

A New Look at Evolutionary Rates in Deep Time: Uniting Paleontology and High-Precision Geochronology

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Figure 1. The Permian-Triassic boundary at Meishan, China, showing dates for the ash beds described in Bowring et al. (1998). The end Permian mass extinction is recorded within the last 1 m below the lowest ash bed (left). This ash bed lies about 10 cm below the Permian-Triassic boundary as defined on the basis of conodonts, and just below the major isotopic excursion. The upper two ash beds are in Lower Triassic strata.

ABSTRACT

It is now possible to routinely determine the age of 200–600-m.y.-old volcanic rocks interlayered with fossil-bearing deposits to uncertainties of less than 1 m.y. with uranium-lead zircon geochronology. This level of precision, coupled with the recognition that volcanic ash beds are much more common in fossiliferous rocks than previously realized, opens new opportunities for the study of evolutionary rates in deep time. It is now possible to constrain rates of evolutionary radiations, mass extinctions, and other evolutionary events as well as evaluate potentially diachronous biostratigraphic boundaries. For example, a combination of detailed biostratigraphic and chemo-

stratigraphic data with new U-Pb zircon dates for the late Neoproterozoic and Early Cambrian has demonstrated that the soft-bodied Ediacaran fossils immediately underlie the Cambrian, that the base of the Cambrian is much younger than previously recognized, and that the Cambrian explosion lasted 10 m.y. or less. Other recent studies have shown the Middle and Late Cambrian each lasted only about 10 m.y., suggesting that the duration of the included trilobite zones was similar to those of Jurassic ammonites. Recent data from the Late Permian and earliest Triassic of south China now constrain the duration of the most profound mass extinction in the history of life to less than 1 m.y. Collaboration between paleontologists

and geochronologists offers the prospect of accurately assessing the rates of evolutionary processes, from speciation to evolutionary radiations and mass extinctions, throughout the Phanerozoic.

"How fast, as a matter of fact, do animals evolve in nature? That is the fundamental observational problem that the geneticist asks the paleontologist" (Simpson, 1944).

INTRODUCTION

Answers to Simpson's question about evolutionary rates have generally lacked precision, particularly for the pre-Cenozoic. Although many paleontological

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In Memoriam

Saul Aronow
Beaumont, Texas
May 15, 1998

Robert E. Barnett
Washington Court House,
Ohio

Bruce B. Hanshaw
McLean, Virginia
July 18, 1998

Laurence B. James
Folsom, California
June 8, 1998

Louis Pavlides
College Park, Maryland
April 8, 1998

Grover Reinbold
Reno, Nevada
April 24, 1998

Mark Springett
Boulder, Colorado
July 16, 1998

Leonard R. Wilson
Norman, Oklahoma
July 15, 1998

CORRECTION: July Science Article

The illustration in the center of the July 1998 issue (p. 16 and 17) is Figure 2 (not Figure 3) of the paper "Probing the Archean and Proterozoic Lithosphere of Western North America" by Deep Probe Working Group. The Figure 2 caption on p. 4 should be on p. 16, and the Figure 3 caption on p. 16 should be on p. 4.

On p. 3, leftmost column, the fourth line under the head Seismic Observations: Three Province-Related Seismic Signatures should be: Cheyenne belt (Fig. 2; see p. 16–17), and the footnote at the bottom of the leftmost column on p. 4 should be: Figure 2 is on p. 16–17.

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issues have revolved around evolutionary rates, the inadequacies of the geologic time scale have generally precluded their resolution. Yet, accurate determination of rates is critical to answering important questions: How does the rate of speciation vary in different environments? How long do stable community assemblages persist? How much time is involved in evolutionary radiations or postextinction recoveries? How rapidly do species and communities respond to climatic and other environmental changes? And perhaps most significant, have these rates changed through the Phanerozoic? Without good data on the amount of time involved in these events, any determination of rate must be suspect.

Rates of some evolutionary and geologic processes can be determined for the Cenozoic with some precision by means of a variety of techniques (e.g., climatic cyclicity, paleomagnetic reversals; Hilgen et al., 1997). However, farther back in the geologic record, the precision with which we can resolve events decreases, the accuracy of the geologic time scale degrades, and the reliability of information used to assess evolutionary rates falls dramatically. Consequently, much of our current knowledge of rates of change is based on interpolation of absolute time between a few well-constrained tie points used to construct relatively imprecise geologic time scales (e.g., Harland et al., 1990), often with the additional assumption that equal thicknesses of rock represent equal amounts of time.

