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Use of aspartic acid racemization and post-bomb ^{14}C to reconstruct growth rate and longevity of the deep-water slit shell *Entemnotrochus adansonianus*

GLENN A. GOODFRIEND,[1] MICHAELE KASHGARIAN,[2] and M. G. HARASEWYCH[3]

[1]Geophysical Laboratory, Carnegie Institution of Washington, 5251 Broad Branch Road NW, Washington, DC 20015-1305, USA
[2]Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory, PO Box 808, Livermore, CA 94551, USA
[3]Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, USA

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Abstract—Slit shells are living fossils which inhabit the continental slope. Aspartic acid racemization in the nacreous layer of the slit shell *Entemnotrochus adansonianus* is shown to occur at a remarkably high rate, sufficient to provide annual resolution of the ages of samples taken along the growth spiral of the shells, thus providing information on growth rates and longevity. Calibration of the racemization rate was obtained by ^{14}C analysis of a post-bomb specimen. The form of the racemization curve was determined by a heating experiment at 60°C; a cubic transformation of the D/L values was found to be linear with respect to time. In three specimens in which a detailed series of samples was analyzed, juvenile growth was found to be very rapid and adult growth 1–2 orders of magnitude slower; adulthood is reached in 2–4 years. Analysis of lip and apical samples of additional shells (total $n = 9$) shows that individuals reaching adulthood have life spans averaging six years (maximum: 14 yr). The life histories of these deep-water gastropods are thus similar to littoral taxa. Analysis of the prismatic layer shows that this racemizes at a much slower rate than the nacreous layer.

INTRODUCTION

Racemization (or epimerization) of amino acids has traditionally been used for dating of Quaternary samples beyond the range of radiocarbon dating (> ca. 45,000 yr BP). However, recent studies have shown that aspartic acid in corals (Goodfriend et al., 1992), land snails (Goodfriend, 1992), and ostrich eggs (Goodfriend et al., 1991) (and probably in all biogenic carbonates) has a particularly high rate of racemization in very young samples and can, therefore, be used for dating on timescales of years to centuries. In this study, we present a new method for analysis of growth rate and longevity, utilizing the rapid racemization of aspartic acid to determine the age of a time-series of samples taken along the growth spiral of individual shells, from the apex (oldest part of the shell) to the lip (youngest part of the shell).

A variety of methods has been used to determine the ages and growth rates of mollusks. Besides biological methods, such as mark and recapture studies (e.g., Rhoads et al., 1981; Saunders, 1983), several geochemical methods have also been used. Seasonal variations in stable oxygen isotope ratios (e.g., Wefer and Killingley, 1980; Krantz et al., 1987; Jones, 1983) have been used to determine annual growth increments in mollusks living in habitats with seasonal variation in temperature. The number of these growth increments indicates the age of the individual. The main disadvantage of this method is that it requires a very large number of analyses. More commonly it has been used to document whether incremental growth lines on shells are annual, so that ages and growth rate can be determined by counting these lines (Jones, 1983; Weidman et al., 1994). The rapid changes in ^{14}C levels following the thermonuclear bomb tests of the late 1950s have also been used as a short-term dating method to determine ages and growth rates (e.g., Landman et al., 1988). As documented in annual bands of a large, shallow-water coral, ^{14}C levels increased rapidly from 1958–1970, then decreased more slowly to the present (Druffel, 1989). The present rate of change is relatively slow, so that temporal resolution is not as good as prior to the 1970 peak. Short-term radiogenic isotopes, such as $^{210}Po/^{210}Pb$ (Cochran and Landman, 1984) and $^{228}Ra/^{226}Ra$ (Turekian et al., 1983), have also been used for determining the ages of mollusk shells in the deep sea, where post-bomb ^{14}C and oxygen isotope methods would not be applicable.

