A Double Mass Extinction at the End of the Paleozoic Era

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Three tests based on fossil data indicate that high rates of extinction recorded in the penultimate (Guadalupian) stage of the Paleozoic era are not artifacts of a poor fossil record. Instead, they represent an abrupt mass extinction that was one of the largest to occur in the past half billion years. The final mass extinction of the era, which took place about 5 million years after the Guadalupian event, remains the most severe biotic crisis of all time. Taxonomic losses in the Late Permian were partitioned among the two crises and the intervening interval, however, and the terminal Permian crisis eliminated only about 80 percent of marine species, not 95 or 96 percent as earlier estimates have suggested.

The extinctions that brought the Paleozoic era to a close about 245 million years ago constituted the most severe biotic crisis in the history of animal life. About 67% of all genera of marine animals known from the uppermost (Tatarian) stage of the Permian System appear not to have survived into the Mesozoic era (*1–3*). The Guadalupian Stage of the Permian, which precedes the Tatarian, also exhibits a high incidence of apparent extinction; 58% of marine animal genera known from the Guadalupian are unknown from any later interval. This is the highest recorded incidence of extinction for any stage of the past 430 million years except the Tatarian (*2, 4*). This pattern has led some investigators to recognize a protracted interval of heavy extinction at the end of the Paleozoic era (*5*). Indeed, recorded percentages of extinction for major taxa decline more-or-less monotonically backward from the Tatarian to the earliest Permian (Fig. 1). The fossil record is imperfect, however, and since the Signor-Lipps effect was elucidated more than a decade ago, it has seemed possible that the high percentages of extinction measured for pre-Tatarian intervals of the Permian are artifacts of an incomplete fossil record (*6*). The Signor-Lipps effect is the erroneous assignment of extinctions that occurred during a crisis interval to earlier intervals; this misassignment results from failure to discover the extinct taxa in rocks that represent the crisis interval. Even if severe extinction in the Late Permian was actually confined to the Tatarian Age, a strong Signor-Lipps effect could give a false appearance that rates of extinction began to increase earlier.

Because the Tatarian record cannot be perfect, there must be some Signor-Lipps effect for the latter part of the Permian. Nonetheless, three tests that we have devised all indicate that the very high rates of extinction recorded for Guadalupian marine faunas are not artifacts of the Signor-Lipps effect but instead reflect actual extinction. Two of the tests reveal that heavy extinction was concentrated at or near the end of the Guadalupian Age. We conclude that one of the largest mass extinctions of the past half billion years occurred about 5 million years before the even larger crisis that ended the Paleozoic era. This Guadalupian crisis appears to have been as severe as the the one that ended the Mesozoic era. Thus, Late Permian faunas experienced a double mass extinction. This unusual occurrence accounts in part for the very high total rate of extinction that has traditionally been attributed to the terminal Paleozoic crisis.

A First Test: Morphologic Patterns

Our tests are based on the observation that high rates of apparent extinction that result from the Signor-Lipps effect should display different taxonomic, morphologic, and temporal patterns from those that represent true extinction. Our first test focuses on the fusulinacean foraminifera. The history of these organisms is especially well known. They have been intensively studied because of their value for dating rocks: They were unicellular, and their abundant calcitic skeletons became major components of limestones. The fusulinaceans that remained after the Guadalupian were notably small (*7*). Differential preservation could not account for a pronounced morphologic pattern of this kind. The Fusulinacea secreted spindle-shaped tests, a large proportion of which were longer than 6 mm when measured parallel to the axis of coiling (Fig. 2A); the tests of all 14 genera known to have survived into the Tatarian are shorter than 6 mm. All five genera that first appear in the Tatarian are also small. In a bootstrap test, we randomly drew 10,000 samples of 14 genera from the total population of 59 Guadalupian genera and established a probability of about 1% that such a sample would contain only genera shorter than 6 mm by chance. An even lower probability would result if data for all Guadalupian and Tatarian species could be assessed, because the genera and type species of our analysis are surrogates for a much larger group of species that resemble them in size.

The Fusulinacea exhibit a second global pattern as well. Of the 59 genera known from the Guadalupian, all 28 that possessed a keriotheca (a skeletal wall resembling a honeycomb) died out before the start of the Tatarian (*8, 9*). Had the apparent extinction been entirely random with regard to wall structure, the probability would have been $[(59 - 28)/59]^{14} = 0.00012$ that none of the 14 genera known to have survived possessed a keriotheca. Inasmuch as the 28 genera with a keriotheca that died out constituted most of the fusulinacean genera whose uppermost occurrences are in the Guadalupian Stage, it is not surprising that they were typically large.

