

DATES AND RATES:
TEMPORAL RESOLUTION IN THE DEEP TIME STRATIGRAPHIC RECORD

Douglas H. Erwin
Department of Paleobiology, MRC-121
National Museum of Natural History
PO Box 37012
Washington, D.C. 20013-7012
erwind@si.edu

and

Santa Fe Institute
1399 Hyde Park Road
Santa Fe, NM 87501

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Abstract: The level of achievable stratigraphic resolution determines the nature of the ecological, evolutionary and geological questions for which a reasonable answer may be expected. Advances in correlation techniques and in high-resolution radiometric dating and their integration with the fossil record through quantitative biostratigraphy and potential orbital cyclicity now allows many questions to be extended into deep time.

“How fast, as a matter of fact, do animals evolve in nature? That is the fundamental observational problem of tempo in evolution. It is the first question the geneticist asks the paleontologist. Some attempt to answer it is a necessary preliminary for the whole consideration of tempo and mode.” (Simpson 1944: p. 3)

MOTIVATION

When George Gaylord Simpson opened his magnificent book “Tempo and Mode in Evolution” with the words above, the use of radiometric dating to define the geologic time scale was still in a rather prolonged infancy. Later on that first page Simpson continues: “...absolute time cannot yet be accurately measured for paleontological materials, and it is desirable to examine relative as well as absolute rates.” Simpson’s book continues to be a powerful statement for the role of the fossil record as the ultimate arbiter of the range of evolutionary rates, but he understood that realizing his vision would require a far more accurate geologic time scale than existed in 1937 when he began writing “Tempo and Mode”.

The development of relative and eventually absolute dating schemes for the geological record has reflected a desire to answer three distinct but overlapping questions: When did some event occur? Did two (or more) events occur at the same time? And how rapidly or slowly did these events occur? Addressing the first question has led to the production of an increasingly refined geological time scale, including international efforts led by the International Commission on Stratigraphy and their designated

subcommissions on individual periods to define a series of internationally recognized Global Stratotype Section and Point (GSSP's). These GSSP's serve as the agreed lower boundaries of the subdivisions of the chronostratigraphic time scale. Radiometric dating has increasingly provided high-quality dates to these boundaries and many other points in the geologic time scale. Recently, Gradstein et al (2004) released the most recent edition of the Cambridge Geologic Timescale with uncertainties on radiometrically-dated boundaries of one million years or less. (The boundary dates in Gradstein et al. are a mix of actual radiometric dates and interpolated estimates based on radiometric dates from above or below the boundary.)

Since the GSSP's rarely contain readily datable materials, construction of the timescale has required development of a suite of increasingly sophisticated procedures to correlate between sections. These methods also address the question of whether two events occur at the same point in time. Such correlation techniques rely on a range of biological, chemical and physical markers, as discussed further below. Some events, such as volcanic ash beds or reversals in the Earth's magnetic field produce time lines or isochrons. Such time lines form the ideal basis for correlation (although establishing them is often difficult in practice). Other correlation methods approach the isochronicity of time lines but the evolution of a new species, for example, takes some finite interval of time, as does expansion of the species from the initial population. Thus while many other events are treated as isochrones, in the limit they are actually not isochronous.

The question of rate is ultimately the most significant, because the temporal resolution we can achieve in the stratigraphic and paleontological record is a primary control on the questions that geologists and paleontologists can ask, and the reliability of the answers they produce. Without an understanding of the time spans over which events occurred, geologists cannot hope to reliably use the patterns preserved in the stratigraphic record to infer the processes underlying the patterns. For example the rate and duration of a positive shift in carbon isotopes can be diagnostic of the possible sources of organic carbon and how they were released. Similarly, the rapidity of a mass extinction or similar biotic crises is a key indicator of the range of possible causes, from meteorite impact at one extreme, to the slow movements of the continents at the other. While geologists once relied on a qualitative means to assess stratigraphic resolution, the resolving power of a variety of quantitative techniques has advanced to the point that we are increasingly able to produce high-resolution stratigraphic results in deep time.

Kowalewski and Bambach (2003) noted that geologists actually use the term resolution in two different ways. Stratigraphic resolution refers to the scale of stratigraphic units and surfaces that can be defined, traced laterally and correlated. Depositional resolution, in contrast, refers to the relative completeness of the stratigraphic or fossil record within a particular sequence. Thus stratigraphic resolution applies among strata and depositional resolution within individual strata. Since the stratigraphic record is replete with gaps of varying temporal duration, a set of sequences of the same time interval could individually have low depositional resolution within strata, but collectively have high stratigraphic resolution across the collection of strata. Kowalewski and Bambach (2003) beautifully demonstrate this principle with an

illustration from Joseph Barrell's (1917) model of the sedimentary record. The most important limitations on depositional resolution stem from temporal mixing and time averaging of fossils, whether through prolonged residence time in the taphonomically active zone (Flessa et al., 1993; Flessa and Kowalewski 1994), bioturbation or other processes. Behrensmeyer et al., (2000) surveyed estimates of the extent of time-averaging within plant, terrestrial vertebrate and marine shelly invertebrate assemblages. They concluded that time-averaging of most assemblages occurred over months to hundreds of years, with only a few settings producing assemblages time-averaged over thousands of years. Given the maximal attainable temporal resolution in most deep time settings is likely to be at least tens to hundreds thousands of years, only fluvial vertebrate aggregations and marine fossils in shelf deposits and hiatal concentrations are likely to have sufficient time averaging to be relevant to this paper. Thorough reviews of the problems of depositional resolution and time-averaging include Kidwell and Boscence (1991); Behrensmeyer et al., (2000), Kidwell and Holland (2002) and Kowalewski and Bambach (2003).