Data on growth rates and longevity in mollusks from deep water are rather scarce. In the unusual environment of deep-sea hydrothermal vents, bivalves show moderately rapid growth rates and longevities on the order of 10–30 yr (Turekian et al., 1979, 1983; Rhoads et al., 1981), although in some cases only a single specimen was analyzed. Clams from nonhydrothermal deep-sea areas may live longer (Turekian et al., 1975). Data are also available for Chambered Nautilus, a shelled cephalopod living in the upper part of the continental slope; adult ages in the range of 10–15 yr have been determined by various methods (Landman et al., 1988; Cochran and Landman, 1984; Saunders, 1983) and far exceed those for other cephalopods (Heller, 1990).

The subject of this study is the slit shell *Entemnotrochus adansonianus*, a large pleurotomariid gastropod living on the upper part of the continental slope in 100–200 m of water in the tropical Western Atlantic. Slit shells are deep-water animals, *E. adansonianus* being one of the shallowest-dwelling species. Slit shells are of particular interest because, like the Chambered Nautilus, they are living fossils (Eldredge and Stanley, 1984)—surviving remnants of an ancient phylogenetic line. The family dates back to the Triassic, whereas the superfamily Pleurotomarioidea originates in the Cambrian, not long after the first mollusks appear in the fossil record (Knight et al., 1960; Hickman, 1984). Slit shells consist of two shell layers: an outer layer with a prismatic microstructure and an inner nacreous layer (MacClintock, 1967; Erben and Krampitz, 1972).

TABLE 1. Information on slit shell (*Entemnotrochus adansonianus*) specimens analyzed and estimates of their ages, based on aspartic acid racemization (D/L Asp) analysis of the nacreous layer at lip and upper part of the shells.

Specimen	Locality	Depth (m)	Yr of collection	Diameter (mm)	D/L Asp		Est. age (yr)
					lip	upper	
A	Bahamas	91	1970	113	0.067	0.137	13.5
B	Bahamas	116	1992	110	0.065	0.113	6.6
C	Navassa I.	141	1988	145	0.062	0.114	7.0
D	Bahamas	116	1992	107	0.063	0.095	3.4
E	Guadeloupe	177	1989	98	0.058	0.085	2.3
F	Bahamas	105	1993	66*	0.056	0.076	1.4
G	Bahamas	104	1993	104	0.058	0.110	6.3
H	Bahamas	110	1988	111	0.057	0.106	5.7
I	Guadeloupe	177	1989	95	0.057	0.073	1.1

*juvenile

To determine the rate of racemization in this species of slit shell, radiocarbon analysis (by accelerator mass spectrometry) and aspartic acid racemization analysis were conducted on a series of samples from a specimen collected in 1970, at the peak of post-bomb ^{14}C levels (Druffel, 1989). From the radiocarbon measurements, we were able to determine the years of growth represented by the samples. In order to be able to convert the D/L aspartic acid values to ones that are proportional to age, the form of the racemization curve with respect to time was determined through a heating experiment. Regression analysis of these transformed (linearized) D/L values against the year of growth provided a racemization rate calibration. This rate was applied to racemization data from other specimens from similar temperature regimes in order to determine their growth patterns and ages.