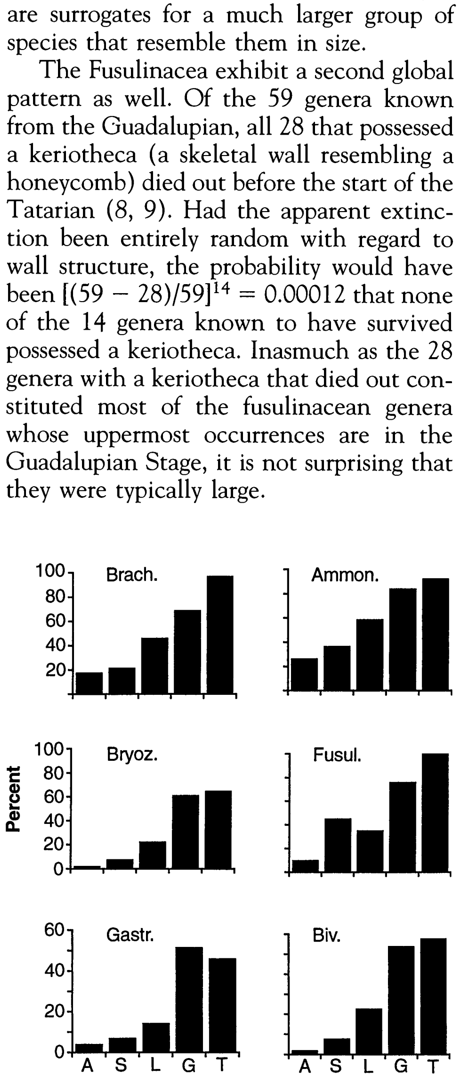

Fig. 1. Percentages of extinction recorded for genera of six higher taxa of skeletonized marine animals [Brachiopoda (Brach.), Ammonoidea (Ammon.), Bryozoa (Bryoz.), Fusulinacea (Fusul.), Gastropoda (Gastr.), and Bivalvia (Biv.)] in the five stages of the Permian [Asselian (A), Sakmarian (S), Leonardian (L), Guadalupian (G), and Tatarian (T)] [data from (*2*), except for Fusulinacea, which are from (*8*) and (*9*)].

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There may have been a slight bias against the preservation of large fusulinid species because they were less abundant than small species. Nonetheless, even the relatively large species were smaller and more abundant than were members of many groups of multicellular animals that left rich Tatarian fossil records. It is therefore inconceivable that lack of preservation could explain the total absence of relatively large fusulinacean genera from the Tatarian Stage throughout the world. Furthermore, because large and small species commonly occur together in Guadalupian rocks (*10*), it is unlikely that Tatarian rocks fail to represent habitats that were suitable for large species. The same arguments hold for species with a keriotheca; they are no less easily preserved than species that lack this structure and frequently occur with such species in the Guadalupian (*10*). The Tatarian record is more extensive than previously believed. A relatively complete stratigraphic sequence exists in Italy, for example, and richly fossiliferous reef facies occur in Greece and China (*11*).

The *Yabeina* fusulinacean zone, which is positioned close to the top of the Guadalupian Stage and extends from Texas to the accreted terranes of British Columbia, contains numerous large fusulinacean species, all of which possessed a keriotheca (Fig. 2B). Sudden extinction is also evident in China, where *Yabeina* and other large fusulinaceans having a keriotheca disappear abruptly at or close to the end of the Maokouan Stage (*8*), which correlates approximately with the Guadalupian (*3*). Had such species survived the transition to the Tatarian Age, it is highly unlikely that their preservation would have ended abruptly at the boundary. Instead, the sudden global disappearance from the fossil record of exceptionally well-preserved taxa characterized by particular morphologies points to a real extinction event in which certain species died out preferentially because they possessed unknown biological traits that rendered them vulnerable to environmental change. This striking pattern further indicates that the excess Guadalupian extinction of these taxa occurred as a brief pulse, at or near the end of the age.

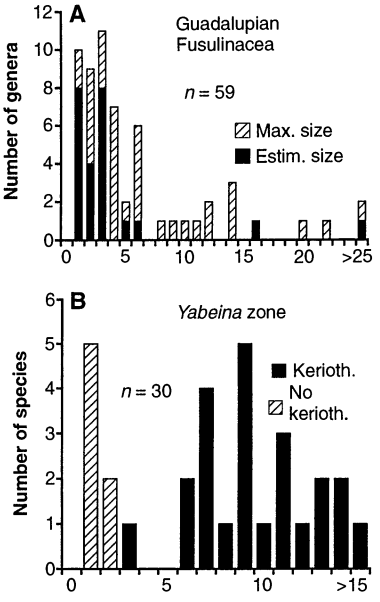

Fig. 2. Size-frequency distributions of Fusulinacea in Guadalupian rocks. (**A**) Plot for all known genera. Where the maximum size for a genus is unknown, the size of the type species is used as an estimate [data derived from (*8*) and (*9*)]. (**B**) Sizes of a large sample of species from the *Yabeina* zone, very close to the top of the Guadalupian Stage of Texas and the Pacific margin of North America [data from (*10*)]. All large species exhibit a keriothecal wall structure (kerioth.) (*8*, *9*).

