nisms (Princeton Univ. Press, Princeton, NJ, 1976).
12. To document the pattern of punching and survival of the hard-shelled prey of *Asemichthys*, 176 fish (mean ± SD; 42.3 ± 6.3 mm standard length) were collected in the field and placed in individual holding tanks. Fecal boli from each individual were collected over the next 48 hours and examined for the presence of punched shells and live prey. Hermit crab shells were identified by the presence of exoskelton at the aperture. Gastropods and bivalves were determined to have survived if they demonstrated closing behavior after disturbance. Three ostracods were also recovered alive in the feces. Live gastropods with well-developed operculi have been reported in the feces of an opisthobranch snail [R. T. Paine, *Veliger* **6**, 1 (1966)] and a starfish [A. M. Christensen, *Ophelia* **8**, 1 (1970)].
13. Among the subclasses of gastropods, a snug-fitting operculum is common only among the prosobranchs [L. Schmekel, in *The Mollusca*, E. R. Trueman and M. R. Clarke, Eds. (Academic Press, New York, 1985), vol. 10, pp. 221–267; A. Solem, S. Tillier, P. Mordan, *Veliger* **27**, 193 (1984)].
14. The bivalve species common in the feces, *Entodesma saxicola*, *Lyonasia californica*, and *Hiatella arctica*, lack snug-fitting valves, except *Clinocardium nuttalli*.
15. In the bivalve experiments six *T. tantilla* (1.1 to 3.2 mm in length) were presented to each of 15 *Asemichthys* in individual holding tanks. All uneaten bivalves were removed after 4 hours. Ingested bivalves were collected from the feces after 48 hours and examined for punching and survival.
16. The frequency of punching among *Lacuna* (no sculpture), *Margarites* (spiral sculpture), and *Alvinia* (spiral and axial sculpture) did not differ significantly (G test, $G = 1.75$, $P > 0.25$, df = 2). Nor were there significant differences in the size of punched versus unpunched shells in each genus (*Alvinia*, $t(91) = 1.60$, $P > 0.10$; *Margarites*, $t(30) = 0.228$, $P > 0.75$; *Lacuna*, $t(60) = 0.306$, $P > 0.75$).
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Technical Comments

Testing for Periodicity of Extinction

In several papers (*1–4*), we have argued that the extinction record of the past 250 million years (my) shows a 26-my periodicity. Stigler and Wagner (*5*) have challenged this conclusion on two grounds. First, they have found a 26-my periodicity embedded in the geologic time scale such that any random assignment of extinction events using that time scale has a nontrivial likelihood of showing a 26-my periodicity. Second, they have shown that the tendency for random series to exhibit the 26-my periodicity is enhanced by applying a certain kind of moving average filter (designed to simulate the Signor-Lipps effect).

We consider the challenges here in the order of their presentation by Stigler and Wagner. An interesting irony of the first challenge is that the Stigler and Wagner analysis actually strengthens the case for periodicity.

In our first paper (*1*), we wrote (p. 803): "the results could have been generated by periodic elements in the time scale itself rather than from the distribution of extinctions." This was a natural question to raise because the geologic time scale is based in large part on extinctions (*6*).

The basic geological chronology was developed in the 19th century before the discovery of radioactivity, and most of the named intervals were established on the basis of changes in fossil biotas. It is thus no accident that most of the mass extinctions fall at or near major boundaries in the time scale. The well-known Cretaceous-Tertiary (K-T) extinction at the end of the Cretaceous marks the boundary between two eras (Mesozoic and Cenozoic). The largest mass extinction of all is at or near the Paleozoic-Mesozoic boundary. The Jurassic-Cretaceous boundary is based on an extinction event in the Tithonian stage, and so on.

With the discovery of radioactivity in the 20th century, the fossil-based chronology was calibrated by a few radiometrically dated "tie-points," but the classification of geologic time was not altered by the calibration. Therefore, if extinctions carry some periodic signal, one would expect it to be reflected in the radiometric time scale to the extent that boundaries are located at times of extinction. This is not to say that all boundaries in the time scale are at major extinction events, because other criteria for defining boundaries have been and are used. But the historical connection between the time scale and extinction is incontrovertible.

Because times of extinction so pervade the geologic time scale, it has even been suggested that the best way to look for extinction periodicity is to analyze the placement of the time boundaries rather than to work with the raw data of extinction (*7*). Bayer (*8*) has carried this reasoning further by using an assumption of periodicity to refine the existing radiometric time scale.

