Comp. Biochem. Physiol. Vol. 102B, No. 2, pp. 199–204, 1992
Printed in Great Britain

0305-0491/92 $5.00 + 0.00
Pergamon Press Ltd

MINI REVIEW

OVERVIEW OF AMINO ACID GEOCHRONOLOGY

D. S. KAUFMAN* and G. H. MILLER

Center for Geochronological Research, INSTAAR and Department of Geological Sciences, University of Colorado, Boulder, CO 80309-0450, U.S.A. (Tel: 303 492-6962; Fax: 303 492–6388)

(*Received* 9 *October* 1991)

INTRODUCTION

The ages of Quaternary (past 1.6 million years) geological, climatological and archeological events older than the range of radiocarbon dating (>40,000 yr) are often poorly known and controversial. Improving their chronological control would elucidate the history of, and interrelations between, global climate fluctuations, paleoenvironmental changes and hominid evolution. Reconstructing regional and global paleoenvironments requires, at a minimum, accurate stratigraphic correlations; understanding the forcing mechanisms and rates of paleoenvironmental change requires a reliable absolute time scale. Amino acid geochronology has received increasing research attention as a promising means of providing relative chronostratigraphies and, in some cases, independent dates for organic-bearing deposits well beyond the range of radiocarbon. Because all living organisms contain amino acids, the technique offers a wide range of possible applications over diverse depositional settings.

Since the first use of amino acids to date fossil mollusc shells in the late 1960s (e.g. Hare and Mitterer, 1967), their utility as a geochronological and paleoclimatological tool has advanced significantly. The technique is now widely accepted as a standard chronostratigraphic tool for Quaternary research. The purpose of this paper is to provide a brief overview of the principles and applications of the technique, particularly as they relate to carbonate fossils, and to highlight some recent advances.

PRINCIPLES

Fossil remains of biogenic carbonate contain trace quantities of indigenous organic matter which is preserved for an extended period of geologic time (Abelson, 1955). In many skeletal remains the organic matter is composed of thin protein membranes that play an active role in the biomineralization process (Crenshaw, 1980). After death of the organism, the proteins degrade through a complex series of chemical reactions. Large proteins are hydrolyzed into smaller polypeptide chains, eventually forming free amino acids; some amino acids are converted into simpler amino acids, or decompose into non-amino-acid molecules. By evaluating the extent to which these chemical changes have progressed, the length of time elapsed since death of the organism can be estimated.

For most geochronological purposes, the most reliable of the complex network of interrelated reactions involved in protein diagenesis is amino acid racemization, which involves the inversion of L-(*levo*) amino acids to their D-(*dextro*) isomeric configuration. When organisms are living, they utilize amino acids exclusively of the L-configuration. Upon death and the removal of biological constraints, the L-amino acids begin to racemize to their D-configuration. The abundance of D- relative to L-forms (D/L) of a specific amino acid defines the extent of racemization; the ratio increases with time after death until the rate of formation of D-amino acids is compensated by the reverse reaction, and the ratio reaches an equilibrium value of approximately 1.0–1.3, depending on the particular amino acid.

Of the approximately 20 amino acids found in carbonate shells, isoleucine and leucine are most widely used for geochronological applications. Both racemize relatively slowly, are stable acids that are not created by decomposition of other more complex forms, and are uncommon as contaminants (Miller and Brigham-Grette, 1989). Unlike most other amino acids, isoleucine contains two centers of asymmetry (chiral carbon atoms). For L-isoleucine, inversion occurs about the alpha-carbon atom, producing the new molecule D-alloisoleucine ("allo" for "other") through the process of epimerization. The diastereomers D-alloisoleucine/L-isoleucine (termed "A/I" by some workers) are distinct enough chemically to be separated by conventional ion-exchange liquid chromatography. Analytical separation of other D- and L-enantiomers is usually accomplished by gas chromatography. Analyses are most commonly performed on the total population of amino acids after acid hydrolysis in the laboratory. In some cases, a separate preparation of the naturally hydrolyzed free amino acid fraction has also been used (e.g. Miller, 1982).

A wide range of biogenic carbonate systems have been used for amino acid geochronology including bivalves, gastropods, foraminifera, coral and avian eggshells; non-carbonate fossil such as wood, teeth and bone are also used, although with less success.

*Current address: Department of Geology, Utah State University, Logan, UT 84322-4505, U.S.A.