A Second Test: Taxonomic Patterns of Extinction and Fossilization

If the high overall rate of apparent extinction recorded for the Guadalupian Age reflects real extinction, we might predict the existence of two patterns. First, rates of extinction recorded for particular taxa in the Guadalupian Stage should correlate with rates recorded for the Tatarian Stage. This prediction follows from the observation that certain higher taxa characteristically suffered severe extinction during major biotic crises, whereas other groups repeatedly experienced lighter casualties (*12*, *13*). We subtracted an estimate of background extinction (extinction representing the typical rate for a noncrisis interval) from the total extinction recorded for each taxon in each of the two Late Permian stages. Background extinction is so weak that estimates need only be approximations. As estimates of background rates, we used rates recorded for the Asselian (lowest Permian) Stage. Of all Paleozoic stages above the Lower Cambrian, the Asselian displays the lowest overall rate of extinction for marine taxa (*4*); thus, no large pulses of extinction occurred during Asselian time. Excess extinction for the Guadalupian and Tatarian is the extinction that exceeds the background rate. For six major taxa, percentages of excess extinction are correlated for the Guadalupian and Tatarian ages (Fig. 3A). We selected these taxa for study because their Permian representatives are relatively diverse and well studied; we had no prior knowledge of their relative rates of extinction for the Guadalupian and Tatarian ages.

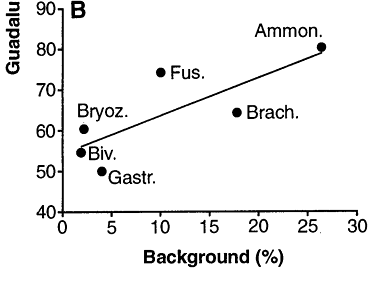

Fig. 3. Relative rates of extinction for genera of the six higher taxa depicted in Fig. 1. (**A**) Correlation between apparent excess extinction for the Guadalupian and Tatarian ages [correlation coefficient (r) = 0.86]. Apparent excess is the percentage above the background percentage (fraction of genera that should have died out during the age at the rate of 1.25%/My recorded in the Asselian Stage). (**B**) Correlation between apparent excess Guadalupian extinction and percentage of extinction for the Asselian (r = 0.80).

Second, if the high overall rate of extinction recorded for the Guadalupian is real, percentages of excess Guadalupian extinction for various taxa should correlate with background rates. This prediction follows from the observation that rates of extinction in crisis intervals often represent the intensification of extinction in proportion to background rates (*12*, *14*). The data show such a correlation (Fig. 3B). Because excess Tatarian extinction correlates with excess Guadalupian extinction for the various taxa, it also correlates with background extinction.

The correlations displayed in Fig. 3 are consistent with the proposition that the high overall rate of apparent extinction recorded for the Guadalupian Stage represents real extinction. Nonetheless, the Signor-Lipps effect might yield at least a weak correlation of this type. Tatarian rates might represent the intensification of background rates, and then any taxon that suffered especially severe losses during the Tatarian would have produced a relatively large pool of extinctions that might erroneously be attributed to the Guadalupian. We can conduct an independent test, however, based on the alternative proposition that the Signor-Lipps effect accounts for the high overall rate of apparent Guadalupian extinction. The test is based on the observation that the effect should be most pronounced for those higher taxa whose species were least likely to be fossilized. In general, probability of preservation varies inversely with body size, because large animals tend to have small populations and long generation times. For a given body size, species with skeletons of calcite are generally more likely to be preserved than are species with skeletons of aragonite, which is less stable at Earth surface conditions.

We can calculate what the magnitude of the Signor-Lipps effect would have been if all of the apparent Guadalupian extinctions in excess of the background rate represented the Signor-Lipps effect. We do this by assigning these extinctions to the Tatarian, in effect restoring hypothetical Signor-Lipps losses (Fig. 4A). Then, for each higher taxon, we calculate the percentage of excess Tatarian extinction that the transfers from the Guadalupian represent. We make the same calculation for excess extinction recorded for the Leonardian and Guadalupian stages combined. These calculations fail to match Signor-Lipps predictions.