A reasonable conclusion from the foregoing is that, *if* extinctions in the geologic

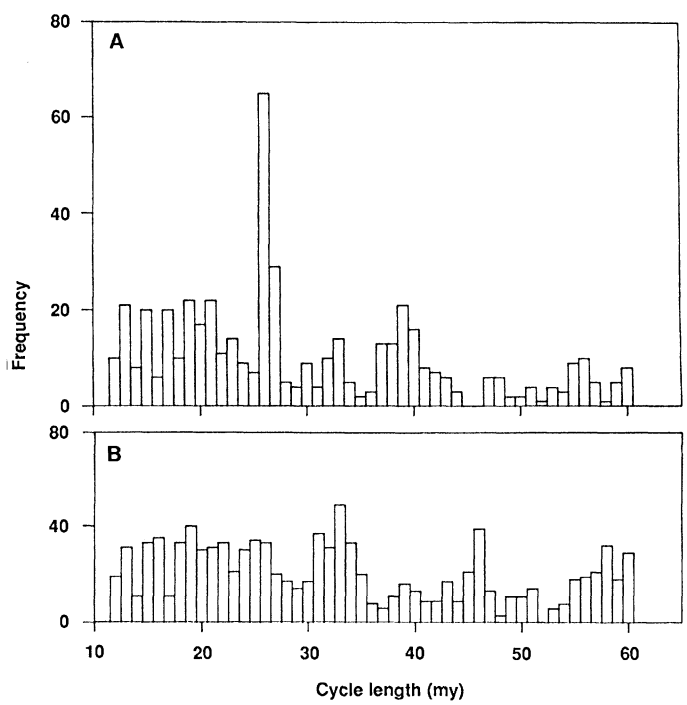


Fig. 1. The frequency distribution of the best fitting period for pseudorandom series (**A**) 500 simulations using the 40-interval Harland time scale for comparison with Stigler and Wagner's figure 4 (*5*). (**B**) One thousand simulations using the 51-interval time scale of Sepkoski (*4*). With the coarser Harland scale, a preference for the 26-my period is evident, but this preference is absent with the finer 51-interval scale.

record are periodic, some trace of the same periodic signal ought to be evident in the placement of the principal boundaries in the geologic time scale. If no trace of periodicity were found in the time scale, this would have to be explained. In this sense the "discovery" of Stigler and Wagner supports our claim of periodicity.

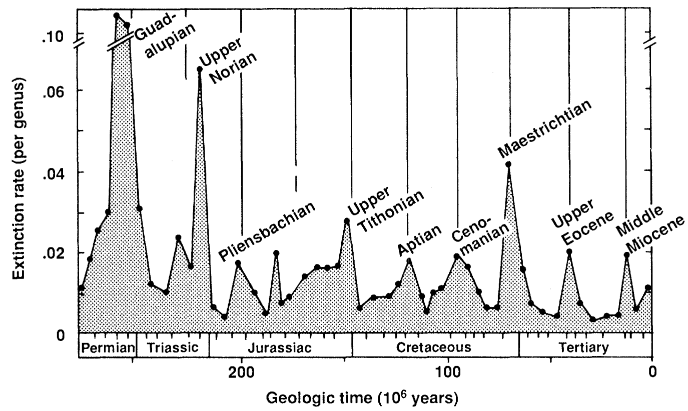
All our time-series analyses recognized the time scale effect, and we tried to segregate the influence of the periodic element in the time scale. Our conclusion in (*1*) was that the time scale has a small but measurable influence on significance levels for rejection of the hypothesis of randomness. Specifically, when the time scale effect is present, the hypothesis is rejected with $P = 0.0045$ (virtually the same as Stigler and Wagner's estimate of $P = 0.0057$); but when the time scale effect is removed by randomization, the significance level changes to $P < 0.0001$ (*1*, p. 803). This provided a rough estimate of the influence of the periodic signal embedded in the time scale.

Thanks to Stigler and Wagner's new simulation technique, however, we now have a more rigorous way to measure the time scale effect. In their stimulation (*5*, figure 4), extinction events were chosen randomly from 40 times boundaries in the Harland time scale, and the best fitting period was found for each pseudorandom series. They observed a "sharp propensity" for the pseudorandom series to have best fitting periods at 26 my. Actually, only 9% of the series show this: a plurality but hardly a "sharp propensity."