Protein concentrations in most of these biogenic carbonates are high enough and detection capabilities sensitive enough that 2 mg of sample is sufficient for an analysis.

Kinetics of amino acid racemization in carbonate systems

The kinetics of the racemization/epimerization (hereafter, simply "racemization") reaction have been evaluated for a variety of biogenic materials by measuring D/L values in samples subjected to isothermal high-temperatures for known lengths of time (e.g. Mitterer, 1975; Miller, 1985; Brooks *et al.*, 1990). These pyrolysis experiments attempt to simulate, in a short period of time, slower processes that take place in natural samples at lower temperatures. The results demonstrate that, for samples held under isothermal conditions, the rate of racemization follows an exponential function of time; it dsecreases as the relative concentration of the D-isomer and, therefore, the rate of the reverse reaction increases (Fig. 1a). This relationship holds true in laboratory experiments as well as in fossil foraminifera recovered from deep-sea sediments where temperatures have remained relatively stable and sample ages can be determined independently by radiocarbon dating (Fig. 1b; Müller, 1984).

Like other chemical reactions, the rate of racemization is dependent primarily upon the temperature of the reaction medium. The present mean annual air temperature (MAT) can be used to gauge the temperature dependency of the reaction in fossil materials. For equatorial sites (MAT > 25°C), the equilibrium D/L ratio for the amino acid isoleucine (*ca* 1.3) is attained after 100,000–300,000 yr; in contrast, at Arctic sites (MAT < 10°C), equilibrium requires more than 10 million yr (Miller and Brigham-Grette, 1989). By heating samples in the laboratory over a range of temperatures, pyrolysis experiments provide a more well-controlled environment for evaluating the temperature sensitivity of the rate of racemization. The results show that the rate approximately doubles for every 4°C rise in ambient temperature (Miller and Mangerud, 1985). The exponential relation between temperature and the rate of racemization is exemplified by studies of molluscan shells that are independently dated to the last interglacial high-sea stand (125,000 yr) and have been subjected to a range of post-depositional thermal regimes (Fig. 2; Hearty and Miller, 1987).

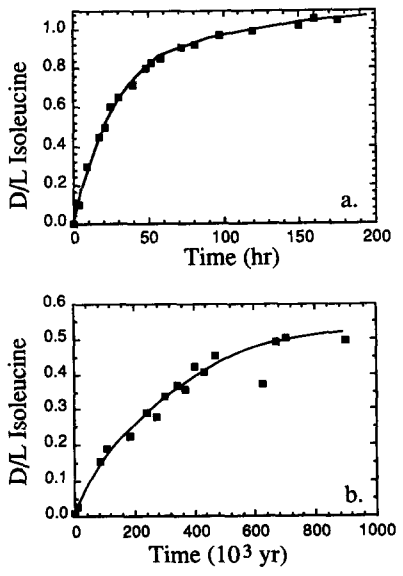

Fig. 1. Relation between the extent of amino acid (isoleucine) racemization (D/L) and time as determined in: (a) the molluscan genus *Mercenaria* subjected to high-temperature (152°C) pyrolysis experiments (from Mitterer and Kriausakul, 1989); and (b) the foraminifera *Globorotalia* from eastern Atlantic deep-sea core 13519-2 dated independently by radiocarbon (from Müller, 1984). D/L ratios follow an exponential function of time for both laboratory-induced and natural diagenetic racemization.

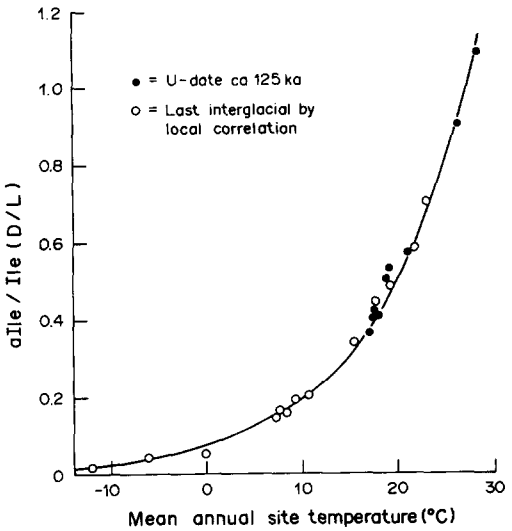

Fig. 2. Mean D/L ratios in samples from deposits of the last interglaciation (125,000 yr ago) worldwide. Ratios are measured in genera that racemize at a similar rate (from Hearty and Miller, 1987).