About People

GSA Fellow Daniel Jean Stanley, National Museum of Natural History, Washington, D.C., was chosen by Italian universities to receive the Golden Trident Medal, a first for a North American scientist. He was also inducted as a member of Italy's Accademia Internazionale di Scienze e Tecnica.

GSA Fellow Julia Ann Tullis, Brown University, Providence, Rhode Island, will receive the 1998 Outstanding Educator Award from the Association for Women Geoscientists Foundation.

NEW DIRECTOR FOR IEE

Cathleen May has joined the headquarters staff at GSA as the Director of the Institute for Environmental Education. Cathleen previously directed the national paleontological resources management program for the U.S. Forest Service. More recently, she has consulted to government and professional societies on resource management and legislative issues, and to the entertainment industry on issues of scientific accuracy and literacy.

May earned undergraduate degrees in geology and in secondary science education at the University of Wyoming and her doctorate in integrative biology at the University of California at Berkeley. Her primary research has focused on macroevolutionary patterns in the terrestrial Triassic, particularly as recorded in northwest Argentina, and on geocological contingency in modern ecosystems. May brings to the IEE her long-standing commitment to the crucial role of the geosciences in building scientific literacy, environmental problem-solving, and Earth-system science. Contact May regarding the IEE and its programs at cmay@geosociety.org, or IEE administrative support person Stacey Ginsburg at sginsbur@geosociety.org.



Cathleen May

For Paleozoic and Mesozoic rocks, high-precision U-Pb geochronology of zircons can be exploited to yield uncertainties of 1 m.y. or less. The continued refinement of chemical separations of U and Pb from zircon and the improvement of mass spectrometry allow high-precision analyses of single grains of zircon containing as little as 10 picograms (10^{-12} g) of radiogenic Pb (Mundil et al., 1996; Bowring et al., 1998). The ultimate test of the resolving power of the technique occurs when multiple volcanic horizons are interlayered with fossil-bearing rocks and the calculated ages do not violate stratigraphic order.

The integration of geochronology, paleontology, and chemostratigraphy has revolutionized our knowledge of several important episodes in geologic history, including the sudden major increase of animals during Neoproterozoic to Cambrian time and, most recently, the most extensive mass extinction in the history of life, the end-Permian event (Fig. 1).

EVOLUTIONARY RATES

Although Simpson (1944) identified and focused on the importance of determining fine-scale evolutionary rates, he was handicapped by lack of data on absolute dates. Kurten (1959) found that rates of morphological change in Pleistocene mammals exceeded mammalian evolutionary rates during the Tertiary. Subsequent work has established that these higher rates were an artifact: Evolutionary rates are inversely related to time scale. The shorter the time period studied, the faster the observed rates of change, whether the object of study is morphology (Gingerich, 1983, 1993), or sedimentation (Sadler, 1981). This is simply because slow long-term rates are difficult to measure over the short term and because fast long-term rates are generally unsustainable over

the long term. Since evolutionary rates are strongly dependent upon the interval of time over which they are measured, they can only be meaningfully compared when the same time scale is used (Gingerich, 1993; Foote, 1994).

More recently, the determination of precise evolutionary rates has faded from current paleobiological research in favor of identification of large-scale macroevolutionary patterns. This is in part because temporal resolution has been too coarse to allow evaluation of finer-scale processes (Campbell and Marshall, 1987). Recent developments in geochronology suggest that it is time for a new examination of the issue of evolutionary rates, at the scale envisioned by Simpson (1944).

GEOCHRONOLOGY

Since stratigraphic thickness cannot be simply extrapolated to geologic time, a large number of high-precision ages from interstratified volcanic ash beds are required in order to evaluate rates of geological change. In the past 10 years there has been a dramatic increase in the number of studies concerned with calibration of the time scale (e.g., Tucker et al., 1990; Tucker and McKerrow, 1995; Claoue-Long et al., 1991; Mundil et al., 1996; Tucker et al., 1998). The U-Pb method applied to zircons separated from stratabound volcanic layers is a powerful method for dating sedimentary rocks because it exploits two independent decay schemes ($^{238}\text{U} \rightarrow ^{206}\text{Pb}$ and $^{235}\text{U} \rightarrow ^{207}\text{Pb}$) within each zircon sample. This method provides independent age information and a test for the degree to which the systems were closed following crystallization. If a closed system has been maintained, the two U-Pb dates ($^{238}\text{U}/^{206}\text{Pb}$ and $^{235}\text{U}/^{207}\text{Pb}$) and the Pb-Pb date ($^{207}\text{Pb}/^{206}\text{Pb}$) for a zircon analysis should be the same within uncertainties and are referred to as concordant.