This review will focus on temporal resolution of the stratigraphic record in deep time, and I will focus on our growing ability to resolve absolute time rather than differences in relative time. The problems and possibilities of the more recent part of the record are distinct from the deeper past and beyond the scope of this discussion. The wealth of detailed paleoecological studies of Quaternary biomes (Jackson and Overpeck, 2000; Jackson and Williams 2004) reflects both the greater number of recent records as well as the greater achievable stratigraphic resolution. Noller et al (2000) provide an excellent survey of the range of geochronological techniques that can be applied to the youngest part of the record. The problems and possibilities of the more recent part of the record are distinct from the deeper past and beyond the scope of this discussion. The wealth of detailed paleoecological studies of Quaternary biomes (Jackson and Overpeck, 2000; Jackson and Williams 2004) reflects both the greater number of recent records as well as the greater achievable stratigraphic resolution. Noller et al (2000) provide an excellent survey of the range of geochronological techniques that can be applied to the youngest part of the record. I begin with a discussion of the range of methods to assess temporal resolution including radiometric dating, magneto- and biostratigraphy and orbital cyclicity. I will then turn to the limits to paleontological and stratigraphic resolution, and finally to the issue of the level of temporal resolution needed to address various questions.

RESOLVING TIME

Although those interested in temporal resolution in deep time possess a smaller toolbox than those working on Neogene or Quaternary questions, there is a wide range of methods available. As noted above, there are two distinct problems to resolving time: establishing the relative order of events through a variety of correlation techniques to build a chronostratigraphic timescale, and assigning absolute age dates to this framework through the use of various isotopic decay schemes to produce a geochronometric scale. None of the techniques is a panacea however, particularly in the Paleozoic where the key to successful temporal resolution lies with integrating biostratigraphy, chemostratigraphy,

magnetostratigraphy, high-resolution radiometric dating and possibly orbital cyclicity where practicable.

Radiometric Dating

The utility of volcanic ash falls as stratigraphic markers has long been appreciated by field geologists. Pursual of old US Geological Survey Professional Papers will reveal identification of even very thin volcanic ash beds and their use as regional isochrons for stratigraphic correlation. Despite their ubiquity in older reports, ash beds appear to be under-recognized today, and are certainly under-utilized for resolving time. Geochemical fingerprinting has allowed regional and even inter-continental correlation of ash beds, greatly improving stratigraphic work (e.g. Huff et al., 1992). Advances in radiometric methods over the past decade or so now permit very high-resolution dating. These developments have permitted the rapid refinement of the geologic timescale, but even more importantly, they have been applied to help unravel the history of the Earth and its biota.

Currently the two most commonly used systems for determining radiometric dates on stratigraphic materials are uranium-lead (U-Pb) and potassium-argon (Ar-Ar) decays series. The first relies principally on the zircon crystals from volcanic ash-falls, debris flows and lavas, and to a lesser extent baddeleyite, monzaitite and xenotime. The $^{40}\text{Ar}/^{39}\text{Ar}$ system relies upon crystals of hornblende, biotite and sanadine. A critical difference between the two systems is that there are two different uranium-lead decay series but only a single potassium-argon series. Consequently U-Pb dating contains an internal control on whether the crystals have lost or gained either lead or uranium since their formation, what geochronologists describe as open-system behavior. This internal check is absent from K-Ar. Argon geochronologists do have techniques to test for open-system behavior, and in younger rocks the advantages of U-Pb are mitigated. Unfortunately at the moment, there is also a consistent bias of between 0.7 and 1.5% between U-Pb and Ar-Ar systems. Geochronologists are currently working to resolve this discrepancy, but until these studies are completed, one must clarify whether dates are presented in Ar or U-Pb years (an excellent recent review of U-Pb geochronology as applied to the stratigraphic record is Bowring and Schmitz 2005). That geochronologists now have to worry about U-Pb and Ar-Ar years is a measure of the increasing precision of the field, and the prospects for rapid advances in the geologic time scale.

The two predominant means of U-Pb analysis of zircons are the sensitive high resolution ion microprobe (SHRIMP) and the more conventional isotope dilution analysis using thermal ion mass spectrometry (IDTIMS). Each method has advantages and disadvantages for time-scale work, (see a thorough discussion in Bowring and Schmitz 2005). A few points are worth emphasizing, however. SHRIMP analyzes minute portions of a single zircon grain, while IDTIMS analyzes an entire grain. This greater spatial precision gives SHRIMP an advantage for complex zircons with overgrowths, as can happen as zircons cycle through magma chambers. SHRIMP also requires calibration against standard zircons of known age. Consequently, the errors associated with SHRIMP are substantially larger than with IDTIMS. IDTIMS is not without problems, and has a number of sources of error, including measurement, calibration and common lead in the

analysis. At the present time, IDTIMS is probably still preferable for most high-resolution geochronology in deep time.

Current best-practice U-Pb IDTIMS and Ar-Ar radiometric methods produce dates with a precision of at least 0.1% back to the Cambrian, although the ability to achieve this depends on the availability of datable material, closed-system behavior and the rigor of the laboratory analysis. Other methods, including SHRIMP and older radiometric techniques such as Rb-Sr analyses are too coarse for Phanerozoic studies of the geologic time scale or of geological and evolutionary rates. Estimations of the currently attainable precision for different methods are shown in Figure 1. Two examples from recent studies demonstrate the power and potential of high-resolution geochronology:

THE PERMO-TRIASSIC TRANSITION The end-Permian mass extinction was the most severe of the Phanerozoic (Erwin 2006) and there has been a long history of controversy over the rate and causes of this episode. In the early 1990s the event was viewed as prolonged over millions of years, and possibly related to marine regression, oceanic anoxia or a combination of causes (Erwin 1993). In the exception that proves the rule that abundant ash beds rarely occur where they are most needed, the Permo-Triassic boundary section recently selected as the GSSP at Meishan, China, has numerous volcanic ash beds. These beds range in thickness from mm to cm and occur both above and below the boundary. Given the pre-existing detailed paleontological and geochemical data, this was an ideal setting to test the ultimate resolving power of U-Pb geochronology (Bowring and Erwin 1998) as well as attempt to resolve the rate of the extinction and the (almost?) correlative shift in carbon isotopes.