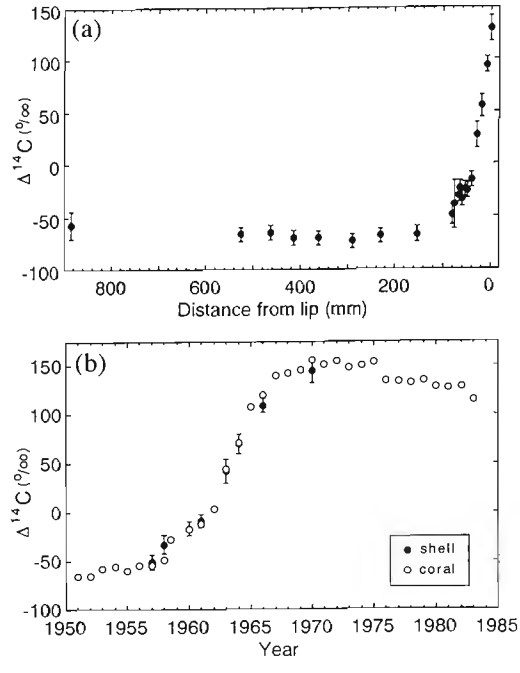

FIG. 1. Radiocarbon measurements, slit shell specimen A (in Δ units, or parts per mil deviation from modern ^{14}C level). (a) Radiocarbon in serial samples taken from the lip (distance = 0) up to near the apex of the shell (left). (b) Slit shell radiocarbon measurements (corrected for difference in reservoir effect; see text) in relation to radiocarbon measurements of annual bands of a shallow-water coral (from Druffel, 1989).

MATERIALS AND METHODS

Nine live-collected specimens of *Entemnotrochus adansonianus* were analyzed (Table 1). Eight of these were collected using a Johnson Sea-Link submersible and one (specimen A) was collected by a SCUBA diver.

Samples for analyses were ground off, using a hand-held Dremel motorized tool, fitted with a fine tapered bit. Positions of the samples were measured along the periphery and suture of the shell relative to the lip. For AMS radiocarbon analysis, ca. 5–10 mg of the outer (prismatic) layer was collected and converted to a graphite target (Vogel et al., 1987). For aspartic acid racemization analysis, ca. 2–6 mg of the part of the nacreous layer immediately underlying the prismatic layer was collected, except for samples from the lip of the shells, where the inner surface of the nacreous layer (the portion most recently laid down) was ground off. Several samples of the prismatic layer were also analyzed for racemization.

For the heating experiments, a piece of shell was cut from the lip of a live-collected specimen and the outer prismatic layer was removed by means of a motorized tool fitted with an abrasive tip, so that only the nacreous layer remained. A series of pieces of ca. 20 mg were then cut perpendicular to the lip using a thin, 1″ diameter saw blade attached to the motorized tool. The shell material was kept wet during this procedure to avoid heating. One of these shell pieces were sealed under N_2 into each of a series of glass tubes partially filled with sand with distilled water (120 μL) present. The tubes were heated in a block in an oven at 60°C and a single tube was withdrawn at intervals of 2–3 days for a twenty-day period. Details of the procedure are given in Goodfriend and Meyer (1991).

D/L aspartic acid values were measured using an HP5790 gas chromatograph with a Chirasil-val column, after derivatization of the hydrolyzed and desalted samples to N-trifluoroacetyl isopropyl esters. Details of the procedures are given in Goodfriend (1991).

RADIOCARBON RESULTS

Radiocarbon levels in specimen A (collected in 1970) were found to increase steadily toward the lip, starting at 80 mm from the lip (Fig. 1a). Radiocarbon levels in the earlier part of the shell (886–155 mm) showed a constant value, within analytical error. This pattern closely reflects the radiocarbon variations documented in shallow-water coral before 1970 (Druffel, 1989; Fig. 1b, open symbols). However, the $\Delta^{14}C$ value for the lip of the shell, presumed to represent 1970