The past 15 years have seen marked improvement in high-precision isotope dilution-thermal ionization mass spectrometry (IDTIMS) U-Pb dating of zircons (Krogh, 1982; Parrish and Krogh, 1987). This is largely the result of being able to analyze small amounts of zircon that may contain as little as $10\text{--}25 \times 10^{-12}$ g of radiogenic Pb. This capability is the result of low analytical blanks ($0.5\text{--}2.0 \times 10^{-12}$ g of common Pb) and improvement in mass spectrometry, especially ion-counting techniques. Although these methods have revolutionized our understanding of how geological time is distributed in the rock record, only recently has the full potential of this technique begun to be realized. High precision for its own sake is often not an efficient strategy. We feel that the calibration of evolutionary rates is an example of a problem that requires the maximum resolving power of the U-Pb technique. For example, Tucker et al. (1990) showed through high-precision zircon geochronology that the mean duration of Ordovician graptolite zones is 1–2 m.y. and recognized that with this approach, evolutionary rates of Paleozoic fauna could be evaluated. Hughes (1995) used available U-Pb geochronology to constrain durations of Silurian graptolite zones; the range was 0.44–1.43 m.y.

Calibration of the Time Scale

Geochronometric calibration of a relative, chronostratigraphic time scale is straightforward. Ideally, a volcanic rock is found very close to the point in a stratigraphic section chosen as the global stratotype for the boundary between two geologic intervals, and the volcanic rock contains a mineral, such as zircon or monazite, for which a precise crystallization age can be determined. Such ideal situa-

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tions are uncommon, and so calibration requires dating rocks elsewhere in sections that can be correlated to the stratotype by means of bio-, chemo-, and magnetostratigraphy. The late Neoproterozoic-Cambrian boundary, for example, is defined as a point in rock in a section located in southeastern Newfoundland (Landing, 1992), but no volcanic rocks are present at or in close proximity to the boundary (Myrow and Hiscott, 1993; Landing, 1992). Consequently, the age of the boundary can be calibrated only through correlation with other sections that contain datable volcanic rocks in close proximity to the boundary.

It is a useful exercise to consult your favorite time scale to see how the age of a particular boundary was determined. The chronostratigraphic time scales that we all depend on (Harland et al., 1990; Shergold, 1995; Gradstein et al., 1995) typically assign an absolute age for a biostratigraphic boundary that reflects averaging of several, often imprecise age determinations and estimates; in many cases the uncertainty is several million years. As the geochronological resolution and the number of calibration studies has increased dramatically in the past ten years, existing time scales have been rendered inadequate, especially for the Paleozoic (Fig. 2).

Methods

Pb analyzed from zircon samples is a mixture of radiogenic and common Pb. Radiogenic Pb is produced by the decay of U in the zircon crystal. A small amount of common Pb is sometimes incorporated into the zircon when it crystallizes, and common Pb is added to the sample via sample processing (analytical blank). When calculating a date for a zircon, one must subtract the common Pb from the total Pb, and in doing so, one must assume a composition of both the blank and any indigenous common Pb. In general, the uncertainties associated with making blank and common Pb corrections can be minimized with large radiogenic Pb/common Pb ratios, which generally scale with sample size. Sources of systematic error may include error in spike calibration and uncertainty in the decay constants for uranium. These later uncertainties would apply to all analyses done in a particular lab; although they might affect absolute age determinations, the relative age differences between beds are not affected. Systematic errors can be a problem when comparing dates obtained by different methods.