Of the six higher taxa, the fusulinaceans have the known fossil record of highest quality, for reasons that we have already given. Brachiopods also secreted calcareous skeletons but are less abundant because they were larger, multicellular animals. Bivalves and gastropods resembled brachiopods in size but secreted shells that were largely aragonitic; they have also been less thoroughly studied in the Permian than have brachiopods. Of these two molluscan classes, the gastropods have the poorer fossil record because they are more aragonitic, on average, and their record is less well known because they have been less intensively studied. Despite these contrasts, the four taxa differ little in the magnitudes of their hypothetical Signor-Lipps effects; in fact, the calculated magnitude is greatest for the fusulinaceans, although they are the best-preserved and best-studied group. The quality of the known fossil record is more difficult to assess for the bryozoans, which are well preserved but poorly studied, and the ammonoids, which are well studied but poorly preserved. Even so, these two groups so closely resemble the other four taxa in the magnitudes of their hypothetical Signor-Lipps effects that their ranking as to quality of known fossil record is immaterial to our analysis.

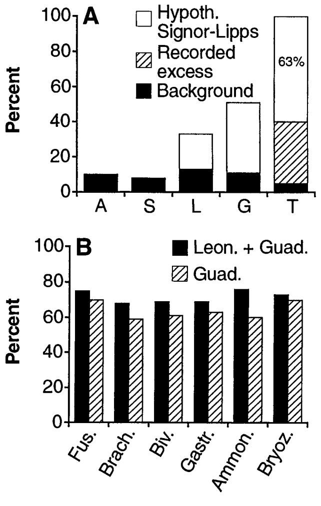

Fig. 4. Hypothetical incidence of the Signor-Lipps effect for the taxa depicted in Figs. 1 and 3, with the assumption that all apparent excess extinctions for ages before the Tatarian actually occurred during Tatarian time. (**A**) Illustration for a model taxon in which the hypothetical Signor-Lipps extinctions, transferred from the Leonardian and Guadalupian, constitute 63% of the total Tatarian excess. (**B**) Hypothetical Signor-Lipps extinction as a percentage of the Tatarian excess for the six higher taxa in Figs. 1 and 3, calculated for the Leonardian and Guadalupian, together [as in (A)] and for the Guadalupian alone. Taxa, such as the Fusulinacea, that are relatively well preserved and well studied do not exhibit a weak hypothetical Signor-Lipps effect.

We conclude that the correlation between rates of extinction recorded for the Guadalupian and Tatarian stages (Fig. 3A) reflects differences in the vulnerability of various higher taxa to extinction rather than differences in quality of preservation and intensity of study. Only a small proportion of the high overall rate of extinction recorded for the Guadalupian represents the Signor-Lipps effect.

A Third Test: Post-Guadalupian Rates of Extinction and Speciation

If the Signor-Lipps effect were to account for the high apparent rates of extinction in the Guadalupian Age, the lower part of the Tatarian record should also display elevated rates. Data for brachiopod species from the excellent Permian fossil record of China (*15*) provide for a test. To eliminate possible distortion caused by variations in the quality of fossil data and in the relative amounts of time represented by Chinese substages, we assess changes in rates of extinction by calculating for each substage the ratio of recorded extinctions to recorded speciations. In a plot of such ratios, the final substages of the Guadalupian and Tatarian stand out as crisis intervals, with recorded extinctions outnumbering recorded speciations by factors of more than 8 and 9, respectively; in contrast, recorded speciations nearly balance extinctions or outnumber them for each of the three intervening substages (Fig. 5). This disjunct pattern is inconsistent with a major role for the Signor-Lipps effect; it points, instead, to two discrete pulses of actual extinction.

Additional evidence of severe Guadalupian extinction is the rampant speciation of brachiopods immediately after the end of the Guadalupian. Of all the Guadalupian and Tatarian stages of China, the first substage of the Tatarian displays the highest ratio of first appearances to last appearances of brachiopod species (the reciprocal of the ratio plotted in Fig. 5). This kind of rebound would be expected to follow a biotic crisis. The Fusulinacea also rebounded after the Guadalupian, although less rapidly; of 133 species recorded from the Changxingian (the latter portion of the Tatarian) in China, 90 are new (*8*).

Physical Evidence of Abrupt Events

All three of our tests indicate that the Signor-Lipps effect contributes relatively little to the high rates of extinction recorded for the Guadalupian Stage. The data for Chinese brachiopods (Fig. 5) indicate that the terminal Permian crisis was confined to the latter part of the Tatarian, just as the earlier crisis appears to have occurred near the end of the Guadalupian.

