_1} \right) / 2(t_2 - t_1), \quad (3)$$

(modified from Bada and Protsch, 1973).

This approach to paleotemperature analysis was applied to fossil land snails from Jamaican cave deposits by Goodfriend and Mitterer (1988). It has also

been used with marine mollusk shells (Miller, G.H. *et al.*, 1987).

The precision of the estimates are limited by the precision of the dating of the samples and of the D/L amino acid ratio measurements. Other problems, however, may affect the accuracy of the estimates. Prime among these is whether the kinetics of modern snails used in the heating experiments to determine  $E_a$  are comparable to the kinetics of the fossils throughout their lifetime. The rates of racemization or epimerization are strongly dependent on the structure of the proteins or peptides (Kriausakul and Mitterer, 1980; Smith and de Sol, 1980). Consequently, differences in the pattern of diagenetic alteration of shell proteins in the fossils vs. the heated modern shells could cause differences in the kinetics. Differences in the racemization/epimerization kinetics of fossil and modern shells of the same species have recently been demonstrated (Goodfriend and Meyer, 1991). The formulation presented in Eqs 1–3 assumes that racemization/epimerization follows first-order reversible kinetics. This is not the case for some amino acids (Goodfriend, 1991b). For other amino acids, such as isoleucine, the first-order kinetic model fits well at lower D/L values (Goodfriend, 1991b), but not at higher values (Mitterer and Kriausakul, 1989). Because of these various problems, experimental analysis of the kinetics of samples used in paleotemperature analysis is desirable in order to ensure accurate results.

#### SOME POTENTIAL USES OF LAND SNAILS IN PALEOENVIRONMENTAL STUDIES

There remain a number of as yet unexplored possibilities for extracting paleoenvironmental information from fossil land snails. A few of these potential uses are mentioned here.

Investigations of the stable isotope composition of H and N in land snail organic matter have not yet been carried out. The D/H ratio of these organics should relate primarily to that of the plants that the snails eat; fossil land snails may constitute an isotopic record of

these plants where the plant remains themselves no longer exist. Stable isotopes of H in plants have been used to infer various paleoenvironmental conditions, such as rainfall amounts (Krishnamurthy and Epstein, 1985; Dubois and Ferguson, 1985) and the isotopic composition of rainfall (Yapp and Epstein, 1977). But recent studies on modern plants have pointed out a number of complications in the interpretation of the stable H isotope composition of plants in terms of climate (Sternberg, 1988; Yakir *et al.*, 1990). However, if future studies could locate and isolate particular H atoms of certain compounds which were added on by the snail during the synthesis of these compounds from other organic precursors, their isotopic composition would relate to that of snail body water, which relates in turn to precipitation  $\delta D$  values. Combined with information on precipitation  $\delta^{18}O$  values derived from analysis of shell carbonate, the deuterium excess parameter (Dansgaard, 1964) could be estimated and this is of interest in determining past rainfall sources and precipitation processes. Nitrogen isotopes have been studied mainly in plants and in the collagen of mammal bones. In plants, the nitrogen isotope composition varies according to whether the plant is a nitrogen fixer or not (see references in DeNiro and Epstein, 1981). Mammal bones will reflect the inclusion of nitrogen-fixing plants such as legumes in the diet of the animal as well as other influences. It has been shown, for example, that  $\delta^{15}N$  values in mammal bone collagen correlate with rainfall (Heaton *et al.*, 1986; Sealy *et al.*, 1987). The basis for this correlation has been suggested to be in variation in the amount of urea excretion in the animals in relation to their water balance; evidence points to urea production being an isotopically fractionating process (Ambrose and DeNiro, 1986). Both of these environmental influences, i.e. legumes in the diet and moisture conditions as reflected in water balance, may also be detectable in

the nitrogen isotope composition of organic matter in land snail shells.

Periodic growth lines of both living and fossil marine mollusk shells have been studied to obtain information on life history properties such as age and growth rate (Jones, 1980, 1983). From these life history properties, information on environmental or paleoenvironmental conditions, such as temperature, can be obtained (Jones, 1981). Analysis of growth lines has also been used to determine the seasonality of collection of mollusk shells found in archeological sites (see, e.g. reviews by Deith (1985) and Rollins *et al.* (1990)) and to infer the occurrence of temperature (hot or cold) stress (Pallant, 1990). Growth line analysis has not yet been applied to terrestrial mollusks, even though they commonly display growth lines (e.g. Pollard *et al.*, 1977). In terrestrial mollusks, growth lines are a consequence of disruptions of growth due to unfavorable conditions for activity, such as cold temperatures or lack of rain. Where annual growth lines occur, the annual growth rate can be determined from the shells and this is likely to correlate with environmental conditions such as rainfall. Such studies thus hold good potential for providing paleoenvironmental information.