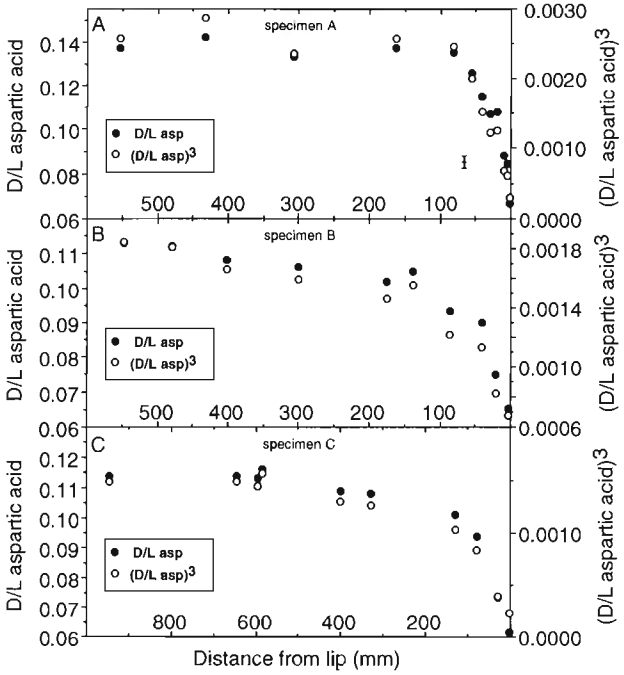

FIG. 2. D/L aspartic acid values in serial samples of the nacreous layer taken from the lip (distance = 0) up to near the apex (left) of three shells. Also plotted are the cubic transforms of the D/L values. (A) specimen A, (B) specimen B, (C) specimen C. The average error (±1 S.D.) for replicate preparations of a standard shell powder with D/L = 0.095 is shown on the right side of (A). This error is ±3.1% of the D/L value (n = 11).

growth, is depleted by ca. 15‰ relative to the 1970 coral value. This is the expected pattern, since there is a delay caused by the time required to mix the bomb ^{14}C signal from the surface of the ocean down to the depth at which the slit shell was collected (91 m). In 1970, a $\Delta^{14}C$ difference of some 250‰ between the surface and 600 m depth was documented for bicarbonate in the central Florida Straits (Mathews et al., 1973). Interpolation of these data for 100 m depth yields an estimated $\Delta^{14}C$ of ca. 120‰, similar to the value measured in the lip of slit shell specimen A. In order to correct for this offset, the $\Delta^{14}C$ value of each sample was adjusted by +15‰. We were then able to match the shell $\Delta^{14}C$ values with those of the coral and thus determine the year when the part of the shell represented by each of the samples was deposited (Fig. 1B, solid symbols). The sample at 155 mm from the lip corresponds with 1957 but earlier samples (>155 mm) could not be assigned ages because there is only a very weak trend in the coral $\Delta^{14}C$ values prior to 1957. These earlier samples might all represent the same year or could span several years.

On the basis of these radiocarbon results, specimen A appears to be at least 13 yr old (1957–1970). The growth rate for the last 80 mm is shown to have been very slow, lasting some twelve years (average of 7 mm/yr).

ASPARTIC ACID RACEMIZATION RESULTS

Aspartic acid racemization analyses were carried out on a series of samples from three specimens of slit shells, including specimen A. In each specimen (Fig. 2), a regular increase in

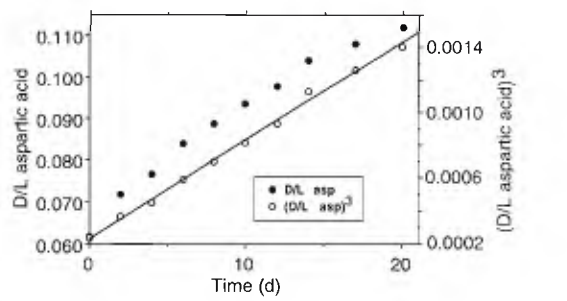

FIG. 3. Aspartic acid racemization in fragments of the nacreous layer heated at 60°C. Also plotted are the cubic transforms of the D/L values, which show a linear relation to time ($[D/L]^3 = 5.91 \times 10^{-5}t + 2.32 \times 10^{-4}$, where t = time in days).

the D/L value from the lip of the shell up toward the apex was observed. This increase was rapid near the lips and slow in the upper parts of the shells. Before further consideration of these results, however, the form of the racemization curve with respect to time must be evaluated.

Results of the heating experiment (Fig. 3, solid symbols) show the pattern typical of aspartic acid racemization kinetics: a curve with the rate decreasing with increasing D/L. Transformation of the D/L values to the third power (Fig. 3, open symbols) was found to linearize the data with respect to time (R^2 = 0.999).