A temporary global shift in isotopic ratios of carbon during the final 100,000 years of the Tatarian (*16*) presumably relates in some way to the severe Tatarian extinction and thus also suggests that this extinction was concentrated at the end of the age. It may be no coincidence that the total continental area flooded by seas declined abruptly at the end of both the Guadalupian and Tatarian ages (*16*), although we lack explanations for these eustatic events and have no evidence as to how they may have related to the extinctions. A massive outpouring of flood basalt in Siberia also occurred very close to the end of the Tatarian and may have played a role in the extinction (*17*).

Impact of the Terminal Crisis

Rates of extinction measured for all skeletonized marine genera are 58% for the Guadalupian and 67% for the Tatarian; corresponding rates at the family level are 27 and 38% (*2*). The Signor-Lipps effect is probably slightly stronger for the total fauna

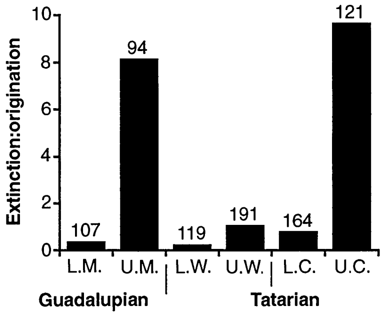

Fig. 5. Ratios of last to first appearances for brachiopod species in the Upper Permian of China. Numbers above bars give total species known from each interval. The abbreviations L and U signify upper and lower substages of the Maokouan (M), Wujiapingian (W), and Changxingian (C) intervals [data from (*15*)].

than for the six higher taxa included in this study, because the total fauna includes some taxa with poor fossil records. Although the apparent incidence of Guadalupian extinction must be slightly elevated by the Signor-Lipps effect, the crisis at the end of this interval was comparable in magnitude to the mass extinctions at the ends of the Triassic and Cretaceous periods. The recorded percentages of extinction for the final stages of the latter periods were actually lower: 46 and 47%, respectively, for genera and 23 and 17% for families (*2*, *4*). For each of the these stages, as for the Guadalupian, a small percentage of the recorded extinctions represents background extinction. We conclude that the Guadalupian event would long ago have been recognized as one of the great mass extinctions of the Phanerozoic Eon if its effects had not been lumped with those of the terminal Permian event, which took place only about 5 million years later.

Evidence that many Permian taxa died out in a pulse of Guadalupian extinction complicates efforts to assess the magnitude of the crisis at the end of the Permian. The fossil record of the Fusulinacea, which we have shown to be distorted very little by the Signor-Lipps effect, displays the apparent extinction of 76% of genera during the Guadalupian, followed by total extinction at the end of the Tatarian. Because the Tatarian added only 5 recognized genera to the 14 known Guadalupian survivors, however, only 19 extinctions of fusulinacean genera are recorded for the terminal Permian extinction, as compared with 45 for the earlier Guadalupian crisis. Thus, although it is impressive that the terminal Permian catastrophe was powerful enough to eliminate all existing species of this group, the actual number of extinctions was relatively small.

Even as a percentage of existing taxa, the terminal Permian extinction was somewhat less severe than some estimates have suggested. Raup's frequently cited estimate for loss of species, based on rarefaction curves, was 88 to 96% (*18*). The rarefaction technique yields estimates of the percentage of extinction at the species level that would be expected to have caused particular percentages of extinction at higher taxonomic levels, which can be measured more accurately from fossil data. Applying rarefaction curves for modern echinoids, Raup estimated that the observed loss of 52% of families and 17% of orders in the latter part of the Permian would have resulted from the extinction of 96% of species; the recorded loss of about 65% of genera yielded the lower estimate for species of 88%. These estimates were not for the Tatarian alone, but for the three final stages of the Permian, which encompass about 24 million years (*3*). Using the same rarefaction curve for genera, Sepkoski estimated that 93 to 95% of species disappeared at the end of the Permian, but to estimate percentage of generic extinction, he pooled data for the Guadalupian and Tatarian stages (*19*).

To evaluate the taxonomic pattern of extinction at the end of the Tatarian, we constructed rarefaction plots of genera against species for 12 extant higher taxa of marine animals. Although the curves vary substantially, most of the individual taxa contain relatively few species, and the composite curve formed by averaging them (Fig. 6) closely resembles Raup's curve for the Echinoidea (a large class of 894 species). Pooling of the data for the 12 taxa also yields a virtually identical curve. Furthermore, these curves nearly coincide with one we constructed for another large extant group, the gammaridean amphipods, which includes 2889 species (*20*). We have used our composite curve to estimate rates of Tatarian extinction at the species level, but the echinoid and amphipod curves would yield almost identical results.