The 9% figure is important because it represents the first hard estimate of the strength of the 26-my signal in the Harland time scale. The algorithms for the fitting process are not trivial, however, and the results of Stigler and Wagner suggest a problem at cycle lengths under 20-my, as indicated by the large number of series showing a best fitting cycle in this range. Therefore, we have repeated the analysis and the results are shown in Fig. 1A. The overall distribution is much flatter than in Stigler and Wagner's figure 4 but, more important, the peak at 26 my is sharper, with 13% of pseudorandom series showing a best fit at 26 my Thus, although it would be difficult to establish periodicity on the time scale alone, the preference for 26-my cycles in the time scale is clear.

Although Stigler and Wagner make much of the fact that "the time scale exerts an intrinsic bias toward a best fitting period of 26 m.y." (*5*, p. 943), they stop short of saying that the bias nullifies our claim for periodicity in the extinction data. This is because the hypothesis of randomness can be rejected at a high significance level even if the time scale effect is viewed as an independent signal which, of course, it is not. By adding the moving average effect, Stigler and Wagner are able to argue against our statistical conclusions.

Fig. 2. Record of percent extinction (per million years) computed from the records of 9773 genera of marine fossil animals [from (*4*, figure 3), with the addition of the 26-my periodicity in best fitting position]. Tics along the abscissa indicate standard stages and are not sampling intervals; dots are placed at the centers of the 51 sampling intervals.



The problem here is what is known as the Signor-Lipps effect. Because the fossil record is imperfect, the youngest known fossil of a species (or of a larger group) may predate the actual extinction of the species (or group). Thus, time ranges are often truncated by nonpreservation or nondiscovery of critical fossils, and this sometimes has the effect of smearing extinction peaks backward in time. This is an ever-present problem in paleontology, and considerable efforts were made in our statistical analyses to confront the problem.

In our most detailed investigation of the Signor-Lipps effect (*3*), we isolated two extinction events, Late Permian and Late Triassic, for special attention. For these two events, we noted (*3*, p. 835) that "The Signor-Lipps effect is probably severe, causing a backward smearing of apparent extinctions due to artificial truncation of ranges." Good geologic sections for these two events are rare and smearing is likely. For this reason, we analyzed the entire time series using the four possible combinations of plausible ages for the Permian and Triassic extinctions. We found (after adjustment for multiple testing) that the hypothesis of randomness could be rejected at an acceptable level in three of the cases, but not in the fourth. Because of the doubt raised by the fourth case, we were conservative in drawing final conclusions and said only that the case for a 26-my periodicity "is strong enough to merit further search for conforming evidence" (*3*, p. 836).

The placement of most of the other extinctions events is well established from several lines of independent evidence (*2*) and is not subject to the Signor-Lipps effect. Most of these events have been known for many years from stratigraphic studies, and their identification and dating are not dependent on the familial and generic data we analyzed. Although smearing due to the Signor-Lipps effect undoubtedly operates at small scale in these cases, it is most unlikely that it could be severe enough to cause misplacement of extinction events at the scale of the time-series analysis being considered here. The K-T event is a good example. Although there is legitimate argument over the precise timing of the event in the Late Cretaceous, a geologist would not be likely to argue that the extinctions were actually concentrated in the Paleocene (Tertiary) that follows the Cretaceous, as would be suggested by the Stigler and Wagner analysis.

The Stigler and Wagner treatment of the smearing problem ignores the geology of the situation and ignores our treatment. Instead, they apply what they describe as "a simple model that qualitatively reflects what has been called the Signor-Lipps effect" (*5*, p. 944), and they apply it uniformly over the entire time series. They find that with certain parameter values, their model (operating in concert with the time scale effect) enhances the 26-my periodicity. Stigler and Wagner show results (their figure 6) of a simulation with parameters set so that 50% of each interval's extinctions are mistakenly located. This is an extreme Signor-Lipps intensity, far more than any reasonable value. For the better known sections that dominate the Mesozoic and Cenozoic records, biostratigraphers could not have so misplaced the major events.

Because the Stigler and Wagner model is heuristic, being only qualitative; because it requires extreme parameter values to be effective; and because it ignores independent stratigraphic assessments, we cannot take the challenge seriously.

Although Stigler and Wagner cite all four of our published papers (*1–4*), they concentrate heavily on the first (*1*). This is particularly unfortunate, because the data base has expanded so much since 1984. The original analysis was based on 567 families and 39 sampling intervals. In subsequent analyses, about 10,000 records at the genus level replaced the family data, and the time scale was refined to contain 51 sampling intervals (*4*).