Claoue-Long et al (1991) reported a SHRIMP U-Pb date of 251.1 ± 3.4 Myr for bed 25 at the event horizon in the GSSP section at Meishan (although technically about 10 cm below the base of the Triassic as defined by conodonts). Renne et al (1995) published a $^{40}\text{Ar}/^{39}\text{Ar}$ date for bed 25 of 250 ± 1.5 Myr and both of these studies suggested the age of the extinction overlapped the eruption of the Siberian flood basalts. Bowring et al (1998) reported a series of zircon analysis from a number of ash beds through the Meishan sequence, with uncertainties of 300 k.y and less, and with an estimated age for the boundary of 251.4 ± 0.3 at Meishan. The inclusion of datable ash beds from the base of the Changhsingian, the final stage of the Permian, and others from below the the apparent onset of the extinction, these results suggested the mass extinction had occurred in less than 1 Myr (probably appreciably less), and further supported a correlation to the Siberian eruptions. Jin et al (2000) performed a statistical analysis of the pattern of extinction and provided new, closely sampled carbon isotope results. These established the presence of a single extinction horizon at Meishan at the top of bed 24. Mundil et al (2001) reported additional results from the Meishan section but many of the dates violate stratigraphic order, which is perplexing. Further details on the geochronology are in Erwin et al. (2002), Bowring and Schmitz (2005) and Erwin (2006), but the important message is that geochronologists are now disagreeing about hundreds of thousands of years, a remarkable level of precision. Figure 2 shows the evolution of the Permo-Triassic timescale over the past four decades. As discussed further in the next

section, the geochronologic results are sufficiently fine that they have had a significant impact on interpretations of the shifts in stable isotopes. Currently geochemists and paleontologists are investigating other, less stratigraphically condensed sections in hope of establishing whether the isotopic shifts occurred before, after or coincident with the extinction.

THE CAMBRIAN RADIATION The Ediacaran-Cambrian radiation of animals is a second critical episode in earth history where our understanding has been transformed by high-resolution geochronology. The rapid appearances of virtually all durably skeletonized animals, along with an equally dramatic diversification of zooplankton and trace fossils has been one of the most perplexing events in the history of life. Despite abundant geologic evidence to the contrary, many paleontologists had argued for a relatively stately unfolding of the soft-bodied Ediacaran organisms, followed by the appearance of the first skeletonized fossils in the Lower Cambrian, and the plethora of soft-bodied forms glimpsed through the Lagerstätten of the Early Cambrian Chengjiang and Middle Cambrian Burgess Shale faunas (e.g. Knoll and Carroll 1999; Erwin in press). The duration of these intervals were poorly constrained until Bowring and colleagues established a rigorous temporal framework based on U-Pb zircon analyses.

In 1993 Bowring et al. published a date of 543 Myr for a volcanic ash from Siberia that was overlain by small shelly fossils and trace fossils diagnostic of the late Neoproterozoic-Cambrian boundary at the GSSP in Newfoundland, Canada. Although such a young date had been previously suggested by French geologists, it was tens of millions of years younger than most workers had expected. (I recall one field conversation where several senior geologists dismissed the Bowring et al result as being 'obviously' wrong, even though they could not point to any reliable radiometric results that contradicted it.) This was followed by a continuing series of papers which sequenced events from the late Neoproterozoic glaciations through the Cambrian (Isachsen et al., 1994; Grotzinger et al., 1995; Davidek et al., 1998; Martin et al., 2000; Thompson and Bowring 2000; Amthor et al., 2003; Hoffman et al., 2004; see discussion in Bowring and Erwin 1998; Bowring and Schmitz 2005). The result (Figure 3) is a tightly defined temporal framework in which to analyze the evolutionary patterns and processes and the geologic context in which they occurred.

Dating of volcanic rocks interbedded with sedimentary rocks does require deposition and recovery of a discrete volcanic component. In addition, both U-Pb zircon geochronometry and Ar-Ar systems actually date the time of closure of the minerals rather than the time of eruption (Bowring and Schmitz 2005). If residence time in a magma chamber is appreciable, there may be an appreciable gap between the closure of the minerals and eruption and deposition of the ash, affecting the geochronologic results. Redeposition of ash beds is an additional complication. To alleviate these problems some workers have studied alternative systems to more directly date the time of formation of the sedimentary deposits. Earlier efforts include glauconite, illite, monzanite and similar systems. Each of these has problems, including large uncertainties, which have precluded widespread adoption. Rasmussen (2005) has suggested xenotime dating of diagenetic overgrowths within sediments. If the diagenesis begins soon after deposition, the resulting dates can closely approximate the age the sedimentary unit was formed but it is

difficult to test this assumption, and to date the method has been most useful in Archean and Proterozoic metamorphic rocks.

Another alternative is dating embedded paleosols (e.g. Rasbury 1998) or diagenetic calcite (e.g. Becker et al. 2002). These methods currently have large errors and while continued development is appropriate they currently only appear useful for settings where no other chronologic information is available, and the dates are too coarse for use in evaluating rates.