The rate of aspartic acid racemization was determined in specimen A by plotting the transformed D/L values against the year of growth, as determined from radiocarbon measurements (Fig. 1B). These data show a linear trend with age (Fig. 4) and indicate a racemization rate (in $[D/L]^3$/yr) of 1.79×10^{-4} (R^2 = 0.95). This racemization rate was used for determination of growth rates and ages of other specimens.

By replotting the D/L data for specimens A–C as $(D/L)^3$ (Fig. 2, open circles), the slope becomes inversely proportional to growth rate. Each individual is seen to have had a very rapid initial growth rate, followed by a slow growth rate for the last 80–150 mm of the shell. These rates were estimated by performing a simple linear regression of the transformed D/L values on distance from lip for the earlier and later portions of each shell, and then converting these values to linear growth per unit time by using the rate calibration given in the preceding paragraph. For specimen A, growth from the apex (890 mm from the lip) to 80 mm from the lip occurred at a rate of 440 mm/yr, whereas the growth rate from

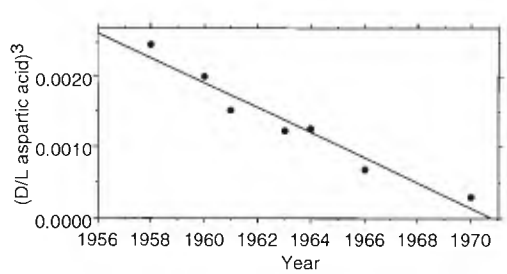

FIG. 4. Calibration of aspartic acid racemization rate in the nacreous layer, based on slit shell specimen A. Cubic transforms of D/L aspartic acid values are plotted in relation to the year of growth, as determined from radiocarbon measurements (Fig. 1B).

80 mm to the lip was 7 mm/yr. For specimen B, the estimated rates are 210 mm/yr from the apex (740 mm from the lip) to 140 mm from the lip and 29 mm/yr from 140 mm to the lip. For specimen C, the estimated rates are 300 mm/yr from the apex (1280 mm from the lip) to 130 mm from the lip and 27 mm/yr from 130 mm to the lip. We interpret this dramatic change in growth rate as representing the point of sexual maturation of the animals, with the former estimates representing juvenile growth rates and the latter, adult growth rates. The age at maturity for specimens A, B, and C was determined by dividing the total length of the juvenile shell (up to the point at which the growth rate changed) by the estimated juvenile growth rate. These ages were estimated to be 1.8 yr, 2.8 yr, and 3.8 yr, respectively, or ca. 2–4 yr. The aspartic acid data indicate that the early whorls of specimen A, whose age was not resolved by radiocarbon, were laid down over a period of less than 2 years.

The ages of slit shell specimens A–C as well as six additional specimens (one of which was obviously a juvenile) were determined through comparison of the D/L values at the lips of the shells and the upper part of the shells, using the rate calibration from specimen A (Table 1). The estimated ages of the adults ranged from 13.5 yr for specimen A to 1.1 yr for specimen I and averaged 5.7 yr. This indicates that individuals that survive to adulthood have an average longevity of ca. 6 yr. The juvenile (F) had an estimated age of 1.4 yr. A precise correspondence between size and age is not seen, indicating that there is some variation among sites and individuals.

These age estimates would be affected by a difference in temperature between the site where the specimens were collected and the calibration site (in the Bahamas). All the Bahamian specimens were collected at similar depths (91–116 m; Table 1). But the Navassa Island and Guadeloupe specimens came from greater depths (141 and 177 m, respectively). Temperatures measured at these sites at the time of collection are within the range of those measured at various times of year in the Bahamas at 105–116 m (21.8–23.8°C; $N = 4$), so no correction for temperature differences has been made. If the average temperatures at the deeper sites were actually slightly cooler, then the ages would be slightly older than our estimates (a temperature 1°C cooler would reduce the racemization rate and increase the estimated age by 19%, for an activation energy of 30 kcal/M).