The kinetics of the racemization reaction are typically modelled mechanistically as a first-order reversible reaction. Based on this kinetic theory, D/L ratios measured in laboratory-heated samples can be related to the forward rate constant of the reaction; the rate constant, in turn, can then be related to the reaction temperature using the Arrhenius equation. This approach, however, is limited by the complexities within biogenic systems; amino acids racemize at different rates depending on their position within the protein or peptide chain. Racemization is faster for amino acids in terminal positions, and slower for those that are internally bound; amino acids that have been completely hydrolyzed from the peptide chain to form free molecules racemize slowest. Because the reaction network involved in protein diagenesis includes the transfer of amino acids from their bound to free states, the overall (apparent) rate of racemization does not follow the theoretical pathway predicated by first-order reversible kinetics. Adding to the complexity of the reaction network in some biogenic systems is the slow loss of amino acids with time, due partially to post-depositional leaching and perhaps microbial decay (Haugen, 1990). As a result of these

complexities, the rate of racemization in most carbonate systems slows beyond the decrease predicted by the reversible first-order rate law for D/L ratios greater than about 0.3, eventually reaching a rate that is about a tenth of the initial phase (Mitterer and Kriausakul, 1989). Because the mechanistic model fails to satisfy the data beyond the initial stages of racemization, some workers have adopted empirical models, including parabolic (Mitterer and Kriausakul, 1989; Kaufman, 1992) and other exponential functions (Wehmiller *et al.*, 1988), to approximate the overall result of the complex diagenetic processes responsible for the degradation of proteins and their constituent amino acids within the carbonate matrix.

An important exception was recently observed for fossil and pyrolyzed ostrich eggshells in which the rate of racemization follows first-order kinetics beyond a D/L ratio of 1.0 (Brooks *et al.*, 1990). This behavior must be related to the greater integrity of the eggshell system as compared to other carbonate matrices. The eggshell approximates a closed system with respect to indigenous amino acids, minimizing the loss of amino acids by diffusional processes that otherwise affect the apparent rate of racemization in other, less ideal, systems. In addition, the kinetics of racemization in ratite eggshell appears to be less sensitive to the relative position of the particular amino acid in the peptide chain, compared to other carbonate matrices (Miller *et al.*, 1990). These properties indicate that amino acid racemization in ostrich eggshells offers particularly high precision for geochronological purposes.

An additional factor governing the rate of racemization in biogenic systems is taxonomy. This taxonomic effect results from differences in the sequences of amino acids and the variable bonding strengths between adjacent amino acids within the protein. To minimize the taxonomic effect, analysis and interpretation of D/L ratios are typically restricted to one or a few of the most commonly occurring genera. The most suitable taxa are those in which D/L ratios vary minimally within a shell and are reproducible between individuals of the same age (Miller and Brigham-Grette, 1989).

APPLICATIONS

Relative-age chronologies

Converting D/L ratios to absolute ages is often difficult because the precise temperature history of a fossil is rarely known. A simpler and more reliable application of D/L ratios is as relative age indices. Within a limited geographic area, where the thermal history is uniform, D/L ratios can be used directly to construct a regional relative chronostratigraphic framework. This application, termed "aminostratigraphy" (Miller and Hare, 1980), is independent of assumptions regarding the rate of racemization, so that differences in D/L ratios are interpreted exclusively as differences in age. Thus, groupings of samples with similar D/L ratios, termed "aminozones" (Nelson, 1978), represent intervals of sediment accumulation within a sedimentary sequence. Aminozones can be used to correlate sedimentary units across disjunct exposures.