Resolution of time with uncertainties of 1 m.y. or less in volcanic rocks provides a special set of problems. The most significant is the ability to distinguish small amounts of Pb loss and/or inheritance. It is common in airfall ash deposits to find

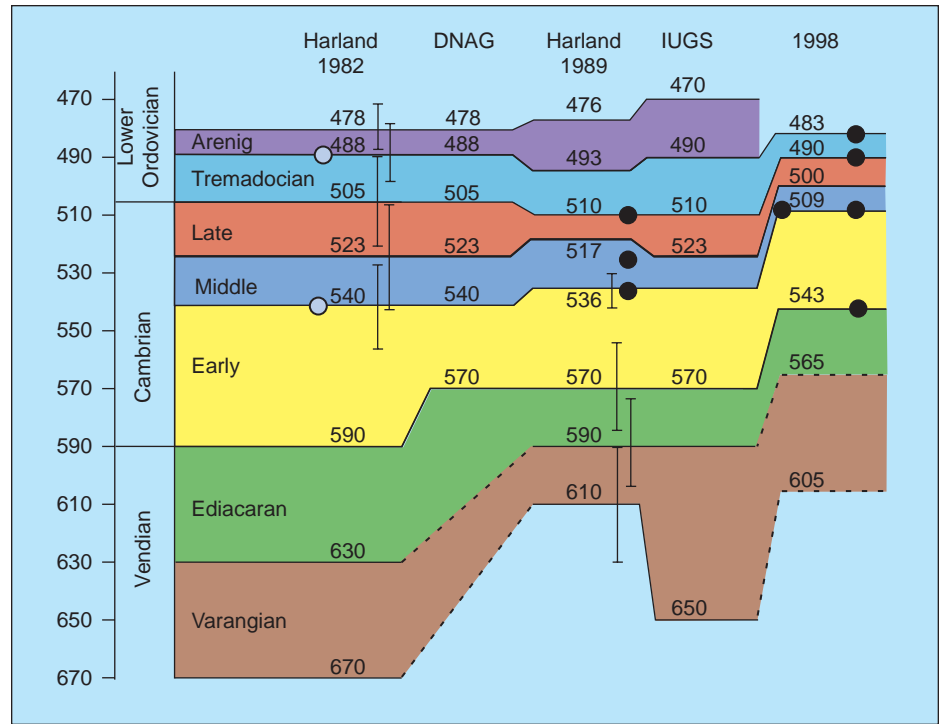


Figure 2. Changing views of late Neoproterozoic–Early Ordovician time. The estimated boundary dates shown are from Harland et al. (1982), the Decade of North American Geology (DNAG) in 1983, Harland et al. (1990), the International Union of Geological Sciences (IUGS; Cowie and Bassett, 1989), and the latest evidence (1998) discussed in this paper. The open circles represent poorly constrained geochronologic tie-points and the black circles better-constrained tie-points. Error bars are shown for the Harland et al. time scales. Note that the Manykaian stage was added to the Cambrian in 1992, and that the subdivisions of the late Neoproterozoic have not been firmly established.

zircon grains, probably incorporated into the eruption column, that are identical in morphology to the indigenous population, but which can be <1 to >10 m.y. older (Landing et al., 1998). This problem can be minimized by analyzing single grains of zircon. A zircon crystal's size and its concentration of radiogenic Pb ultimately determine whether or not single-grain analysis is feasible. One seeks as high a ratio of radiogenic to common Pb as possible for each analysis. In this way, the uncertainty on all three dates ($^{206}\text{Pb}/^{238}\text{U}$, $^{207}\text{Pb}/^{235}\text{U}$, and $^{207}\text{Pb}/^{206}\text{Pb}$) is low (0.1%–0.5%), and the difference between the $^{206}\text{Pb}/^{238}\text{U}$ and $^{207}\text{Pb}/^{235}\text{U}$ dates can be evaluated for inheritance of slightly older grains and/or Pb-loss. In the case of complex zircons, it is often necessary to relax precision requirements so as to be able to analyze a single grain or grain fragment. It is this trade-off that requires the super-high-resolution ion microprobe (SHRIMP) to rely on the $^{206}\text{Pb}/^{238}\text{U}$ date when determining the age of Paleozoic zircons (e.g., Claoue-Long et al., 1995).

In the best-case scenario, a statistically significant cluster of concordant analyses is obtained for each sample, and weighted mean $^{206}\text{Pb}/^{238}\text{U}$, $^{207}\text{Pb}/^{235}\text{U}$ and $^{207}\text{Pb}/^{206}\text{Pb}$ dates are calculated. More commonly, a suite of zircons is discordant and defines a linear array that intersects concordia. In these cases, uncertainty in

the age of the zircons can be calculated for the intersection of the discordant array with the concordia curve (Ludwig, 1980), or, more often, the weighted mean of the $^{207}\text{Pb}/^{206}\text{Pb}$ dates can be used (e.g., Tucker et al., 1998; Bowring et al., 1993). When this approach is used, the minimum uncertainty in age is generally 1–2 m.y. There is no question that the best results are obtained from concordant zircons, and in older rocks they become increasingly difficult to find. Our technique could be termed the “brute force” approach. We typically attempt to analyze a minimum of 5–10 fractions of zircon for each ash bed to assess our reproducibility and to reduce errors in the age (this does not include the analyses that show evidence for inheritance, severe Pb loss, high common Pb, etc.). The test of our approach is to analyze multiple samples of the same horizon, as well as different beds in stratigraphic order (Grotzinger et al., 1995; Bowring et al., 1998).