Racemization in the prismatic (outer) layer was examined in specimen B (Fig. 5). Racemization was observed to show a net increase from the lip to the apex to the lip, but this trend is very weak (slope of 7.4×10^{-6}; $R^2 = 0.06$) and not statistically significant. Thus, in this layer in the living snails, racemization occurs at too slow a rate to quantify during the ca. 7-year life span of this individual. Noteworthy, however, is the very high D/L value found for each of the samples (mean of 0.18), which is discussed below.

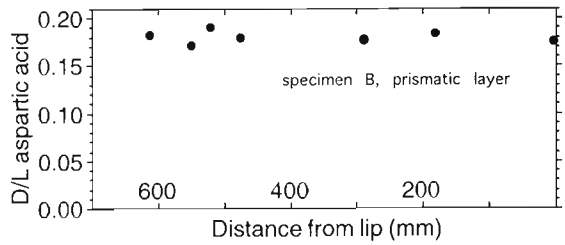

FIG. 5. Aspartic acid racemization in a series of samples from the prismatic layer of slit shell specimen B, in relation to distance from the lip of the shell.

DISCUSSION

The pattern of rapid early growth followed by a greatly reduced growth rate in the adult phase is prevalent in gastropods that lack determinate growth (Frank, 1969; Williamson and Kendall, 1981). Both the average and maximum ages of these slit shells are similar to those of most shelled gastropods and shelled cephalopods (Heller, 1990). The few reports of gastropod life spans in excess of twenty-five years are based on extrapolations that assume constant growth rates and are, therefore, questionable. Within the Mollusca, life spans over fifty years appear to be restricted to the Bivalvia.

A range of rates of racemization of aspartic acid have been observed in various types of samples. Although vertebrate teeth (composed of a calcium phosphate mineral) have intrinsically relatively slow rates of aspartic acid racemization, at the high temperatures of the body, significant racemization occurs within the lifetime of the organism (Helfman and Bada, 1975) and has thus been used to determine ages of humans (e.g., Ohtani et al., 1988). In coral samples, the initial rate of racemization is rapid enough (0.04 in 10 yr) to provide annual resolution of ages, as in the nacreous layer of slit shells; but going back 1–3 centuries, rates are an order of magnitude slower (0.04/100 yr) (Goodfriend et al., 1992). The initial rates of racemization observed in land snails of various species from several different subtropical and tropical areas and also during indoor storage are rather slower than in the slit shell nacreous layer or the corals, with ca. 0.05 racemization during the first 100 yr, or ca. 0.01 per 20 yr (Goodfriend, 1992). The lack of observed racemization in the prismatic layer of the slit shells over a time span of ca. 7 yr is thus consistent with the racemization rates observed in land snails.

The possibility of different rates of racemization in different shell layers within the same individual, due to different protein composition of the layers, has been recognized for some time (Mitterer, 1975), but has not been studied systematically. Brigham (1983) found no evidence for differences in epimerization of isoleucine among five different regions of shells of a marine bivalve; but the particular layers within these regions were not separated. The data presented here on racemization rates in the prismatic and nacreous layers of slit shells point to the existence of very large differences among different types of shell microstructure. Careful sampling from a particular layer of a shell may, therefore, be important in obtaining reproducible results for amino acid racemization dating.

The very high D/L aspartic acid values found consistently in the prismatic layer are very surprising. D/L aspartic acid values in modern mollusk shells, corals, and ostrich eggshell are in the range of 0.03–0.08 (Goodfriend, 1992; Goodfriend et al., 1991, 1992; G. A. Goodfriend, unpubl. data). It is assumed that no D-Asp is present in modern proteins and that the D/L values observed in preparations of modern samples represent racemization induced by preparation procedures, primarily the hydrolysis step. Although the proteins in the nacreous layer racemize much more rapidly in the shell than those

in the prismatic layer, the racemization induced by preparation is much lower (ca. 0.06; Table 1, lip samples). It may be that the proteins in the prismatic layer contain Asp (or Asn) moieties which racemize relatively slowly in intact proteins but which racemize particularly rapidly when they become exposed to terminal positions during protein hydrolysis at high temperature in the laboratory (cf. Kriausakul and Mitterer, 1980).

