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Cycles in fossil diversity

Robert A. Rohde & Richard A. Muller

Department of Physics and Lawrence Berkeley Laboratory, University of California, Berkeley, California 94720, USA

It is well known that the diversity of life appears to fluctuate during the course of the Phanerozoic, the eon during which hard shells and skeletons left abundant fossils (0–542 million years ago). Here we show, using Sepkoski's compendium[1] of the first and last stratigraphic appearances of 36,380 marine genera, a strong 62 ± 3-million-year cycle, which is particularly evident in the shorter-lived genera. The five great extinctions enumerated by Raup and Sepkoski[2] may be an aspect of this cycle. Because of the high statistical significance we also consider the contributions of environmental factors, and possible causes.

Sepkoski's posthumously published *Compendium of Fossil Marine Animal Genera*[1], and its earlier versions, has frequently been used in the study of biodiversity and extinction[3,4]. For our purposes, diversity is defined as the number of distinct genera alive at any given time; that is, those whose first occurrence predates and whose last occurrence postdates that time. Because Sepkoski references only 295 stratigraphic intervals, the International Commission on Stratigraphy's 2004 time scale[5] is used to translate the stratigraphic references into a record of diversity versus time; details are given in the Supplementary Information. Although Sepkoski's is the most extensive compilation available, it is known to be subject to certain systematic limitations due primarily to the varying availability and quality of geological sections[6,7]. The implications of this will be discussed where appropriate.

Figure 1a shows a plot of diversity against time for all 36,380 genera in Sepkoski's *Compendium*. In Fig. 1b we show the 17,797 genera that remain when we remove those with uncertain ages (given only at epoch or period level), and those with only a single occurrence. The smooth trend curve through the data is the third-order polynomial that minimizes the variance of the difference
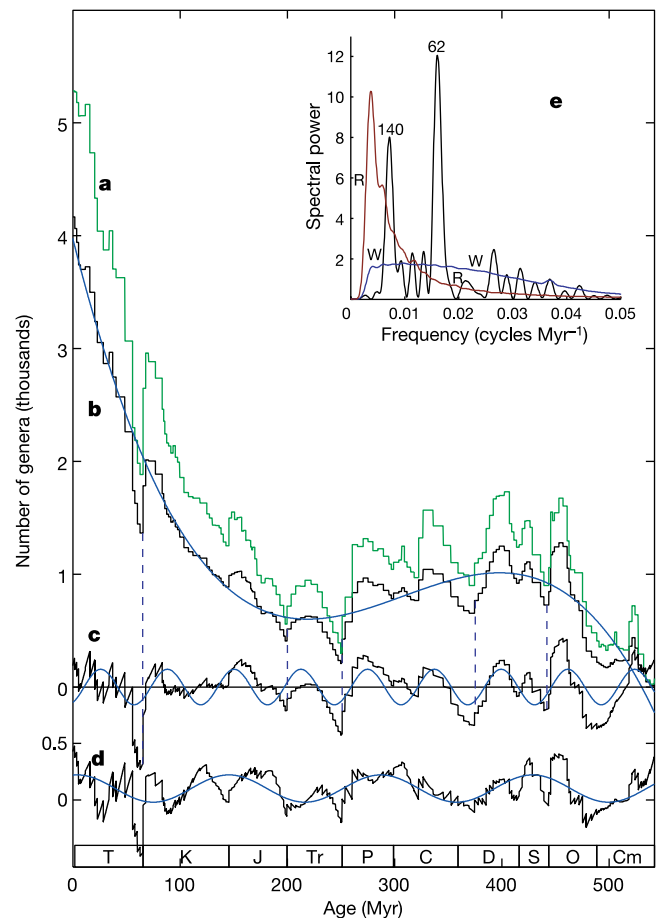