The primary application of aminostratigraphy has been in studies of the relative chronology of mollusc-bearing coastal sediments deposited during high-sea stands of the late Pliocene and Pleistocene. It has been successfully applied in a wide range of environments from the Arctic to lower middle latitudes. Regional studies include the Canadian Arctic (Miller, 1985), northwestern Alaska (Brigham-Grette and Carter, 1992; Kaufman, 1992), Norway (Miller *et al.*, 1983), Northwest Europe and the UK (Miller and Mangerud, 1985; Bowen *et al.*, 1985), the Pacific coast of the US (Kennedy *et al.*, 1982; Wehmiller, 1984) and Peru (Hsu *et al.*, 1989), the US Atlantic Coastal Plain (York *et al.*, 1989; Wehmiller *et al.*, 1988), and the Mediterranean (Hearty *et al.*, 1986). The technique has been employed with equal success to chronostratigraphic studies of terrestrial deposits, including those of the UK (Miller *et al.*, 1979; Bowen and Sykes, 1988), Eastern Europe (Oches and McCoy, 1990), interior US (Scott *et al.*, 1983; McCoy, 1987a; Miller *et al.*, 1987; McCoy and Miller, 1990), and the Negev Desert (Goodfriend, 1987). The technique has also been used in deep-sea chronostratigraphy by studying the extent of racemization in downcore samples of foraminifera from the Arctic Ocean (Sejrup *et al.*, 1984), North Sea (Sejrup *et al.*, 1987), Gulf of Mexico (Johnson, 1990), and the equatorial Pacific and Atlantic Oceans (Müller, 1984; King, 1977). A thorough and up-to-date review of many of these studies is provided by Wehmiller (1990). Figure 3 illustrates examples from five sites, where D/L ratios were instrumental in devising local chronostratigraphies.

The technique is applicable not only to *in situ* samples collected from superposed stratigraphic units, but is also useful in the case of transported shells from redeposited sediment. Because an aminozone is defined solely on the basis of clusters and gaps in the distribution of D/L ratios, it need not correspond to bio- or lithostratigraphic subdivisions of a sedimentary sequence. Nor must an aminozone necessarily be represented by any *in situ* lithostratigraphic unit; instead, it may be composed of reworked material contained in glacial debris (e.g. Andrews *et al.*, 1983) or even mine tailings (e.g. Kaufman, 1991). Likewise, a single lithostratigraphic unit may contain multiple aminozones separated by lithologically indistinguishable depositional hiatuses.

By analyzing a number of individuals from a single stratigraphic horizon, D/L ratios can be used to detect mixed-age assemblages and to test if samples are contemporaneous. A unimodal distribution of D/L ratios reflects a single-age population probably deposited contemporaneously with the enclosing sediments, whereas a multimodal distribution indicates the presence of a mixed-age population. The method serves as a valuable screening tool, whereaby D/L ratios are measured in a group of shells to determine their relative-age distribution. Individual shells representative of each relative-age class can then be analyzed by other geochronologic methods (Miller *et al.*, 1987; Walters, 1988).

Absolute-age chronologies

Perhaps the most problematic application of acid geochronology is determining the absolute (numerical) age of a sample. Accurate age determinations

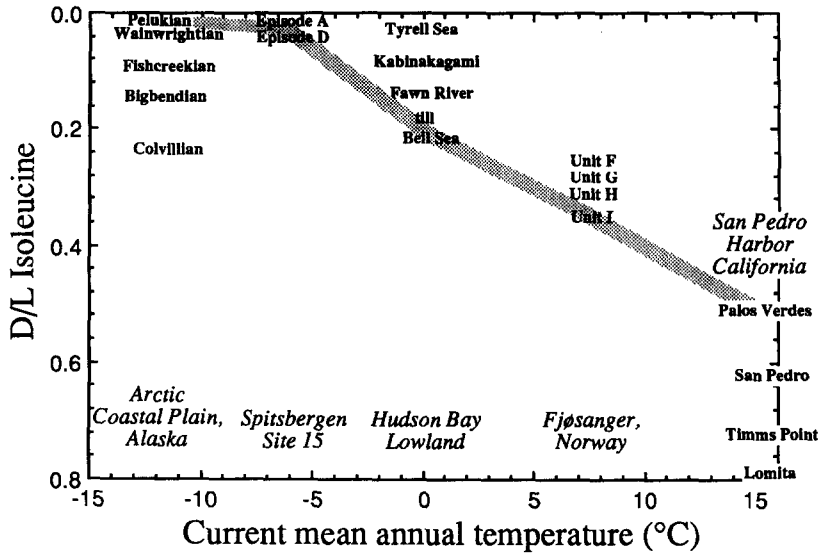

Fig. 3. Litho- and aminostratigraphy at five sites ranging from −12 to +15°C present mean annual temperature. Stratigraphic units are arranged according to their physical superposition and by their mean D/L ratio. The patterned line connects units believed to date to the last interglaciation (125,000 yr BP). D/L ratios were measured in the molluscan genera *Hiatella* and *Mya* (which racemize at a similar rate) for all but the San Pedro Harbor site where *Mercenaria* was used. Arctic Coastal Plain data from Brigham-Grette and Carter (1992), Spitsbergen from Miller *et al.* (1989), Hudson Bay Lowland from Andrews *et al.* (1985), Fjøsanger from Miller *et al.* (1983) and San Pedro Harbor from Wehmiller (1984).

require a secure reconstruction of the integrated post-depositional thermal history of a site and a valid model of racemization kinetics. In most cases, neither is well-constrained. Nonetheless, the extent of amino acid racemization in a fossil organism does contain primary chronological information, which, when interpreted prudently, can offer valuable temporal information.