Chemostratigraphy

Marine carbonates record variations in the ocean geochemistry of stable isotopes of carbon, oxygen and strontium. Fluctuations in these values have proven vital in both regional and inter-continental correlation and potentially provide great insight into the causes of mass extinctions and other biotic events. Beyond their utility in correlation, the source of a shift in stable isotopes is a major factor in the duration of an isotopic shift, and thus in the level of temporal resolution associated with them.

For example, there is an approximately 3-4‰ $\delta^{13}\text{C}_{\text{carbonate}}$ shift at the Permo-Triassic boundary. Many causes for this shift have been proposed, from deposition of organic carbon from the extinction itself to release of large volumes of sea-floor methane and oxidation of marine organics during regression (see discussion in Erwin 2006). It is very difficult to test these alternatives in the absence of some constraints on the duration of the isotopic shift. When Holser et al (1989) produced their detailed carbon isotope curve from the Gartnerkofel-1 core in western Austria they estimated (based on the assumption that conodont biostratigraphic zones were about 1 million years in duration) that the isotopic excursion lasted some 3 million years. This favored explanations that involved a shift in the isotopic values of the whole ocean, rather than a shift primarily restricted to surface waters. However, once we established that the mass extinction at the Permo-Triassic boundary and the associated isotopic shift occurred in significantly less than 1 million years (Bowring et al 1998; Jin et al 2000) there was too little time for a whole-ocean shift to be plausible (see Erwin et al 2002). Attention then turned to mechanisms that could produce a very rapid shift in surface waters, in part associated with a change in primary productivity, perhaps accompanied by a smaller whole-ocean isotopic shift. Currently geochemists and paleontologists are investigating other, less stratigraphically condensed sections than the GSSP at Meishan in hopes of establishing whether the isotopic shifts occurred before, after or coincident with the extinction. While stable isotopic shifts are critical in establishing correlations between sections they rarely provide unique information about temporal duration.

Magnetostratigraphy

The episodic reversals in the Earth's magnetic field are, like changes in stable isotopes, a vital tool in correlation. However neither the duration of a reversal nor the length of time over which the magnetic field switches direction can be determined a priori. Thus despite the undoubted use of this tool in correlation it provides no direct information on temporal resolution. Once the magnetic reversal sequence has been calibrated against a geochronometric standard, it can be of great use in the absence of

further radiometric results in establishing the duration of various intervals. Olsen and Kent (1999) used a combination of radiometric dates and detailed orbital cyclicity (see the next section) to calibrate the magnetic reversal record of the Late Triassic basins in eastern North America and propose a high-resolution Late Triassic timescale).

Orbital cyclicity

Recurrent sequences of rock are ubiquitous in the stratigraphic record (e.g. Einsele et al 1991; House and Gale 1995) and are frequently interpreted as evidence of the preservation of various orbitally-induced climatic changes, particularly Milankovitch cycles (see Hinov 2000, 2004 for recent reviews). Climatic changes impact temperature, salinity, and precipitation, and through these variables the distribution of clay and dust, oxygen and carbon stable isotopes, microfossil abundance, paleoredox conditions and other variables. Through their influence on climatic variables orbital cycles are known to influence patterns of sedimentation, but they are not the only cause of apparently cyclical sedimentary packages. The stratigraphic record of the past 15 Myr has many examples of such orbital cycles and they have proven of enormous use in stratigraphy, climate studies and evolution, among other areas. Such cycles hold the promise of resolving very high-resolution stratigraphic records in deep time, opening the possibility of addressing a host of fine-scale geological, micro-evolutionary and even ecological questions. But establishing the cause of apparent orbitally-induced cycles deeper in time is more challenging. Hinov (2004) notes that it may be impossible to tie apparent cyclicity older than 20 Myr directly to the orbital record, requiring arguments based on inferred similarity to astronomical cycles (which are themselves still incompletely understood in the Paleozoic) and validation through high-resolution radiometric dating. Moreover, the absence of a deep-sea record before the Jurassic limits studies to shallower sections where gaps in the record are more frequent (Fischer 1995). One of the best case studies of the challenges for orbital forcing in deep time concerns the controversy over and possible Milankovitch cyclicity in the Latemar Middle Triassic carbonate platform in the Dolomites of Italy.

The Latemar contains hundreds of meter-scale sequences representing a carbonate lagoonal facies. Time-series analysis suggested that these cycles represented Milankovitch-induced climatic fluctuations (Goldhammer et al 1987; Hinov and Goldhammer 1991), but U/Pb dating of zircons from correlative strata suggested the buildup was deposited in much less time, and thus must reflect shorter cycles (Mundil et al 1996). Subsequent time-frequency analysis of sedimentological data has been advanced in support of precession and eccentricity components of the Milankovitch cycles (Preto et al. 2001) while new radiometric results (Mundil et al 2003) and extended sedimentological studies (Zuhlke et al 2003) continue to suggest that the most obvious Latemar cycles must have been produced on sub-Milankovitch timescales. Zuhlke et al (2003) have identified bundles of cycles that may represent Milankovitch forcing. This is not the forum to resolve this controversy, but the disagreement does point out the difficulty in using orbital cyclicity in deep time where it has not been confirmed by high-resolution geochronology.

There are pre-Cenozoic records where sufficient high-resolution radiometric dates have been acquired to establish that the apparent sedimentary cycles actually reflect Milankovitch forcing. Prokoph et al (2001) used $^{40}\text{Ar}/^{39}\text{Ar}$ analysis of biotite grains from volcanic ash beds to establish that a sequence through the Cenomanian-Turonian oceanic anoxic event (OAE) had a duration of less than 1 Myr. When combined with statistical analysis of the cyclical sediments, the analysis suggested the OAE lasted about 320 k.y. and the preceding fluctuation in $\delta^{13}\text{C}_{\text{org}}$ lasted about 110 k.y.