RESOLVING THE CAMBRIAN RADIATION

The explosive diversification of higher marine invertebrates in the Early Cambrian is the single most dramatic event documented in the fossil record. Rocks that are late Neoproterozoic in age contain the soft-bodied remains of Edi-

Millions of Years
Before Present

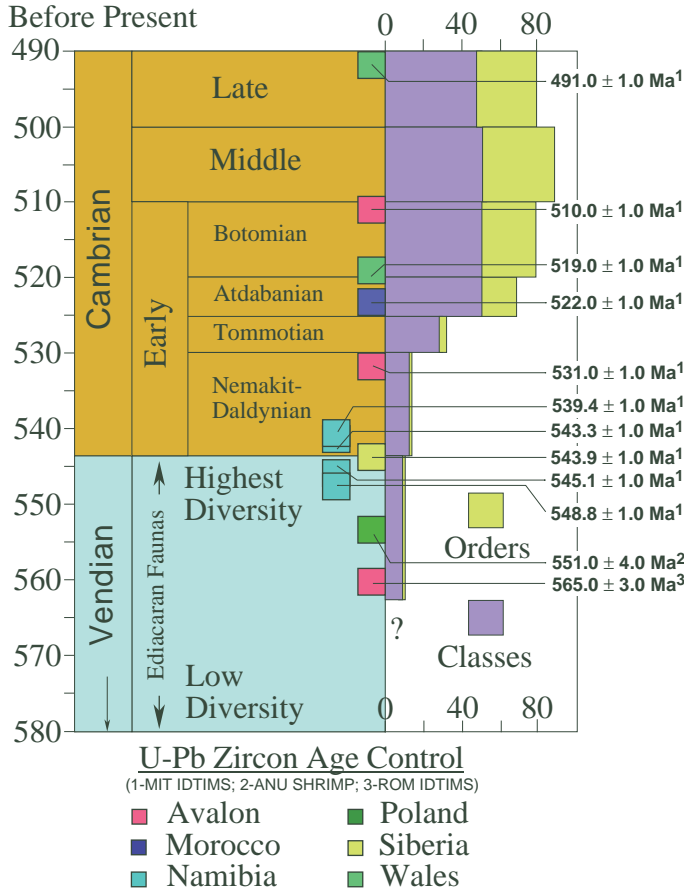


Figure 3. Summary diagram of biostratigraphically and geochronologically well constrained samples that define the late Vendian to Late Cambrian time scale (after Bowring et al., 1993; Grotzinger et al., 1995). Newer data are from: Compston et al. (1995), Landing et al. (1998), and Davidek et al. (1998). MIT IDTIMS is Massachusetts Institute of Technology, isotope dilution-thermal ionization mass spectrometry; ANU SHRIMP is Australian National University, super-high-resolution ion microprobe; ROM is Royal Ontario Museum.

Ediacaran fossils and a small assemblage of skeletonized tubes, as well as recently discovered fossil embryos and sponge spicules (ca. 570 Ma; Xiao et al., 1998; Li et al., 1998). The first Cambrian shelly fossils occur in carbonates near the base of the Manykaian Stage, currently the basal stage of the Cambrian. Trace fossils, skeletal fossils, and spiny organic microfossils diversified rapidly during the ensuing Tommotian and Atdabanian stages, so that by the end of the Atdabanian, most durably skeletonized phyla and classes of marine invertebrates are recognized. Controversy continues over the rapidity of this radiation and the possibility that considerable diversity existed long before the base of the Cambrian, but has not been recognized in the fossil record because of small size or low preservation potential.