There are two general approaches to converting the D/L ratios of a fossil to an absolute time scale: the first is a calibrated approach, in which the D/L ratio is used to interpolate between, or extrapolate beyond, the known ages of one or more independently dated aminozones within a limited geographic region where temperature histories are similar. In the second approach, the effects of time and temperature on the extent of racemization are determined in modern shells subjected to high-temperature laboratory experiments. This relationship, together with a model of racemization kinetics, is used to calculate the age of a sample if its D/L ratio and temperature history are known. In practice, some combination of the two approaches is typically employed. For example, a kinetic model is used to estimate the age of an undated sample by extrapolating beyond a calibration point, or a calibration curve developed for one thermal regime is applied to another using a kinetic model to adjust the reaction rate for differences in site temperature.

The most appropriate and frequent use of D/L ratios as absolute-age indicators is in providing reasonable constraints on the likely age range of a sample. For example, a Holocene rate constant can be calculated using radiocarbon-dated samples of the last 10,000 yr. This rate constant can then be applied to D/L ratios measured in older, late Pleistocene samples from the same area. Because temperatures during the Holocene were generally warmer than during the late Pleistocene, the age calculated using the Holocene rate constant must underestimate the true age of the late Pleistocene sample. In some cases, the late Pleistocene temperature depression can be determined using independent paleoclimatic evidence, which in turn, can be used to evaluate the time/temperature combinations needed to explain a particular D/L ratio.

The dating of stratified cave deposits containing ostrich eggshells in association with archeologically significant material provides a recent example of the use of the racemization reaction to derive absolute ages. Ostrich and other ratite eggshells are ubiquitous in prehistoric sites of Africa, Australia and the Middle East where early humans used the eggs for food, water vessels and more recently, for beads. Brooks *et al.* (1990) measured D/L ratios in ostrich eggshells from radiocarbon and uranium-series dated sites in Africa to calibrate the racemization rate constant; using this rate constant, the ages of older Middle Stone Age levels were estimated at 65,000–85,000 yr BP. The technique was also useful in demonstrating the stratigraphic integrity or admixture within particular levels.

In a companion study, Miller *et al.* (1991) used D/L ratios in ostrich eggshells associated with lacustrine deposits to date the history of Quaternary lake level fluctuations at Bir Tarfawi and Bir Sahara East, two depressions in the present-day hyperarid eastern Sahara. Using uranium-series dates on algal mats contained within some lake beds for calibration, the D/L ratios in eggshells associated with other lacustrine sediments were used to date the most recent Pleistocene lacustrine interval to about 100,000 yr BP, and two older intervals, one about 200,000 ± 25,000 yr BP, and another that occurred prior to 250,000 yr BP. These estimates indicate that the lacustrine intervals

apparently coincided with Northern Hemisphere solar-radiation maxima.

Paleothermometry

Because the extent of racemization is dependent on both temperature and time, the average post-depositional temperature can be determined from the D/L ratio if the sample age is known independently. By integrating the entire post-depositional temperature history of a deposit, the amino acid data provide a more reliable means of evaluating long-term climate changes, as compared to the geologically instantaneous paleoenvironmental evidence contained within the deposits themselves. This is particularly true for high-sea-level deposits which are necessarily biased toward peak-interglacial conditions. The potential of amino acids for paleotemperature reconstructions was reviewed by McCoy (1987b). He concluded that D/L ratios can be used to measure paleotemperatures with a precision of about ± 3°C. Where paleotemperatures are calculated from samples of different age, the temperature difference between the two periods is accurate to within ± 1°C.

In a recent study, D/L ratios were measured in AMS-^{14}C-dated planktonic foraminifera recovered from upper-Quaternary marine sediment from the Indian, mid-Pacific and mid-Atlantic Oceans to determine the magnitude of bottom-water temperature changes during the last glacial–interglacial transition (Johnson *et al.*, 1990). Paleotemperature calculations based on these measurements together with analyses of pyrolized foraminifera indicate that temperature of oceanic bottom water in the Indian Ocean increased by about 3°C during this period. This provides an independent confirmation of temperature changes previously estimated by changes in the oxygen-isotopic composition of fossil benthic foraminifera.