One of the longest orbitally-tuned records is from the Newark Series rift basins Late Triassic and Early Jurassic of eastern North America. This 26 Myr long record reveals several different Milankovitch cycles, including long-period cycles of ca. 404 k.y., 700 k.y., 1 m.y., and 1.75 m.y. The 1.75 myr cycle was not predicted based on modern day astronomical patterns (Olsen and Kent 1999). Olsen and Kent did not report radiometric dates from these sections, but correlate using fossils to other sections (Olsen and Kent 1996). By combining the frequency analysis with biostratigraphy and 58 magnetostratigraphic zones Olsen and Kent (1999) produced a high-resolution timescale for the Late Triassic, and could suggest the likely duration of many magnetic reversals.

Strong support for the 404 k.y. cycle identified by Olsen and Kent (1999) comes from recent computation of the dynamics of astronomical forcing cycles back to 250 Myr (and forward another 250 Myr: Laskar et al 2004). Laskar and colleagues conclude that this cycle, corresponding to the largest amplitude in the orbital eccentricity, provides the best tool for astronomical calibration of the Mesozoic time scale, with uncertainties of 0.1% to 100 Myr and 0.2% to 250 Myr, comparable to stated uncertainties on high-resolution U/Pb dates.

The debate over the Latemar cycles illustrates the problem in assessing whether apparent cyclical packages of sediment are due to astronomical forcing, particularly into the Paleozoic (e.g. Late Cambrian carbonates: Osleger and Read, 1991; Silurian: Landing and Johnson 1998). Establishing the causes and evaluating the potential astronomical forcing has proven difficult. The chaotic relationships among the inner planets render computational solutions increasingly suspect further back in time. While the 404 k.y. beat should persist for some period into the Paleozoic, assertions of astronomical forcing must be supported by high-resolution radiometric dates. Most of Paleozoic studies lack sufficient geochronology to confirm that particular cycles have been preserved. Several authors have constructed arguments for orbital forcing. For example, Jeppsson's (1998) model of Silurian ocean cyclicity was developed to explain apparently cyclical patterns of conodont diversity but explicitly invoked Milankovitch cyclicity as the cause of the climatic events driving the diversity dynamics. In Jeppsson's model cool, humid climates with extensive weathering, erosion of terrigenous clastics and cold, oxygenated deep waters alternate with episodes of warm, dry climates favoring widespread carbonate production and anoxic deep waters. Shifts between states are shorter than the oceanic mixing time (c. 1000 years today) and thus occur over at most a few cm of sediment. Aside from the lack of statistical assessment of the reliability of Jeppsson's patterns, the imputation of Milankovitch cyclicity is free of any radiometric evidence.

Biostratigraphy and Correlation

Using fossils and fossil assemblages to establish biostratigraphic zones and correlations is the traditional basis of stratigraphy and still forms the foundation of most fine-scale analyses. But biostratigraphic units contain no a priori information about their duration and so must be calibrated against a chronographic standard to assess the level of temporal resolution.

The recent development of interval-free biostratigraphic methods relies on the overlap, or conjunctions, in fossil ranges of a large number of species. These overlaps are used to establish the position of each species in a temporal sequence through one of several available computer programs. This permits the establishment of many finer-scale intervals than is generally possible with the standard approach of using a limited number of fossils that are believed to be of biostratigraphic utility. Computer-based sequencing can also incorporate a wide variety of other stratigraphic information, including isochrons such as volcanic ash-falls, magnetic reversals and stable isotope excursions. Sadler (2004) reviews a variety of such methods and their application to specific paleontological problems. Some of these methods rely upon a sequence of fossils within stratigraphic range charts, others use isolated collecting localities with no a priori organization into stratigraphic order. These methods hold the promise of a 10-fold increase in temporal resolution over current methods (Sadler 2004).

LIMITS TO PALEONTOLOGIC AND STRATIGRAPHIC RESOLUTION

Currently available geochronologic limits suggest a dating error of few hundred thousand years for Cambrian-age rocks using radiometric methods. With no further temporal information, the potential temporal resolution would depend upon the density of the dated ash beds, and require linear interpolation of estimated sedimentation rates between the dates. The potential of extending the 404 k.y. orbital cycle back into the Paleozoic and of quantitative biostratigraphy suggest that when these techniques are used in combination even finer temporal resolution is possible into the early Paleozoic. Sadler (2004) describes two particularly well worked out examples of biostratigraphic correlation that suggest that even with widely spaced radiometric control resolution of as short as 50,000 years or less may be achievable back to 100 Myr. In the first of these examples Alroy (1992, 1994, 2000) sequenced 6475 events for 3243 taxa derived from 4978 lists of occurrences of Cenozoic North American land mammals. With some 186 dated events, Sadler (2004) suggests the potential resolution of events could be as little as 10,000 years. In their analysis of Ordovician to Early Devonian graptolites, Sadler and Cooper (2003; Cooper and Sadler 2003; Cooper et al., 2004) sequenced 2856 events for 1410 taxa from 256 range charts; they used 22 ash beds. The estimated temporal resolution is some 50,000 years. As with other methods, the reliability of the results are dependent upon the density of the dated ash beds and the accuracy with which they have been studied.

In determining the limits of temporal resolution of stratigraphic sequences it is worth distinguishing between studies that focus on single sections (as in the Permian-Triassic sequence at Meishan) where datable ash beds are present to provide direct control, and perhaps orbital cyclicity may be applied, and regional or global compilations

which rely on correlation to control points (as in the Ediacaran-Cambrian example). Different issues of resolution arise for these two distinct problems.