Since 1990, U-Pb geochronological studies have constrained the age of the late Neoproterozoic-Cambrian boundary, the duration of diverse Ediacaran fossils, the burst of innovations during the Tommotian-Atdabanian, the Lower-Middle Cambrian boundary, and the Cambrian-Ordovician boundary (Compston et al., 1992, 1995; Bowring et al., 1993; Isachsen et al., 1994; Grotzinger et al., 1995; Landing et al., 1997, 1998; Davidek et al., 1998). Figure 3 is a revised time scale for the Cambrian Period showing the control

provided by U-Pb zircon ages on biostratigraphic boundaries.

Although volcanic rocks are uncommon interbedded with Ediacaran fossils, the fossils generally postdate Varanger-aged glaciogenic rocks (ca. 600 Ma) in eastern North America. In Newfoundland, Benus (1988) reported an age for volcanic rocks immediately overlying Ediacaran fossils at 565 ± 3 Ma. Compston et al. (1995) reported for volcanic rocks from the subsurface of Poland which are correlated with Ediacaran-bearing strata in Ukraine an age of 551 ± 4 Ma. Grotzinger et al. (1995) and Narbonne et al. (1997) have documented Ediacaran fossils including the new genus *Swartpuntia* immediately below the basal Cambrian in Namibia; this deposit is younger than 543.3 ± 1 Ma. Grotzinger et al. (1995) also showed that diverse small shelly fossils overlap with the Ediacaran fossils in Namibia. Although the Cambrian is often viewed as lacking Ediacaran fossils, several exceptions have appeared recently (Crimes et al., 1995; Conway Morris, 1993; Jensen et al., 1998). The lack of any obvious gap between the last Ediacaran fossils and the onset of Cambrian fossils leads to the simple conclusion that the Cambrian explosion is part of a continuous evolutionary radiation that started in the late Neoproterozoic (Grotzinger et al., 1995). The bios-

trigraphically defined boundary does not mark a sudden event or explosion in the diversification of life, but instead serves as an important reference point in an increasingly rich evolutionary record.

Carbon isotope stratigraphy is an essential tool for correlating latest Neoproterozoic rocks. Globally, many stratigraphic sections have yielded very similar fluctuations in carbon isotopes (Kaufman et al., 1997; Narbonne and Knoll, 1994). This pattern of isotopic variation provides an independent framework for correlation between sections and allows, in some cases, calibration of the isotopic shifts by dating volcanic layers. In Namibia, Grotzinger et al. (1995) showed that an isotopic interval known as the +2 plateau has a duration of about 5-6 m.y. and coincides with occurrence of the most diverse Ediacaran assemblages.

Temporal calibration of past global events, correlated using bio-, chemo-, and magnetostratigraphic data sets, is possible only with the precise absolute age control offered by U-Pb zircon dating of volcanics interlayered within sedimentary sequences. This temporal framework has important implications for our understanding of biological diversification and its possible links to contemporaneous tectonic, biogeochemical, and climatic changes. Exciting problems remain unresolved. What is the lower boundary of the Ediacaran faunas? Can we resolve time sufficiently during the late Neoproterozoic to identify distinct assemblages of fossils or migration between different biogeographic regions? Will additional data on the Manykaian Stage allow better temporal constraints on the gradual expansion of the small shelly fossils? Is the distribution of Ediacaran organisms diachronous?

NEW RESULTS FOR THE MIDDLE CAMBRIAN-EARLY ORDOVICIAN

Trilobites dominate Middle and Late Cambrian marine assemblages in both species diversity and numbers of specimens. Rapid speciation in trilobites has allowed biostratigraphers to divide the Middle Cambrian of Laurentia into six biostratigraphic zones, and the Upper Cambrian into seven (but see Geyer and Palmer, 1995). A detailed examination of the evolutionary patterns underlying trilobite history during this time reveals a more interesting pattern, however. In 1965 A. R. Palmer recognized a series of five larger biostratigraphic units, each beginning with a small number of trilobite families unrelated to those in underlying rocks. He traced the rapid diversification of these families across several biostratigraphic zones; the resulting diverse assemblage was finally eliminated by a mass extinction, and the cycle was repeated.

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These extinction events cross a variety of facies and, significantly, are not associated with lithological changes (Palmer, 1965, 1979, 1984; Stitt, 1971, 1975; Thomas, 1995). These biomere events, as Palmer termed them, also affect brachiopods, conodonts, and other taxa.