A similar approach was used by Oches *et al.* (1989) to estimate paleotemperatures in the lower Mississippi River valley during the last glacial maximum (~24,000–18,000 yr B.P.). Using a rate expression derived from D/L ratios measured in radiocarbon-dated and laboratory-pyrolized terrestrial gastropod shells, temperature reductions of about 8–12°C were estimated for several periods bracketing the last glacial maximum. Likewise, in northern United Kingdom, Miller *et al.* (1987) compared D/L ratios measured in marine molluscs from two deposits, one with D/L ratio of 0.055 and a radiocarbon age of 11,500 yr BP, and a nearby site with only slightly higher D/L ratios (0.078) but with a much greater radiocarbon age (>42,000 yr). They calculated that the minimum glacial-age temperature depression required to explain the data was 9°C.

SUMMARY

Amino acid geochronology is an increasingly important chronostratigraphic tool than can be used in a wide range of Quaternary geologic settings. The technique has been applied to deep-sea and coastal marine deposits, terrestrial deposits and archeological sites. Although a wide variety of preserved organic remains have been used, most recent studies have focused on marine molluscs and foraminifera. Studies utilizing bone remain controversial. The most successful applications rely on D/L ratios as relative-age indices that are independent of assumptions regarding post-depositional temperatures. As a relative-age tool, D/L ratios provide a basis for identifying unconformities in stratigraphic sequences, resolving mixed populations of reworked material and evaluating stratigraphic correlations between disjunct exposures. D/L ratios, combined with independent paleoenvironmental evidence, can be used to constrain the reasonable time/temperature range of a stratigraphic unit. Where the ages of units are known from independent determinations, D/L ratios can be used to evaluate the overall temperature history of a deposit. A newly emerging and particularly promising application of the amino acid geochronology is in dating eggshell from archeological sites. The outstanding potential of this application is derived from the integrity of the eggshell carbonate matrix which, better than any other carbonate system, approximates a closed system for the retention of amino acids.

Acknowledgements—Research at the Amino Acid Geochronology Laboratory, University of Colorado, has benefited from the support of the National Science Foundation and other agencies over many years, and through the interaction of colleagues and students too numerous to identify singly here. To these institutions and individuals, we extend our appreciation.

REFERENCES

Abelson P. H. (1955) Organic constituents of fossils. Yearbook 54, pp. 107–109. Carnegie Institution, Washington, DC.

Andrews J. T., Miller G. H., Vincent J.-S. and Shilts W. W. (1985) Quaternary correlations in Arctic Canada. *Quatern. Sci. Rev.* **6**, 243–249.

Andrews J. T., Shilts W. W. and Miller G. H. (1983) Multiple deglaciations of the Hudson Bay Lowlands, Canada, since deposition of the Missinaibi (last-interglacial?) Formation. *Quatern. Res.* **19**, 18–37.

Bowen D. W. and Sykes G. A. (1988) Correlation of marine events and glaciations on northeast Atlantic margin. *Phil. Trans. R. Soc. Lond. B* **318**, 619–635.

Bowen D. W., Sykes G. A., Reeves A., Miller G. H., Andrews J. T., Brew J. W. and Hare P. E. (1985) Amino acid geochronology of raised beaches in southwest Britain. *Quatern. Sci. Rev.* **4**, 279–318.

Brigham-Grette J. and Carter L. D. (1992) Pliocene and early Pleistocene marine transgressions of northern Alaska. Circumarctic correlations and paleoclimatic interpretations. *Arctic* (in press).

Brooks A. S., Hare P. E., Kokis J. E., Miller G. H., Ernst R. D. and Wendorf F. (1990) Dating Pleistocene archeological sites by protein diagenesis in ostrich eggshell. *Science* **248**, 60–64.

Crenshaw M. A. (1980) Mechanisms of shell formation and dissolution. In *Skeletal Growth of Aquatic Organisms* (Edited by Rhoads D. C. and Lutz R. A.) pp. 115–132. Plenum Press, New York.

Goodfriend G. A. (1987) Evaluation of amino acid racemization/epimerization dating using radiocarbon-dated fossil land snails. *Geology* **15**, 698–700.

Hare P. E. and Mitterer R. M. (1967) Non-protein amino acids in fossil shells. Yearbook 65, p. 362. Carnegie Institution, Washington, DC.