Although the rarefaction method is never perfect for estimating percentages of extinction at the species level, it is more accurate when genera, rather than families or orders, are used to provide empirical data. The rarefaction approach assumes that extinction of species was random. If, instead, extinctions were clustered within certain higher taxa, fewer species will usually have died out than would be estimated by the rarefaction approach (*18*). Imagine, for example, that two families that together constitute an order of animals and that contain equal numbers of genera and identical distributions of species within genera each experience the sudden loss of 60% of their genera. Our rarefaction curve (Fig. 6) predicts that each of the families will lose 83.5% of its species; this will therefore be the impact on the order. Alternatively, consider what would have happened if the same total number of genera had been lost from the order but had included 90% of the genera in one family and only 30% of the genera in the other family. Then the same rarefaction curve predicts that the first family will have lost 97% of its species and the second, 56%. Because the two families originally contained the same number of species, the overall loss will be the average for the two, or 76.5%. This is a smaller percentage than in the first example, where extinctions were evenly distributed between the two families. The convex shape of the rarefaction curve explains the difference: The rate at which higher taxa are lost increases with the percentage of species that die out.

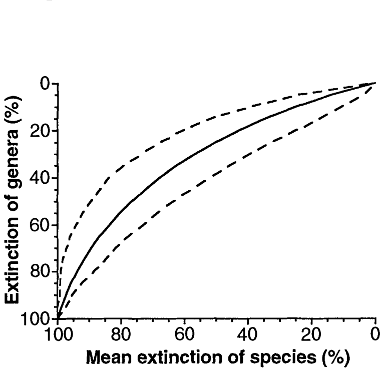

Fig. 6. Rarefaction curve obtained by averaging values for 12 higher taxa of marine animals (*31*). Dashed lines depict two standard deviations. The composite curve is virtually coincident with ones that represent very large individual higher taxa (*18*, *20*) and should approximate the curve for a large marine fauna, such as that of the Late Permian.

That extinction was nonrandom at the end of the Permian is evident from the great variation in rates among major groups of mollusks; the ammonoids nearly died out altogether, whereas the fossil records of gastropods and bivalves reveal losses of only 46 and 58% of genera, respectively (Fig. 1). At a lower taxonomic level, nonrandom extinction is evident for the Fusulinacea at the end of the Guadalupian Age. Eleven of 13 Guadalupian subfamilies (73%) failed to survive to the Tatarian (*12*). This nearly equaled the percentage of genera that died out (45 of 59 = 76%). As noted earlier, the Guadalupian crisis preferentially eliminated genera with a keriotheca. These were confined to 10 subfamilies, all of which disappeared, as compared with just one of the three subfamilies that lacked this feature. Clustering also occurred at the genus level for articulate brachiopods in the Tatarian of southern China, where nearly as large a fraction of genera (85%) as of species (87%) failed to survive to the Mesozoic era (*21*). Sampling of the distribution of species within genera for this region predicts that the random loss of 87% of species would have eliminated only 77% of genera. The higher rates of generic extinction resulted from the concentration of extinction within genera that contained few species.

The effects of clustering of Permian extinctions were inevitably compounded upward through the taxonomic hierarchy. Rarefaction curves for Permian genera will therefore estimate incidence of extinction at the species level more accurately than will curves for families or orders. To estimate the fraction of taxa lost at the end of the Tatarian, it is essential to deduct background extinction from total extinction for the interval. The latest estimate is that 10% of skeletonized marine genera died out during the Asselian Age (*2*, *4*), which lasted about 8 million years (*3*). We use this as an estimate of 6% for background extinction during the Tatarian Age, which lasted about 5 million years (*3*, *22*). Deducting this percentage from the total Tatarian rate of 67%, we obtain 61% as an estimate for losses at the end of the Tatarian. A second method of estimating the background rate suggests that 6% is an underestimate. The reciprocal of 28.4 million years (My), an estimate of mean duration for genera of marine animals (*23*), gives a rate of background extinction of 3.5%/My, or about 17.5% for the Tatarian, leaving 49.5% for extinction in the terminal crisis.

For a loss of 49.5 to 61% of genera at the end of the Tatarian, our rarefaction curve (Fig. 6) yields an estimate of 76 to 84% for loss of species, or a median of 80%. This estimate is subject to several biases. Two factors must depress it artificially. First, the fossil record is relatively poor for genera that contained few species or were geographically restricted and that therefore, on average, experienced relatively high rates of extinction. Second, although we have concluded that most apparent Guadalupian extinctions were real, some small fraction of them must properly belong to the Tatarian because of the Signor-Lipps effect.