The causes of these events have been the subject of considerable debate; some authors have favored shelf-wide declines in water temperature (Stitt, 1971, 1975), perhaps associated with an incursion of anoxic water (Palmer, 1984). Others have favored a model tied to sea-level rise and a migration of deep-water taxa into near-shore environments (Westrop and Ludvigsen, 1987). Testing these alternative explanations and determining how quickly the extinctions and the subsequent adaptive radiations took place require tight constraints on time. The DNAG time scale, similar to other time scales of that vintage (Fig. 2), depicts a Middle Cambrian of 17 m. y. and a Late Cambrian of 18 m. y., yielding an average duration of a biostratigraphic zone of 2.8 m. y. and 2.6 m. y., respectively, with biomes averaging 7 m. y.

High-precision geochronology, while not yet to the level of the Cambrian radiation, has already changed this picture considerably. With the Ordovician boundary at about 490 Ma (Davidek et al., 1998) and the base of the Middle Cambrian at 509 Ma (Landing et al., 1998), the 13 trilobite zones of the Middle and Upper Cambrian now have an average duration of 1.5 m. y. and the biomes average 4 m. y. The trilobite zones are not of equal duration—those early and late in each biome are generally shorter (Shergold, 1995), but the length of these zones now approaches that of Jurassic ammonites, and the rates of speciation, migration, and overturn are all very high. Improved geochronology may help resolve intercontinental problems (e.g., Geyer and Palmer, 1995) and, if the appropriate circumstances are identified, may be combined with biogeographic information and phylogenetic analysis to determine rates of immigration at the base of biomes.

RATES OF THE END-PERMIAN MASS EXTINCTION

The Paleozoic ended at 251 Ma with the most severe mass extinction of the Phanerozoic. An estimated 85% of all marine species disappeared during the Late Permian, along with about 70% of land vertebrates and a significant number of plants and insects (Erwin, 1994; Retallick, 1995). The next largest mass extinction, at the close of the Ordovician, was only half as large. The end-Permian mass extinction eliminated the major marine communities of the Paleozoic, and in its

aftermath an entirely new suite of communities developed which, in many ways, continue to dominate modern oceans.

The causes of this extinction have long been enigmatic, in part because marine sections spanning the critical interval are relatively rare. Over the past decade, considerable advances have been made, and paleontologists, working together with geochemists and others, have established several important aspects of this extinction. Anoxia is present in both deep-ocean (Isozaki, 1997) and shallow-ocean sections (Wignall et al., 1996) across the Permian-Triassic boundary, the latter during a time of marine transgression. Analyses of carbon isotope patterns across the boundary show multiple, brief, negative excursions (Holser and Schonlaub, 1991; Wignall et al., 1996), and are found in both marine and terrestrial sections, demonstrating that extinctions were essentially simultaneous in both realms. There is no evidence for glaciation near the boundary, but there is growing evidence for some degree of global warming in the earliest Triassic. Finally, the mass-extinction patterns are consistent with the effects of poisoning by massive amounts of CO₂ (Knoll et al., 1996).

How did these events interact to trigger this mass extinction? The age of the Permian-Triassic boundary at the classic Meishan section between Shanghai and Nanjing, China was determined to be ca. 251 Ma (Claoue-Long et al., 1991; Renne et al., 1995), but knowing the age of the boundary without additional age constraints provides no reliable estimates of the duration of the extinction. On the basis of rock thickness and the number of biostratigraphic zones, a variety of estimates have been offered for the duration of the Late Permian stages, ranging between 2 and 10 m. y.

Recently, in conjunction with Jin Yugan and his colleagues at the Nanjing Institute of Geology and Paleontology, we have used the techniques described above to date a series of ash beds (Fig. 1) in south China that bracket the Permian-Triassic boundary and are well constrained biostratigraphically (Bowring et al., 1998). Because our results are tied to previous biostratigraphic and chemostratigraphic studies, they are of immediate significance beyond south China, and they provide the first constraints on the rapidity of the extinction and the association between the extinction and the related environmental changes. In particular, Bowring et al. (1998) showed that in the Meishan section, a sharp spike in $\delta^{13}\text{C}_{\text{carb}}$ of -6‰ occurred in less than 160 000 yr and perhaps as little as 10 000 yr (using the dates to calculate accumulation rates within this section). The latest Permian extinction occurred in less than 1 m. y. and could be coincident with the isotopic shift. At the

moment, the geochronological resolution of the extinction pattern is more detailed than the paleontological resolution. Further paleontological studies employing the statistical methods could help to sort out the rapidity of the extinction and help to constrain possible mechanisms. Models for the extinction that involve changes related to aggregation of Pangea at that time (e.g., Faure et al., 1995) seem incompatible with the rapid pulse of extinction. The rapidity implies events at the 100 000 yr level, compatible with proposed oceanographic changes (e.g., Knoll et al., 1996) such as overturn or even bolide impact (Bowring et al., 1998). More work on the fine-scale texture of the extinction and associated geochemical changes is required to further constrain the mechanisms of extinction. Outstanding issues are whether the terrestrial extinction occurred at the same time as the marine, and whether the extinction was globally synchronous. With the ability to resolve time at the 200 000–300 000 yr level, this question is of extreme importance.