Fossil data begins with single occurrences, whether the data is used for stratigraphic purposes or to address other questions, and is subject to the same problems. First, neither the first nor last occurrence of a taxon are expected to coincide with the actual origination or extinction of the group: apparent stratigraphic ranges will always be shorter than true ranges. Some of the quantitative correlation methods described above include corrections for this bias. In other circumstances the application of confidence intervals to apparent ranges may help to correct durations (Marshall 1990, 1994; see Jin et al 2000 for application to the Permo-Triassic boundary and an extension to a different type of range data). Second, most fossil occurrences are time averaged to varying degrees, but as pointed out in the introduction, for most settings the level of time-averaging is less than the achievable temporal resolution. Shelf accumulations of marine invertebrates and fluvial aggregations of terrestrial vertebrates are two settings where time-averaging may begin to impact the temporal resolution. Thus as geochronologists increasingly divide stratigraphic sequences into finer bins issues of taphonomy will become increasingly important and eventually begin to impact the nature of the questions that can be addressed. This is probably already true in some Cenozoic settings.

The combination of the methods described above suggest that an achievable goal with existing methods and technology is a temporal resolution to better than 500,000 years back to the lower Paleozoic by relying on a combination of high-resolution geochronology and the optimized quantitative biostratigraphy outlined by Sadler (2004). In non-fossiliferous sequences, or areas where there are not unique solutions to the optimization problems or where adequate dateable material is absent this goal will not be met. This is, however, a far higher temporal resolution than most geologists and paleontologists are used to considering, and raise the possibility of addressing new questions concerning geological and evolutionary rates and the processes underlying them.

RATES, PROCESSES AND TEMPORAL RESOLUTION

The paleoecology of the 1970s has been characterized, not entirely unfairly, as 'me-to ecology' as paleontologists read back issues of *Ecology* and attempted to replicate the studies of succession and life history strategies in the fossil record. This research program largely came to an end in the early 1980's with papers by Schindel (1990, 1992) and Sadler (1991). These papers two complementary issues of sedimentary completeness and microstratigraphic resolution. Sadler attempted to quantify the ubiquity of gaps in the stratigraphic record. Specifically, he showed that the finer the temporal resolution sought, the less sediment was actually preserved. So in a particular sequence of 20 million years, some rock might represent each 1 million year time interval, but if the desired level of temporal resolution is increased to 100 k.y. there will be more 100 k.y. bins for which no sediment has been preserved. Thus completeness drops as temporal resolution increases. Schindel asked how thin a layer of rock would need to be sampled in different environments to analyze events of different temporal resolution. He based his analysis, as did Sadler, on large compilations of sedimentary deposition rates. Schindel

showed that most ecological processes played out over millimeters of rock, a far finer scale of stratigraphic resolution than most paleoecological studies had achieved.

As a consequence of these studies most paleoecologists concluded that they could not meaningfully address a host of ecological issues in most stratigraphic settings. Older detailed records exist, for example Bell's studies of the evolution of fossil sticklebacks from Miocene lake beds in Nevada sampled at roughly 5,000 year intervals (Bell et al., 1985; Bell 1988), but these were settings which clearly had anomalous sedimentation patterns. Intellectually this was actually a quite beneficial episode as paleoecologists realized that there were a host of broader-scale questions that they could meaningfully address. These have largely concerned changing ecological patterns over tens of millions of years.

While the problems of sedimentary completeness and stratigraphic resolution outlined by Schindel and Sadler have not disappeared, nor have the limits of time averaging, the steady increase in temporal resolution promised by a combination of high-resolution geochronology, quantitative biostratigraphy and potentially orbital cyclicity means that we will be re-entering a zone between 10,000 years and a few hundred thousand years temporal resolution where they are increasingly important.

Figure 4, derived in part from Schindel (1992), depicts the general timescales over which a variety of ecological and biological processes play out. In many cases the combination of stratigraphic incompleteness, time-averaging and insufficient temporal resolution means that investigators will have to make strong arguments that they can actually address questions of population dynamics, ecological succession and some aspects of rapid speciation and resource partitioning. (This is not to say that there are not many cases even into the Early Paleozoic where such studies can be accomplished, only that investigators have a higher hurdle to demonstrate the appropriateness of particular settings.) But at the same time the methods described here, used in combination, promise much more reliable analyses of some of the other processes on Figure 4, as well as issues of rates of morphological change, patterns of diversity dynamics, and macroecological patterns and processes.

DISCUSSION

The field of chronology is little remembered today, but during the Renaissance the proper ordering of the events of human history occupied some of the finest minds in Europe. As clocks spread through Europe consciousness of time transformed the study of the past, as Mercator, Ussher and Newton produced lengthy chronologies and analyzed the relationships between different calendrical systems (Grafton 2003). Chronology provided the fundamental basis for history, but history, freed of concern over the sequencing of events was free to address broader issues of pattern and process.

The earth sciences stand on the threshold of a similar transformation as high-resolution geochronology supplemented by higher resolution studies based on orbital cyclicity and interval-free biostratigraphy promise a highly detailed geologic record back to at least 600 Mya. Freed of the concern over dating the geological timescale, new

generations of geologists will finally have the tools to establish geological, evolutionary and paleoecology rates through the Phanerozoic. This will open up a wide range of new questions for investigation.