Figure 1 Genus diversity. **a**, The green plot shows the number of known marine animal genera versus time from Sepkoski's compendium[1], converted to the 2004 Geologic Time Scale[5]. **b**, The black plot shows the same data, with single occurrence and poorly dated genera removed. The trend line (blue) is a third-order polynomial fitted to the data. **c**, As **b**, with the trend subtracted and a 62-Myr sine wave superimposed. **d**, The detrended data after subtraction of the 62-Myr cycle and with a 140-Myr sine wave superimposed. Dashed vertical lines indicate the times of the five major extinctions[2]. **e**, Fourier spectrum of **c**. Curves W (in blue) and R (in red) are estimates of spectral background. Conventional symbols for major stratigraphic periods are shown at the bottom.

between it and the data. The overall shape of Fig. 1a, b is similar to those previously published for fossil families[2] and for genera[3]. It rises rapidly at the beginning of the Phanerozoic (right side), drops to a nadir near the Permian/Triassic boundary (251 Myr ago), and then rises steeply until the present. These variations might result from evolutionary and environmental drivers[8], observational biases[6] or changes in the number of available geological sections[7]; for example, the sharp rise towards the present might be driven by the greater availability and study of recent sections.

Our focus will be on the short-term variations shown in Fig. 1c, obtained by subtracting the trend from Fig. 1b. The Fourier spectrum of Fig. 1c is shown in Fig. 1e. It is dominated by a strong peak with period 62 ± 3 Myr (frequency 0.0161 ± 0.0009 cycles Myr^{-1}, error is half width at half max.). The sine wave corresponding to this cycle is also shown in Fig. 1c, where it accounts for 35% of the variance. Note that because steep decreases in diversity are often followed by gradual recoveries, the peaks and valleys in the data do not precisely align with those of the sine curve. Also, some abrupt features might appear more gradual because of incomplete records[9]. We indicate the five major extinction events of Raup and Sepkoski[2] by dashed lines. They all occur during declining phases of the 62-Myr cycle, indicating that the 62-Myr cycle might be related to the timing or magnitude of these extinctions. However, as shown in the Supplementary Information, extinctions do not demonstrate as strong a periodicity as that shown in diversity itself.

Figure 1e has a second spectral peak, with period 140 ± 15 Myr (frequency 0.0072 ± 0.0008 cycles Myr^{-1}). To show this cycle directly in the diversity data, we subtracted the 62-Myr sine wave from Fig. 1c; the result is shown in Fig. 1d.

To determine the statistical significance of the cycles, we estimated background in two ways. In model R we assume that all diversity changes reflect a random walk, and simulate this with random permutations of the steps in Fig. 1b. Thirty thousand Monte Carlo simulations were detrended (third-order polynomial) and analysed; their average spectral power is the red line R in Fig. 1e. For model W we broke the detrended data from Fig. 1c into 20 groups and scrambled their order, thus preserving short-term correlations but randomizing the placement of major events. Thirty thousand Monte-Carlo simulations yielded the flatter blue background W. This is a more appropriate background estimate than R if the fluctuations represent perturbations about an independently driven slow trend. On the basis of these backgrounds, the probability of observing peaks at least as strong as the 62-Myr and 140-Myr spectral peaks were computed and are shown in Table 1. In doing so we considered both the significance of finding the indicated peak at the specified frequency and more generally the probability of finding a similar peak at any frequency. The 62-Myr peak is significant, with no more than a 1% chance of a similar feature occurring anywhere in the spectrum. By contrast, the 140-Myr peak can plausibly result from purely random processes, and this is likely if diversity dynamics reflect R-type behaviour. For further technical details of this computation see the Supplementary Information.

The 62-Myr cycle is also present in both first appearances (originations) and last appearances (extinctions and pseudo-extinctions), though in both cases it is weaker. These results are included in the Supplementary Information.

The possible presence of a ~60-Myr cycle in fossil data has been suggested previously[10–12], but no statistical analysis was performed to confirm those qualitative observations. In fact, when we use the older time scales that were then available, we find that the 62-Myr peak would be of only questionable statistical significance. Different parts of the record shift in phase and cancel each other.