Following the biggest extinction in Earth history, life recovered dramatically, although in a fundamentally different world. The recovery period of the Early Triassic provides an opportunity to quantify rates of rapid diversification into a relatively barren ecosystem following the end-Permian extinction. A comparison of evolutionary rates and paleobiogeographic controls may be the best analog to the Cambrian radiation. Comparisons of this sort should help us to better understand the general processes involved in extinctions and recoveries throughout Earth history.

NEW DIRECTIONS FOR THE STUDY OF EVOLUTIONARY RATES

The integration of high-resolution U-Pb geochronology and detailed paleontology offers a bright future to understanding rates of a variety of evolutionary processes. Thin layers of volcanic ash, interbedded with fossiliferous rocks, are more common than is often recognized, and correlations can be made to sections that lack volcanics by using biostratigraphy and chemostratigraphy. In addition, accumulation rates can be precisely evaluated when bracketed by abundant ashes, allowing much-improved resolution. Ideally, when volcanic rocks are regularly interspersed between fossil-bearing layers, reproducibility and precision can be evaluated by dating multiple ash beds within a single stratigraphic sequence.

This linkage between paleontology and geochronology allows us to address several evolutionary questions, especially those that move beyond simple taxonomic approaches. In Precambrian rocks, there is potential for calibrating major branch points or nodes in the tree of life

and comparing these estimates to those derived from analysis of molecular data through molecular clocks. The spectacular morphometric data on Cambrian and Ordovician trilobites produced by Foote (1993) is an excellent example for which high-resolution geochronology could document quantitative rates of morphological change from the Cambrian through the Ordovician radiation and extinction (rather than simply changes in the number of taxa). For this interval, the database is good enough that biogeographic effects could be examined as well. When coupled with high-resolution chemostratigraphy, the approach described in this paper will allow exploration of how subtle changes in climate or ocean chemistry are manifested in the evolutionary record.

Critical to understanding the diversification of life is an accurate chronology of life as preserved in the fossil record. Armed with an accurate chronology, we can begin to evaluate evolutionary rates by merging information on taxonomic, phylogenetic, and morphologic evolutionary patterns. Further, this approach offers the prospect of a more rigorous synthesis of data on molecular evolution and paleontology. When chronology is coupled with chemostratigraphic data, we can begin to understand the linkages between environmental change and evolution and to examine the distribution of time in the rock record with precision.

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GSA Executive Director Donald M. Davidson, Jr., meets Colorado State University Dean of Libraries, Camila Alire, at the Flood Recognition Event in the Morgan Library at Colorado State University. The flood disaster that occurred in Fort Collins, Colorado, on July 28, 1997, extensively damaged the library. In October 1997, GSA donated to the Morgan Library approximately 220 books and about 20 years' worth of the journals *Geology* and the *GSA Bulletin*, valued at over \$11,000.



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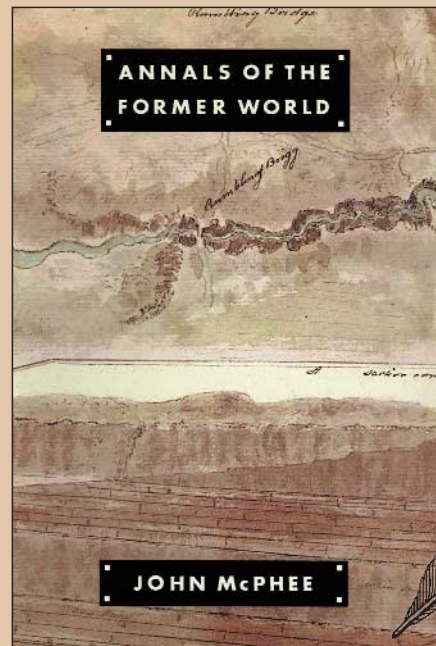
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