Haugen J-E. (1990) Biogeochemistry of amino acids in carbonate fossils and marine sediments. Unpublished D.Sc. Thesis. University of Bergen, Norway.

Hearty P. J. and Miller G. H. (1987) Global trends in isoleucine epimerization. Data from the circum-Atlantic,

the Mediterranean, and the South Pacific. *Geol. Soc. Am.* (Abstracts with Program) **19,** 698.

Hearty P. J., Miller G. H., Sterns C. E. and Szabo B. J. (1986) Aminostratigraphy of Quaternary shorelines in the Mediterranean Basin. *Geol. Soc. Am. Bull.* **97,** 850–858.

Hsu J. T., Leonard E. M. and Wehmiller J. F. (1989) Aminostratigraphy of Peruvian and Chilean Quaternary marine terraces. *Quatern. Sci. Rev.* **8,** 255–262.

Johnson B. J. (1990) The Pleistocene planktonic foraminiferal aminostratigraphy of Ocean Drilling Program hole 625B in the Northeast Gulf of Mexico. Unpublished M.Sc. Thesis, University of Delaware.

Johnson B. J., Lehman S. J. and Miller G. H. (1990) Arrhenius parameters for the foram species *Globorotalia menadii* and deduction of the bottom water temperature changes during the Pleistocene–Holocene transition. *Geol. Soc. Am.* (Abstracts with Program) **22** (7), 146.

Kaufman D. S. (1991) Pliocene–Pleistocene chronostratigraphy, Nome, Alaska. Unpublished Ph.D. Thesis, University of Colorado, Boulder, CO.

Kaufman D. S. (1992) Aminostratigraphy of Pliocene–Pleistocene high-sea-level deposits, Nome coastal plain and adjacent nearshore area, Alaska. *Geol. Soc. Am. Bull.* **104,** 40–52.

Kennedy G. L., Lajoie K. R. and Wehmiller J. F. (1982) Aminostratigraphy and faunal correlations of late Quaternary marine terraces, Pacific coast U.S.A. *Nature, Lond.* **299,** 545–547.

King K. Jr (1977) Amino acid survey of recent calcareous and siliceous deep-sea microfossils. *Micropaleontology* **23,** 180–193.

McCoy W. D. (1987a) Quaternary aminostratigraphy of the Bonneville Basin, western United States. *Geol. Soc. Am. Bull.* **98,** 99–112.

McCoy W. D. (1987b) The precision of amino acid geochronology and paleothermometry. *Quatern. Sci. Rev.* **6,** 43–54.

McCoy W. D. and Miller B. B. (1990) Relative ages of late Cenozoic fossil assemblages from SW Kansas and NW Oklahoma interpreted from isoleucine epimerization in mollusc shells. *Geol. Soc. Am.* (Abstracts with Program) **22** (7) 146.

Miller G. H. (1982) Quaternary depositional episodes, western Spitsbergen, Norway. Aminostratigraphy and glacial history. *Arctic Alpine Res.* **14,** 321–340.

Miller G. H. (1985) Aminostratigraphy of Baffin Island shell-bearing deposits. In *Quaternary Environments—Baffin Island, Baffin Bay and West Greenland* (Edited by Andrews J. T.), pp. 394–427. Allen and Unwin, London.

Miller G. H. and Brigham-Grette J. (1989) Amino acid geochronology. Resolution and precision in carbonate fossils. *Quatern. Int.* **1,** 111–128.

Miller G. H. and Hare P. E. (1980) Amino acid geochronology. Integrity of the carbonate matrix and potential of molluscan fossils. In *Biogeochemistry of Amino Acids* (Edited by Hare P. E., Hoering T. C. and King K., Jr), pp. 415–444. John Wiley and Sons, New York.

Miller G. H., Hollin J. T. and Andrews J. T. (1979) Aminostratigraphy of UK Pleistocene deposits. *Nature* **281,** 539–543.

Miller G. H., Johnson B. J. and Ernst R. D. (1990) Modeling amino acid racemization and decomposition and protein hydrolysis in ratite eggshells. *Geol. Soc. Am.* (Abstracts with Program) **22** (7), 145.

Miller G. H., Jull A. J. T., Linick T., Sutherland D., Sejrup H. P., Brigham J. K., Bowen D. Q. and Mangerud J. (1987) Racemization-derived late Devensian temperature reduction in Scotland. *Nature, Lond.* **326,** 593–595.