Three biases operate in the opposite direction, artificially elevating our estimate. First, there must also be a Signor-Lipps effect that erroneously positions some Early Triassic extinctions in the Tatarian. The stratigraphic record for the first few million years of the Triassic is very poor (*24*), and many Permian taxa unknown from the Lower Triassic reappear in Middle Triassic rocks (*25*); furthermore, genera that were depleted of species by the Tatarian crisis have relatively low probabilities of discovery. Second, rarefaction at the genus level must usually overestimate loss of species because of clustering, even though the effect tends to be weaker at the level of the genus than at higher taxonomic levels. Third, not all taxa recovered fully from the Guadalupian crisis during the Tatarian. The Fusulinacea, for example, lost 45 genera during Guadalupian time and then evolved only 5 new ones during the Tatarian. Some genera that survived the Guadalupian crisis must have remained depleted of species when the Tatarian crisis struck. This implies that, to some degree, the actual rarefaction curve for many Tatarian taxa should have been less convex than average, and relatively few species should have been lost for the recorded percentage of genera.

We have noted two biases that artificially depress our estimate of the impact of the Tatarian crisis on species and three biases that artificially elevate the estimate. It seems unlikely that these biases could produce a large net negative error. We therefore suggest that the fractional loss of marine species was not appreciably larger than our estimate of 76 to 84% and may have been smaller.

A Pair of Mass Extinctions

Since the end of the Paleozoic era, major biotic crises have been separated by intervals of 15 million years or more (*26*). This spacing may reflect a long recovery time for ecosystems (*27*). The occurrence of two mass extinctions within 5 million years of one another during Late Permian time was presumably possible only because the hostile environmental conditions at the end of Guadalupian time disappeared quickly. Certainly, brachiopods in China recovered early in the Tatarian (Fig. 5). Although correlations between marine and nonmarine deposits are imprecise, it appears that terrestrial vertebrates in South Africa, where their Late Permian record is relatively complete, suffered two pulses of extinction, separated by a brief interval of recovery (*28*). The Late Devonian mass extinction may have followed a similar pattern. Reef-building stromatoporoids, for example, suffered heavy extinction at the end of the penultimate (Frasnian) Devonian stage and then recovered somewhat before nearly disappearing at the end of the Devonian (*29*). Also, although the heaviest extinction of marine life is recorded at the end of the Frasnian, the placoderm fishes remained diverse in the subsequent Famennian Age and were not devastated until the end of the Devonian (*30*).

Our calculations do not challenge the conventional view that the Tatarian mass extinction was the largest of the past half billion years. Even so, we conclude that this great crisis eliminated only about 80% of marine species rather than 95 to 96% as some earlier estimates have suggested. A comparable estimate suggests that about 71% of marine species died out in the Guadalupian event.