Stable isotope profiles of land snail shells may also provide important paleoclimatic information. An example of a profile of  $^{18}O$  is shown in Fig. 5. Such studies have been carried out in marine bivalves and have produced information on seasonal temperature variations in the past, (e.g. Killingley, 1981; Krantz, 1987). However, in land snails, these short-term variations in  $^{18}O$  will reflect variations in the isotopic composition of rainfall as well as seasonal temperature variations. This opens up the possibility of using land snails to determine changes in the seasonal importance of different rainfall sources (e.g. variations in monsoon intensity) which may have different isotopic composi-

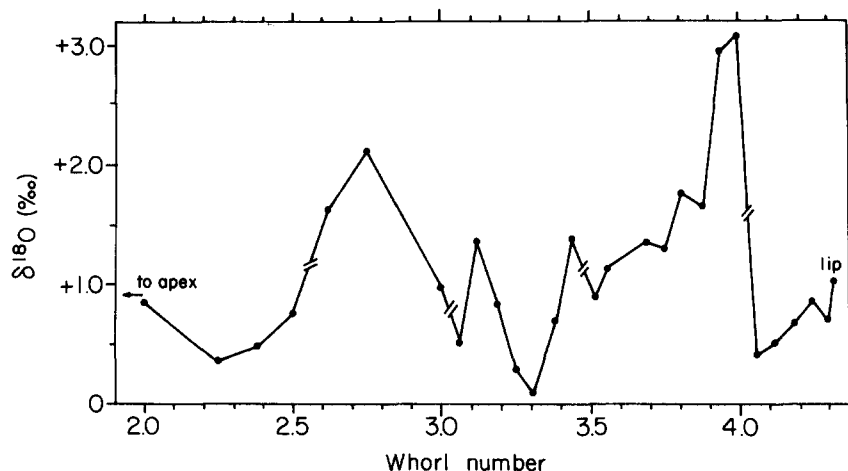


FIG. 5. Serial analysis of  $^{18}O$  in an adult shell of the land snail *Levantina caesareana* from Ein Fawar, Wadi Kelt, NE of Jerusalem. The first sample was taken just after the embryonic shell and the last at the lip of the shell. Sample positions were recorded by whorl number, i.e. the number of whorls (turns) after the apex. The inner layer of shell material, which is laid down over the entire inside of the shell only after the snail reaches adulthood (marked by reflection of the lip), was removed by grinding before samples were taken. Breaks in the line represent growth lines, i.e. places where shell growth ceased and resumed only sometime later. In these snails, these breaks generally occur annually, during the summer dry season.

tions. If growth occurs after every rain event, then each rain will have an isotopic record in the shell. However, such applications would require detailed study of the life history, growth and activity patterns of the snails. Further problems in interpretation come from short-term variations in body water  $\delta^{18}\text{O}$  values relating to physiological processes rather than to environmental influences (Goodfriend *et al.*, 1989). Nevertheless, a detailed investigation of the use of stable oxygen isotope profiles of land snails shells would seem worthwhile.

Pedogenic (soil) carbonates are an important source of paleoenvironmental information. They are deposited only under a limited range of rainfall conditions and their rate of deposition as well as their isotopic composition vary in relation to environmental conditions (e.g. Cerling, 1984; Goodfriend and Magaritz, 1988). Pedogenic carbonates are commonly deposited as a partial coating on buried land snail shells. These would provide the same type of paleoenvironmental information as carbonate nodules within the soil, but they have the advantage that they are relatively pure (i.e. they contain less detrital material because they are deposited as coatings on a solid surface rather than around grains which they incorporate). This means that measured isotopic values and radiocarbon dates will be less affected by the presence of original detrital carbonates. Another advantage of studying the carbonates on shells is that in some cases they may be emplaced later than the time of deposition of the sediments (e.g. in shell middens in rodent burrows; Goodfriend, 1987a). These can therefore be used to study different time periods of soil evolution within a single profile.

## CONCLUSIONS

As is apparent from the foregoing sections, land snails have been relatively neglected as a source of paleoenvironmental information, apart from faunal studies. This is in part due to the fact that the database available in the literature for modern land snails is very limited as compared to that for other organisms such as plants or vertebrates. Consequently most studies of fossil land snails also require the study of modern land snails to serve as a basis for interpretation. Once one accepts this necessity, a wealth of potential paleoenvironmental information is available from fossil land snails.

Land snail shells hold a number of advantages over other materials as sources of paleoenvironmental information. They are strictly local indicators of environmental conditions (since snails move around very little), provided there has been no long-distance post-mortem transport. This is critical in regions with strong environmental gradients where averaging over a broad area would lead to an unrealistic scenario. The shells can generally be dated, so that the paleoenvironmental information obtained from the shells is dated directly. One thus avoids the problems and uncertainties of

dating of paleoenvironmental indicators by stratigraphic association with other datable materials. Furthermore, because most land snail shells are sufficiently large for amino acid racemization/epimerization and AMS  $^{14}\text{C}$  analyses, it is possible to deal objectively with problems of redeposition and resulting mixed-age faunas.

No one method of paleoenvironmental reconstruction may be considered completely reliable — all interpretations depend on assumptions of correct analogies. Yet some methods have advantages over others. In general those features of land snail shells that are under the control of fewer factors are preferred. Thus isotopic methods hold an advantage over methods based on biological properties (such as species abundances and shell morphology) because the rules controlling isotopic fractionation are relatively few and generally well known. Nevertheless, the ambiguity of all methods means that reliable paleoenvironmental analyses require that results be confirmed by another, independent line of evidence.

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