Another unexpected observation is that the D/L aspartic acid values of the nacreous layer at the lip is not much different among the specimens: even the 1970 shell, collected some twenty-four years ago, shows only a marginally higher racemization at the lip than recently collected specimens. Yet within the lifetime of the snails, racemization occurs at a very high rate. The most likely explanation for this is that after the bodies are removed from the shells and the shells are stored in cabinets in the museum, there is not sufficient moisture present in the shells to allow racemization to proceed. However, other types of shells stored in museum collections do show significant racemization during storage (Goodfriend, 1992).

Aspartic acid racemization provides a valuable new method for study of life histories of organisms with accretionary skeletons. The method should prove particularly valuable in the deep sea where uncertainties in the timing of penetration of the bomb ^{14}C signal make its use as a dating technique problematic and where seasonal variations in temperature are too small for use of stable isotope methods.

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REFERENCES

Brigham J. K. (1983) Intrashell variations in amino acid concentrations and isoleucine epimerization ratios in fossil *Hiatella arctica*. *Geology* **11,** 509–513.

Cochran J. K. and Landman N. H. (1984) Radiometric determination of the growth rate of *Nautilus* in nature. *Nature* **308,** 725–727.

Druffel E. R. M. (1989) Decade time scale variability of ventilation in the North Atlantic: high-precision measurements of bomb radiocarbon in banded corals. *J. Geophys. Res.* **94 (C3),** 3271–3285.

Eldredge N. and Stanley S. M. (1984) Living fossils: introduction to the casebook. In *Living Fossils* (ed. N. Eldredge and S. M. Stanley), pp. 1–3. Springer-Verlag.

Erben H. K. and Krampitz G. (1972) Ultrastruktur und Aminosäuren-Verhältnisse in den Schalen der rezenten Pleurtomariidae (Gastropoda). *Biomineralization* **6,** 12–31.

Frank P. W. (1969) Growth rates and longevity of some gastropod mollusks on the coral reef at Heron Island. *Oecologia* **2,** 232–250.

Goodfriend G. A. (1991) Patterns of racemization and epimerization of amino acids in land snail shells over the course of the Holocene. *Geochim. Cosmochim. Acta* **55,** 293–302.

Goodfriend G. A. (1992) Rapid racemization of aspartic acid in mollusk shells and potential for dating over recent centuries. *Nature* **357,** 399–401.

Goodfriend G. A. and Meyer V. R. (1991) A comparative study of amino acid racemization/epimerization kinetics in fossil and modern mollusk shells. *Geochim. Cosmochim. Acta* **55,** 3355–3367.

Goodfriend G. A., Von Endt D. W., and Hare P. E. (1991) Rapid racemization of aspartic acid in mollusk and ostrich egg shells: a new method for dating on a decadal time scale. *Ann. Rep. Director, Geophys. Lab. Carnegie Inst. Wash.* **1990-1991,** 172–176.

Goodfriend G. A., Hare P. E., and Druffel E. R. M. (1992) Aspartic acid racemization and protein diagenesis in corals over the last 350 years. *Geochim. Cosmochim. Acta* **56,** 3847–3850.

Helfman P. M. and Bada J. L. (1975) Aspartic acid racemization in tooth enamel from living humans. *Proc. Natl. Acad. Sci. USA* **72,** 2891–2894.

Heller J. (1990) Longevity in molluscs. *Malacologia* **31,** 259–295.