Miller G. H. and Mangerud J. (1985) Aminostratigraphy of European marine interglacial deposits. *Quatern. Sci. Rev.* **4,** 215–278.

Miller G. H., Sejrup H. P., Lehman S. J. and Forman S. L. (1989) Glacial history and marine environmental change during the last interglacial–glacial cycle, western Spitsbergen, Svalbard. *Boreus* **18,** 273–296.

Miller G. H., Sejrup H. P., Mangerud J. and Anderson B. G. (1983) Amino acid ratios in Quaternary mollusks and foraminifera from western Norway. Correlation, geochronology, and paleotemperature estimates. *Boreas* **12,** 107–124.

Miller G. H., Wendorf F., Ernst R., Schild R., Close A. E., Friedman I. and Schwarcz H. P. (1991) Dating lacustrine episodes in the eastern Sahara by the epimerization of isoleucine in ostrich eggshells. *Palaeogeog. Palaeoclimatol. Palaeocol.* **84,** 175–189.

Mitterer R. M. (1975) Ages and diagenetic temperatures of Pleistocene deposits of Florida based upon isoleucine epimerization in Mercenaria. *Earth Planet. Sci. Lett* **28,** 275–282.

Mitterer R. M. and Kriausakul N. (1989) Calculation of amino acid racemization ages based on apparent parabolic kinetics. *Quatern. Sci. Rev.* **8,** 353–358.

Müller P. J. (1984) Isoleucine epimerization in Quaternary planktonic foraminifera. Effects of diagenetic hydrolysis and leaching, and Atlantic–Pacific intercore correlations. *Meteor Forsch.-Ergenbnisse,* Reiche Co., No. 38, pp. 25–47.

Nelson A. R. (1978) Quaternary glacial and marine stratigraphy of the Qivitu Peninsula, northern Cumberland Peninsula, Baffin Island, Canada. Ph.D. Dissertation, 297 pp. University of Colorado, Boulder, CO.

Oches E. A. and McCoy W. D. (1990) Aminostratigraphic evaluation of central European loess deposits. New data from the Pleistocene of Hungary. *Geol. Soc. Am.* (Abstracts with Program) **22** (7), 146.

Oches E. A., McCoy W. D. and Clark P. U. (1989) Amino acid paleotemperature estimates for the last glacial maximum, lower Mississippi Valley. *Geol. Soc. Am.* (Abstracts with Program) **21**(6), 210.

Scott W. E., McCoy W. D., Shroba R. R. and Rubin M. (1983) Reinterpretation of the exposed record of the last two cycles of Lake Bonneville, Western United States. *Quatern. Res.* **20,** 261–285.

Sejrup H. P., Aarseth I., Ellingsen K. L., Reither E. and Jansen E. (1987) Quaternary stratigraphy of the Fladen area, central North Sea. A multidisciplinary study. *J. Quatern. Sci.* **2,** 35–58.

Sejrup H. P., Miller G. H., Brigham-Grette J., Lovlie R. and Hopkins D. (1984) Amino acid epimerization implies rapid sedimentation rates in Arctic cores. *Nature, Lond.* **310,** 772–775.

Walters J. (1988) Glacial geology of Countess of Warwick sound, Baffin Island, Arctic Canada. Unpublished MS thesis, University of Colorado, Boulder, CO.

Wehmiller J. F. (1984) Interlaboratory comparison of amino acid enantiomeric ratios in fossil Pleistocene mollusks. *Quatern. Res.* **22,** 109–120.

Wehmiller J. F. (1990) Amino acid racemization. Application in chemical taxonomy and chronostratigraphy of Quaternary fossils. In *Skeletal Biomineralization—Patterns, Processes and Evolutionary Trends* (Edited by Carter J. G.), pp. 583–608. Reinhold, New York.

Wehmiller J. F., Belknap D. F., Boutin B. S., Mirecki J. E., Rahamin S. D. and York L. L. (1988) A review of the aminostratigraphy of Quaternary mollusks from United States Atlantic Coastal Plain sites. In *Dating Quaternary Sediments* (Edited by Easterbrook D. J.), pp. 69–110. Geological Society of America Special Paper 227.

York L. L., Wehmiller J. F., Cronin T. M. and Ager T. A. (1989) Stetson Pit, Dar Country, North Carolina. An integrated chronologic, faunal and floral record of subsurface coastal sediments. *Palaeogeog., Palaeoclimatol., Palaeoecol.,* **72,** 115–132.