Although the 140-Myr cycle is unexpected and of ambiguous significance, we do note that it is consistent with the periods of other cycles reported in climate[13] and cosmic rays[14], and on those grounds it might merit further investigation. We also note that several authors[15,16] have reported cycles of 26–32 Myr in diversity or extinctions. Although the 62-Myr cycle is the dominant cycle in Sepkoski's diversity data, the existence of secondary features in the middle of some cycles (Silurian, Upper Carboniferous, Lower Jurassic and Eocene) might have influenced previous reports of this ~30-Myr cyclicity.

A particularly simple way to show the appearance of the 62-Myr cycle is to separate the diversity of the 13,682 'short-lived' genera (those that endured for 45 Myr or less) from the 'long-lived' ones. This is shown, without detrending, in Fig. 2. Although the short-lived genera represent, on average, 44% of the diversity at any instant in the geological record, they are responsible for 86% of the amplitude in Fig. 1c. By contrast, the long-lived genera show few significant variations and only strongly participate in one extinction, the Permian/Triassic. We note from Figs 1c and 2a that the 62-Myr cycle is somewhat less regular and well developed during the last ~150 Myr. It is unclear whether this represents a change in the cycle or is merely an obscuring effect due to the large apparent increase in total diversity during this time.

To understand the 62-Myr cycle, it is necessary to consider environmental and causal factors that might be involved. However, given the large sampling biases affecting Sepkoski's work[6,7], we must also acknowledge that the cycle could be driven by a physical process affecting the fossil record, such as changes in sedimentation, rather than by a process that directly affects diversity. Another potential concern is that the durations of several geological periods (Carboniferous, Devonian and Ordovician plus Silurian) are ~60 Myr.
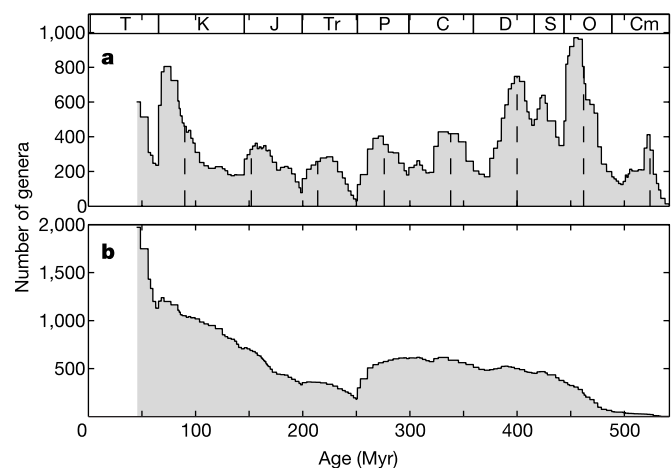

Figure 2 Diversity of short-lived and long-lived genera. This plot shows, with no detrending, the diversity of all genera that have both a first and last appearance resolved at the stage or substage level, and persisted for either 45 Myr or less (**a**) or more than 45 Myr (**b**). Genera with only single occurrences were excluded. Vertical dashed lines indicate the times of maxima of the 62-Myr sine wave of Fig. 1c. Conventional symbols for major stratigraphic periods are shown at the top.

Table 1 **Likelihood of similar cycles**

Probability of peaks	At this frequency		Anywhere in spectrum	
	R	W	R	W
62 Myr	$<5 \times 10^{-5}$	3.6×10^{-4}	<0.0013	0.010
140 Myr	0.12	0.0056	0.71	0.13

The probabilities of observing the 62-Myr and 140-Myr cycles, given the R or W background models as described in the paper, are shown. These are stated both in relation to finding the spectral peak in its current position and as the probability of finding a similar peak anywhere in the spectrum. For details, see the Supplementary Information.

However, most period boundaries were defined by major biological and geological events long before their ages were known. This suggests that any regularity in period durations is likely to be a response to the periodic changes influencing diversity rather than its cause.