Hickman C. S. (1984) *Pleurotomaria:* Pedigreed perseverance? In *Living Fossils* (ed. N. Eldredge and S. M. Stanley), pp. 225–231. Springer-Verlag.

Jones D. S. (1983) Sclerochronology: Reading the record of the molluscan shell. *Amer. Sci.* **71,** 384–391.

Knight J. B. et al. (1960) *Treatise on Invertebrate Paleontology, Vol. I, Mollusca 1.* Univ. Kansas Press.

Krantz D. E., Williams D. F., and Jones D. S. (1987) Ecological and paleoenvironmental information using stable isotope profiles from living and fossil molluscs. *Palaeogeogr., Palaeoclim., Palaeoecol.* **58,** 249–266.

Kriausakul N. and Mitterer R. M. (1980) Some factors affecting the epimerization of isoleucine in peptides and proteins. In *Biogeochemistry of Amino Acids* (ed. P. E. Hare, T. C. Hoering, and K. King, Jr.), pp. 283–296. J. Wiley.

Landman N. H., Druffel E. R. M., Cochran J. K., Donahue D. J., and Jull A. J. T. (1988) Bomb-produced radiocarbon in the shell of the chambered nautilus: rate of growth and age at maturity. *Earth Planet. Sci. Lett.* **89,** 28–34.

Mathews T. D., Fredericks A. D., and Sackett W. M. (1973) The geochemistry of radiocarbon in the Gulf of Mexico. In *Radioactive Contamination of the Marine Environment,* Proc. Intl. Atomic Energy Agency Symposium, Seattle, WA, 10–14 July, 1972, pp. 725–734. Intl. Atomic Energy Agency.

MacClintock C. (1967) Shell structure of the patelloid and bellerophontoid gastropods (Mollusca). *Bull. Peabody Mus. Nat. Hist. Yale Univ.* **22,** 1–140.

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

Ohtani S. et al. (1988) A study on the use of the amino-acid racemization method to estimate the ages of unidentified cadavers from their teeth. *Bull. Kanagawa Dental Coll.* **16,** 11–21.

Rhoads D. C., Lutz R. A., Revelas E. C., and Cerrato R. M. (1981) Growth of bivalves at deep-sea hydrothermal vents along the Galapagos Rift. *Science* **214,** 911–913.

Saunders W. B. (1983) Natural rates of growth and longevity of *Nautilus belauensis. Paleobiol.* **9,** 280–288.

Turekian K. K., Cochran J. K., and Bennett J. T. (1983) Growth rate of a vesicomyid clam from the 21°N East Pacific Rise hydrothermal area. *Nature* **303,** 55–56.

Turekian K. K. et al. (1975) Slow growth rate of a deep-sea clam determined by ^{228}Ra chronology. *Proc. Natl. Acad. Sci. USA* **72,** 2829–2832.

Turekian K. K., Cochran J. K., and Nozaki Y. (1979) Growth rate of a clam from the Galapagos Rise hot spring field using natural radionuclide ratios. *Nature* **280,** 385–387.

Vogel J. S., Southon J. R., and Nelson D. E. (1987) Catalyst and binder effects in the use of filamentous graphite for AMS. *NIM Phys. Res.* **B29,** 50–58.

Wefer G. and Killingley J. S. (1980) Growth histories of strombid snails from Bermuda recorded in the O-18 and C-13 profiles. *Marine Biol.* **60,** 129–135.

Weidman C. R., Jones G. A., and Lohmann K. C. (1994) The long-lived mollusc *Arctica islandica:* A new paleoceanographic tool for the reconstruction of bottom temperatures for the continental shelves of the northern North Atlantic Ocean. *J. Geophys. Res.* **99 (C9),** 18,305–18,314.

Williamson P. and Kendall M. A. (1981) Population age structure and growth of the trochid *Monodonta lineata* determined from shell rings. *J. Mar. Biol. Assoc. U. K.* **61,** 1011–1026.