REFERENCES AND NOTES

1. J. J. Sepkoski, *Milw. Public Mus. Contrib. Biol. Geol.* **51**, 125 (1982).
2. J. J. Sepkoski, unpublished compilation.
3. We follow the convention that divides the Upper Permian into the Guadalupian and Tatarian stages, which correspond to formal ages of geologic time. The Guadalupian, defined in Texas, may actually overlap slightly with the Tatarian, defined in the Ural Mountains [H. Kozur, *Neues Jahrb. Geol. Palaeontol. Abh.* **187**, 99 (1992)]. In China, the Maokouan correlates approximately with the Guadalupian, and the Wujiapingian and overlying Changxingian correlate with the Tatarian. We use absolute ages from W. B. Harland *et al.*, *A Geologic Time Scale* (Cambridge Univ. Press, Cambridge, 1989); here the base and top of the Tatarian are 250 and 245 million years ago.
4. J. J. Sepkoski, *Geotimes* **39**, 15 (March 1994).
5. S. M. Stanley, *Extinction* (Freeman, New York, 1987), chap. 5; D. H. Erwin, *The Great Paleozoic Crisis* (Columbia Univ. Press, New York, 1993), chap. 3.
6. P. W. Signor and J. H. Lipps, *Geol. Soc. Am. Spec. Pap.* **190**, 291 (1982).
7. D. J. Gobbett, in *Atlas of Palaeobiogeography*, A. Hallam, Ed. (Elsevier, Amsterdam, 1973), pp. 152–158.
8. R. Gu, *Minist. Geol. Miner. Resour. (China), Geol. Mem. Ser.* **2** (no. 6), 42 (1987).
9. A. R. Loeblich and H. Tappan, *Foraminiferal Genera and Their Classification* (Van Nostrand Reinhold, New York, 1988).
10. M. L. Thompson and H. E. Wheeler, *J. Paleontol.* **16**, 700 (1942); ———, W. R. Danner, *Cushman Found. Foraminiferal Res. Contrib.* **1**, 46 (1950); J. W. Skinner and G. L. Wilde, *J. Paleontol.* **29**, 927 (1955); *Univ. Kans. Paleontol. Contrib.* **4**, 13 (1966).
11. C. Broglio Loriga and G. Cassinis, In *Permo-Triassic Events in the Eastern Tethys*, W. C. Sweet, Y. Zuni, J. M. Dickens, Y. Hongfu, Eds. (Cambridge Univ. Press, Cambridge, 1992), p. 78; J. W. Reinhardt, *Facies* **18**, 502 (1990); E. Flügel and J. Reinhardt, *Palaios* **4**, 502 (1990).
12. S. M. Stanley, *Macroevolution: Pattern and Process* (Freeman, New York, 1979), chap. 10; J. J. Sepkoski, *Geol. Soc. Am. Spec. Pap.* **247** (1990).
13. D. M. Raup and G. E. Boyajian, *Paleobiology* **14**, 109 (1988).
14. D. H. Erwin, *Palaios* **4**, 424 (1989).
15. G. Xu, *Minist. Geol. Miner. Resour. (China), Geol. Mem. Ser.* **2** (no. 6), 45 (1987).
16. W. T. Holser and M. Magaritz, *Mod. Geol.* **11**, 155 (1987). K. Wang, H. H. J. Geldsetzer, H. R. Krouse, *Geology* **22**, 580 (1994).
17. I. H. Campbell, G. K. Czamanske, V. A. Fedorenko, R. I. Hill, V. Stepanov, *Science* **258**, 1760 (1992).
18. D. M. Raup, *ibid.* **206**, 217 (1979).
19. J. J. Sepkoski, *J. Geol. Soc. (London)* **146**, 7 (1989).
20. J. L. Barnard, *U.S. Nat. Mus. Bull.* **271**, 535 (1969).
21. G. Xu and R. E. Grant, *Smithson. Contrib. Paleobiol.* **76** (1994).
22. S. C. Forster and G. Warrington, *Geol. Soc. London Mem.* **10**, 99 (1985); G. S. Odin, *ibid.*, p. 114.
23. D. M. Raup, *Paleobiology* **4**, 1 (1978).
24. B. Kummel, *Can. Soc. Petrol Geol. Mem.* **2**, 557 (1973).
25. D. Jablonski, in *Dynamics of Extinction*, D. K. Elliot, Ed. (Wiley, New York, 1986), p. 183; A. Hallam, *Hist. Biol.* **5**, 257 (1991).
26. D. M. Raup and J. J. Sepkoski, *Proc. Natl. Acad. Sci. U.S.A.* **81**, 801 (1984).
27. S. M. Stanley, *Paleobiology* **16**, 401 (1990).
28. G. M. King, *Hist. Biol.* **53**, 239 (1991).
29. C. W. Stearn, *Geology* **15**, 677 (1987).
30. S. M. Stanley, *Am. J. Sci.* **288**, 334 (1988).
31. Our composite rarefaction curve is based on 12 taxa, containing a total of 844 genera and 4050 species. Each group's name is followed here by its number of species in parentheses: oegopsid squids (180) [M. A. Clarke, *Adv. Mar. Biol.* **4**, 91 (1966)]; jellyfish (165) [A. G. Mayer, *The Medusae of the World. III. Scyphomedusae* (Asher, Amsterdam, 1910)]; shipworm bivalves (66) [R. D. Turner, *A Survey and Illustrated Catalogue of the Teredinidae* (Museum of Comparative Zoology, Harvard University, Cambridge, MA, 1966)]; ovulid gastropods [N. C. Crawford, *The Veliger* **15** (suppl.) (1973)]; pleocyematan lobsters (153) [A. B. Williams, *Lobsters of the World* (Osprey, Huntington, NY, 1988)]; shrimps and prawns (343) [L. B. Holthius, *Food Agric. Org. Fish. Synop.*, no. 125, vol. 1 (1980)]; sharks (344) [L. J. V. Compagno, *ibid.*, vol. 4 (1984)]; clupeoid fish (355) [P. J. P. Whitehead, *ibid.*, vol. 7 (1985)]; muricid gastropods (389) [G. E. Radwin and A. D'Attilio, *Murex Shells of the World* (Stanford Univ. Press, Stanford, CA, 1976)]; sea cucumbers (1423) (S. Smiley and D. L. Pawson, unpublished manuscript); whales (75) [D. W. Rice, *NOAA Tech. Rep. NMFS SSRF 711* (1987)]; and balanomorph barnacles (352) [W. A. Newman and A. Ross, *San Diego Soc. Nat. Hist. Mem.* **9**, 108 (1976)].
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