To help understand the cycles, we examined the following seven geophysical records. First, a strong ~135-Myr cycle in $\delta^{18}O$, a proxy for glaciation and climate, has been found[13], and is statistically indistinguishable from our 140 ± 15-Myr cycle. Cold periods in $\delta^{18}O$ precede our 140-Myr diversity maxima by 20–25 Myr. A 140-Myr cycle has been reported in other glacial indicators, although the results are disputed[14,17–18]. Second, major volcanism is frequently invoked as a possible cause of mass extinctions. Wavelet analysis on the ages of large igneous provinces shows a minor feature near 60 Myr and no cycle near 140 Myr (ref. 19). Third, $\delta^{13}C$ is a proxy for biomass; however, spectral analysis shows no significant 62-Myr or 140-Myr cycle[20]. Fourth, sea level changes[21] have been associated with extinctions[22]. Extreme sea level states correspond to some extremes in our 62-Myr cycle, but not in a consistent way. Spectra of sea level records[21] show peaks near the 62-Myr and 140-Myr periods, but with low statistical significance. (The Exxon sea level data are available at http://hydro.geosc.psu.edu/Sed_html/exxon.sea.) Fifth, ages of impact craters on Earth[23] show no significant periodicity at 62 Myr or 140 Myr, although it is widely believed that many craters of moderate size have never been discovered. Sixth, records of the number of explored geological formations[7] show no 62-Myr or 140-Myr periodicity, although poor resolution could obscure such cycles. Last, a 143 ± 10-Myr cycle in meteorite ages has been reported and attributed to variation in cosmic ray flux[14].

Our searches have found no compelling match for the 62-Myr cycle; however, incomplete records and errors in time scales can obscure true periodicity. The match of our 140-Myr diversity cycle to the climate/glacial/cosmic-ray cycle might be real, because having a peak at exactly that frequency is still relatively unlikely; however, less ambiguous data would be needed to establish the connection and explain the relatively large lag between the diversity and climate cycles.

The 62-Myr cycle is strong. It might be a largely biological process or a variation in the integrity of the fossil record; however, in either case it is also worth considering geophysical processes that could be driving it. We consider seven possibilities. First, periodic passage of the solar system through molecular clouds, Galactic arms or some other structure could periodically perturb the Oort cloud and cause variations in the rate of comet impacts on the Earth[24]. It has been argued[14] that a 140-Myr period between spiral arm crossings is consistent with existing astrophysical constraints, and that such passages can affect climate by varying the cosmic ray flux. Second, laboratory simulations of mantle plumes, under idealized conditions, show relaxation oscillator modes in which plumes reach the surface at regular intervals for six to nine cycles[25]. Similar behaviour in the Earth could cause periodic volcanism. Third, the Sun currently oscillates up and down across the Galactic plane every 52–74 Myr (ref. 26), but plausible responses[24] would seem to occur every mid-plane crossing (namely 26–37 Myr). Moreover, the period is not constant, but decreases to half when we encounter higher-density Galactic arms. Fourth, solar cycles could affect climate, but solar theory[27] predicts that long-period oscillations do not occur. Fifth, Earth orbital oscillations could affect climate. Using an orbital integration package[28] and nine point-mass planets, we found no significant cycles with periods of 62 Myr or 140 Myr. Changes in obliquity were not included in our calculations. Sixth, one or more companion stars to the Sun could trigger periodic comet showers. However, a 62-Myr orbit is unstable to perturbations from passing stars. The interaction of two or more short-period companions could generate a longer periodicity (for example, through beats), but our simulations suggest that mutual perturbations would probably destroy any regularity. Last, 'Planet X' is a proposed large planet that perturbs the Kuiper belt and could yield periodic comet showers on the right time scales[29]. No evidence for it exists.

Although no explanation exists, the 62-Myr cycle is not a subtle signal. It is evident even in the raw data (Fig. 1a), dominant in the short-lived genera (Fig. 2) and strongly confirmed by statistical analysis. We do not know whether this cycle is a variation in true diversity or only in observed diversity, but either case requires explanation and implies that an unknown periodic process has been having a significant impact on Earth's environment throughout the Phanerozoic. Most models seem to make testable predictions, so we are hopeful that the cause of this behaviour will not remain a mystery for long. □

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