Two new interdisciplinary projects have recently begun in the United States to advance this goal. The Earthtime Initiative (earth-time.org/), funded by the US National Science Foundation (NSF), is a community-based, collaborative effort dedicated to integrating new high-resolution radiometric dates with quantitative stratigraphy to produce a very fine scale record of Earth history. Critical to this event will be producing radiometric dates with uncertainties of about 0.1% of the ages. The EarthTime initiative faces several challenges, including pushing forward geochronologic techniques and interlaboratory calibration so that these differences do not continue to hamper comparison of results. Geochronologists must also resolve the current systematic bias between the U-Pb and Ar-Ar systems. Perhaps equally important is education of stratigraphers, paleontologists and other field geologists to collect, report and analyze volcanic ash beds. Our experience has been that intensive field studies identify more volcanic ash beds than were previously known. In collaboration with the following effort, there is a need for increased understanding of how to integrate these diverse sources of temporal information, appropriately propagate errors, and use the results in analyzing geological and evolutionary rates.

Chronos is a related effort, also funded by NSF, to develop a series of databases and related tools (www.chronos.org/) integrating stratigraphic and paleontologic data. The new geochronologic data from EarthTime will flow into Chronos to establish the temporal framework needed for that effort. These efforts began in the US but they are necessarily international in scope and will require full involvement from geologists around the world to be successful.

Paleontologists do not have a firm answer to Simpson's question, posed at the beginning of this review. In part this is because there are actually many evolutionary rates depending on the clade, the setting and the type of evolutionary change being studied. But we are increasingly able to establish the range of evolutionary rates, and this may turn out to be a more interesting answer than the one Simpson originally sought.

SUMMARY

1. Recent advances in high-resolution radiometric dating, particularly ITDMS U-PB dating of zircons as well as Ar-Ar methods now make it possible to produce a very-high resolution geologic time scale back to at least 600 Mya.
2. Computer-based methods of quantitative biostratigraphy, used in combination with high-resolution geochronology have shown the ability to achieve sub-100 k.y. resolution into the Paleozoic.
3. The application of orbital cyclicity has been demonstrated in specific circumstances in the Mesozoic but its use in the Paleozoic remains uncertain. Such claims must be tested against high-resolution geochronology. But if these problems can be addressed, the 404 k.y. cycle in particular may yet prove useful in generating high-resolution records in the Paleozoic.

4. The highest fidelity temporal resolution is likely to be achieved in settings where all these techniques can be applied together.

ACKNOWLEDGEMENTS

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Figure captions

Figure 1 – The predicted ideal 2-sigma errors for different geochronological methods as they propagate through time, including SHRIMP and IDTIMS U-Pb, Ar-Ar, Rb-Sr whole rock and fission track analyses. Note that IDTIMS U-Pb and Ar-Ar have the lowest errors for time-scale work and thus provide the greatest precision in deep time. The lines across each triangle are the reported errors for studies of stratigraphic rocks published in

Geology over a five-year period. The SHRIMP errors are fairly close to the minimum achievable errors with current methods, but both IDTIMS and Ar-Ar studies can probably achieve better results. The probable errors of U-Pb work on soils and K-Ar studies at 1000 myr are shown at the base of the figure.

Figure 2 – The evolution of the Permian and Triassic geologic timescale since 1964. The Permian was only formally divided into Middle and Late after 2000. The data comes from the various Harland et al. (1964, 1982, 1989) timescales, the Geological Society of America (GSA) 1999 timescale, the International Union of Geological Sciences (IUGS) 1999 timescale, the International Commission on Stratigraphy timescale (2000) and the Gradstein et al GTS 2004 timescale (from Erwin 2006).

Figure 3 – The Ediacaran and Early Cambrian radiation of animals and associated geological and geochemical events have now been well constrained by a series of U-Pb IDTIMS studies. The timing and approximate duration of the Marinoan and Gaskiers glaciations, the various shifts in carbon isotopes and the timing of critical biological events are now relatively well dated. From Condon et al. 2003. Used with permission of the American Association for the Advancement of Science and S. A. Bowring.

Figure 4 – Required temporal resolution to analyze a variety of ecological and evolutionary processes. The vertical bar denotes the expected achievable temporal resolution in the Cambrian with radiometric dating and possibly with orbital cyclicity. Derived in part from Schindel (1980).

Figure 1

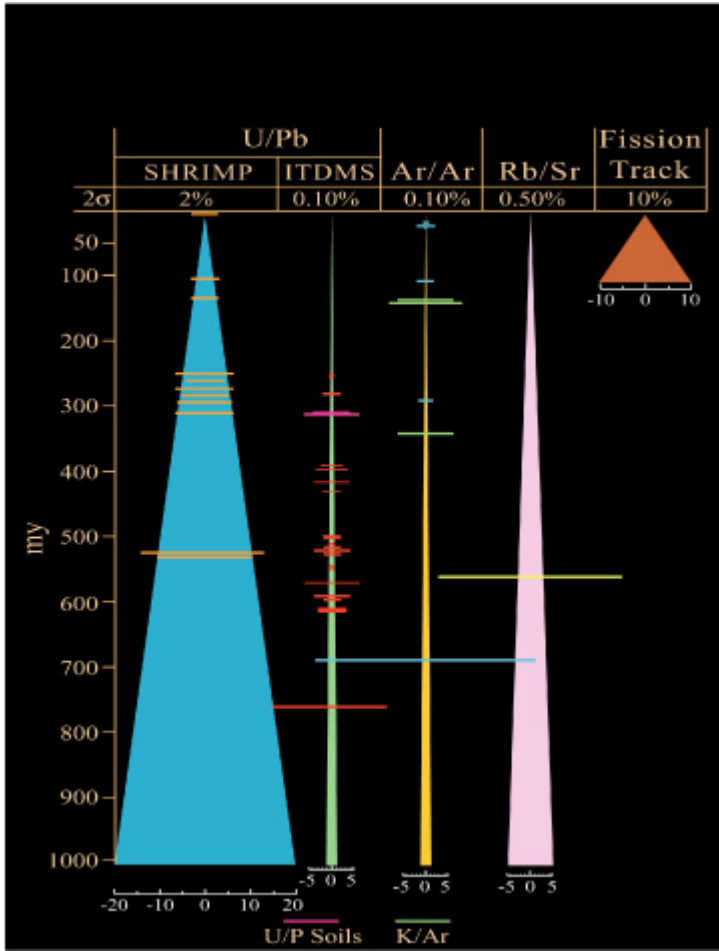


Figure 2.