The refinement of the time scale from 39 to 51 sampling intervals was not done arbitrarily. Rather, recognized substage boundaries were used to break up the longer sampling intervals of the more primitive Harland scale. The new generic data were placed in the substages as accurately as possible. That is, the refinement was not done merely by interpolation from the old time scale. Inevitably, the 51-interval scale includes a higher proportion of minor boundaries defined on criteria other than major extinction events. This should have the effect of diluting the 26-my signal seen in the original time scale (Fig. 1A). This prediction was tested by applying the Stigler and Wagner simulation procedure to the 51-interval scale, and the result is shown in Fig. 1B. The tendency for the time scale to produce a 26-my periodicity has disappeared. Thus, a 26-my signal can be seen in the coarse time scale because it contains a substantial number of boundaries defined by major extinctions. The finer time scale contains 36 of the original 39 boundaries, but the addition of 12 minor boundaries masks the periodic signal.

If our original finding of periodicity had been spurious or a statistical fluke, it is likely that increasing the data base by a factor of 20 would have destroyed or severely altered the signal. Instead, the periodic signal has been considerably strengthened, as shown in Fig. 2, which is based on 9773 generic records and the full 51-interval time scale. The last six events (150 my before present to the present) are clearly delineated and match the 26-my periodicity almost perfectly, although the radiometric dating of the sixth (Tithonian) is uncertain. Earlier events show a poorer fit, as is reasonable in view of the weaker biological and temporal control in the older record.

The case for periodicity in the extinction record is based on statistical inference with messy data, and thus it cannot be proved or disproved in a truly satisfactory manner. Because acceptance of periodicity (and some of its suggested causes) would entail a major shift in the way geologists look at the history of the earth and of life, it is proper that the hypothesis be evaluated as toughly as possible. To this end, the past three years have seen a number of published reinterpretations of the extinction data. Some of these have supported periodicity (*9*) and others, such as the Stigler and Wagner effort, have not (*10*). Some of the negative criticisms have been constructive and have led to important improvements in the testing procedures.

The question of periodicity will not be settled completely until we have new data independent of the extinction record. A number of laboratories are working intensively to provide independent tests, including broad sampling for evidence of climatic changes, meteorite impact, and other signals in environmental history that may corroborate periodicity. Not until these databases are fully developed will we know for sure whether extinction is periodic and, if so, whether the signal is simple or complex. In the meantime, the periodicity idea is a hypothesis being testing in the best tradition of science.

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Response: Fours years ago, Raup and Sepkoski (*1*) created an immense stir with their detailed examination of the bold hypothesis that extinction rates were periodic with a period of 26 million years (my). A major component of that paper was a significance test they performed, decisively rejecting the alternative hypothesis that extinctions have occurred as a totally random process. In our report (*2*), we examined the statistical properties of the test they used (*3*); we replicated their analysis and confirmed their main result (that the recorded series of extinction rates was inconsistent with the hypothesis of a totally random process), but we discovered two things about the test that led us to conclude that the apparent periodicity could well be a statistical artifact. We remain convinced that our conclusion was correct.

In our examination of the significance test, we discovered that the Harland time scale (*4*) as used in the original paper by Raup and Sepkoski (*1*) exerted a peculiar bias toward a best fitting period of 26 my and that the test was as sensitive to measurement error of a type known to be present in the data as it was to truly periodic signals, given the noise levels expected with these data. We speculated that the two factors working together could well have produced an artifactual, statistically significant, "period" of 26 my in the original study. We noted that, even if the time scale were refined to the point of being equally spaced (with a stage duration equal to the average stage duration for the Harland scale), the second factor could produce an artifactual "period" in the range from 25 to 30 my—the strong preference for exactly 26 my would disappear, but the tendency of such models to produce artifactual periods would persist. Our results imply that no valid demonstration of periodicity is possible without allowing for this tendency.

In their comment, Raup and Sepkoski note [as they already had in (*1*)] that the boundaries of several strata are determined at least in part by the fossil record itself, and they suggest that the strong preference for 26 my we found in the Harland time scale might be a reflection of this connection, and indeed that it might therefore be taken as itself evidence of periodicity. We note first that these patterns in the time scale, whatever their nature (whether they are the result of a numerical quirk or a consequence of a true periodicity), are irrelevant to an important part of our analysis. The patterns in the time scale were not responsible for the statis-