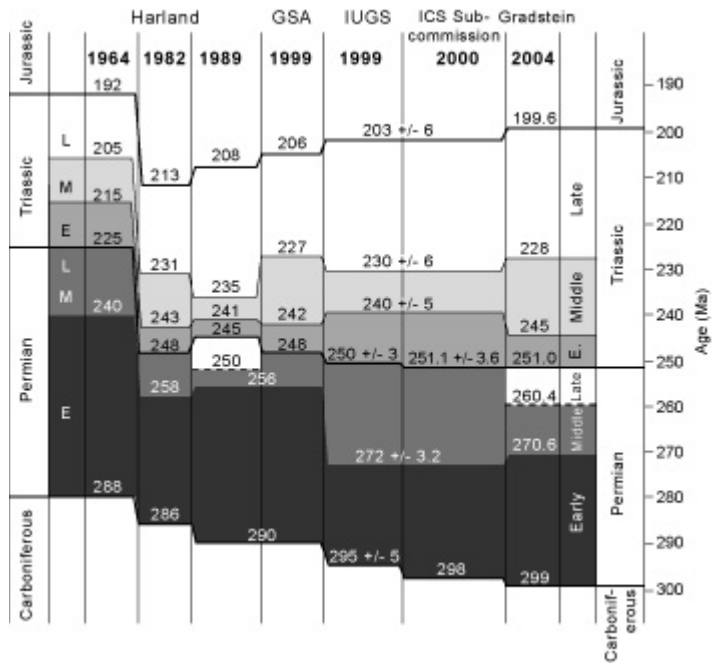


Figure 3

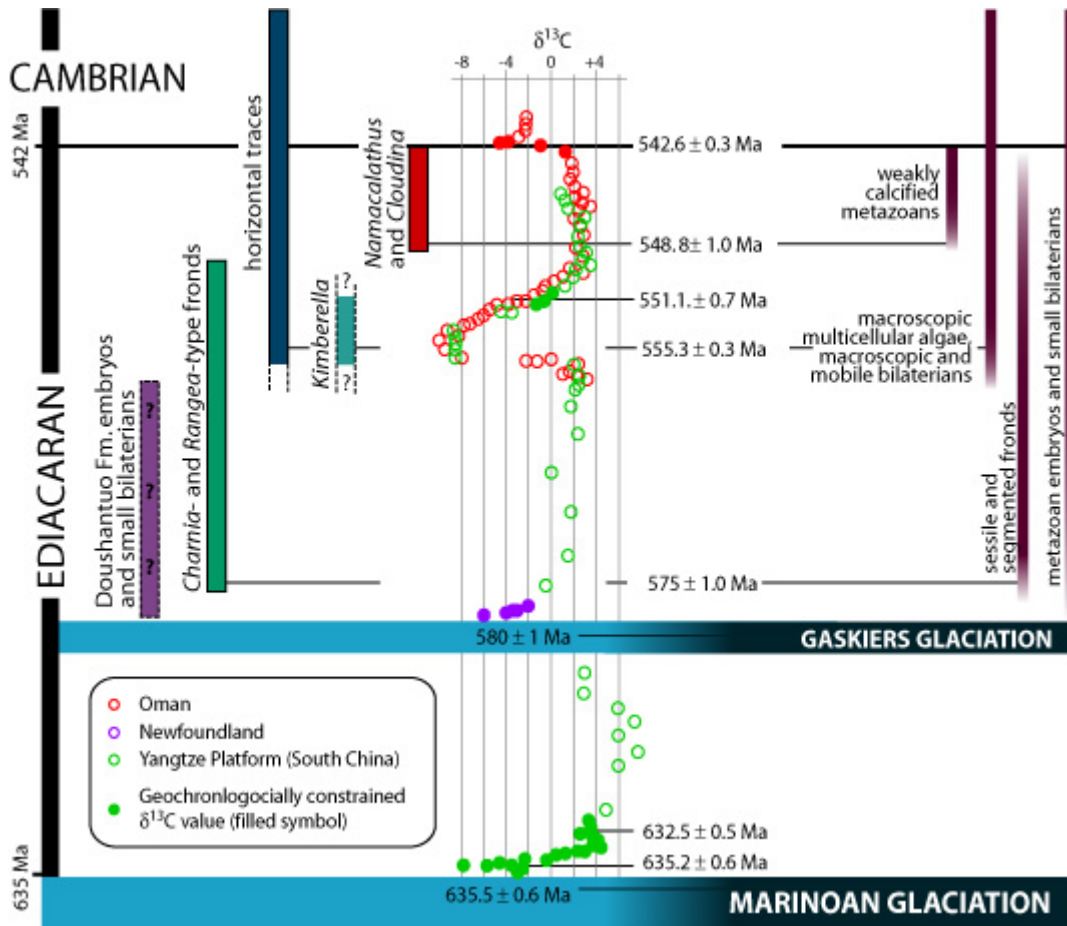


Figure 4

