

## The double mass extinction revisited: reassessing the severity, selectivity, and causes of the end-Guadalupian biotic crisis (Late Permian)

Matthew E. Clapham, Shuzhong Shen, and David J. Bottjer

**Abstract.**—The end-Guadalupian extinction, at the end of the Middle Permian, is thought to have been one of the largest biotic crises in the Phanerozoic. Previous estimates suggest that the crisis eliminated 58% of marine invertebrate genera during the Capitanian stage and that its selectivity helped the Modern evolutionary fauna become more diverse than the Paleozoic fauna before the end-Permian mass extinction. However, a new sampling-standardized analysis of Permian diversity trends, based on 53731 marine invertebrate fossil occurrences from 9790 collections, indicates that the end-Guadalupian “extinction” was actually a prolonged but gradual decrease in diversity from the Wordian to the end of the Permian. There was no peak in extinction rates; reduced genus richness exhibited by all studied invertebrate groups and ecological guilds, and in different latitudinal belts, was instead driven by a sharp decrease in origination rates during the Capitanian and Wuchiapingian. The global diversity decrease was exacerbated by changes in beta diversity, most notably a reduction in provinciality due to the loss of marine habitat area and a pronounced decrease in geographic disparity over small distances. Disparity over moderate to large distances was unchanged, suggesting that small-scale beta diversity changes may have resulted from compression of bathymetric ranges and homogenization of onshore-offshore faunal gradients stemming from the spread of deep-water anoxia around the Guadalupian/Lopingian boundary. Although tropical invertebrate genera were no more likely than extratropical ones to become extinct, the marked reduction in origination rates during the Capitanian and Wuchiapingian is consistent with the effects of global cooling (the Kamura Event), but may also be consistent with other environmental stresses such as anoxia. However, a gradual reduction in diversity, rather than a sharp end-Guadalupian extinction, precludes the need to invoke drastic extinction mechanisms and indicates that taxonomic loss at the end of the Paleozoic was concentrated in the traditional end-Permian (end-Changhsingian) extinction, which eliminated 78% of all marine invertebrate genera.

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### Introduction

Biotic changes during the Permian-Triassic interval restructured marine ecosystems through their severe impacts on diverse Paleozoic groups such as rhynchonelliform brachiopods, crinoids, and stenolaemate bryozoans, enabling molluscan clades to become the most diverse components of marine ecosystems (Erwin 1993). This taxonomic shift from the Paleozoic fauna to the molluscan Modern fauna was one of two fundamental biotic reorganizations during the Phanerozoic (Sepkoski 1981), coincident with changes in guild structure and energetics in the marine biosphere (Stanley 1968; Bambach et al. 2002). Early studies of mass extinctions recognized both

the taxonomic severity and pronounced evolutionary effects of the Permian-Triassic mass extinction (Raup 1979) as well as the existence of significantly elevated extinction rates at the end of the preceding Guadalupian Series (Middle Permian) (Raup and Sepkoski 1982). High extinction rates during the Guadalupian were considered to be part of a prolonged end-Permian crisis, but subsequent studies instead showed that the end-Guadalupian crisis was a separate event (Jin et al. 1994; Stanley and Yang 1994) distinct from the extinction at the close of the Permian (Fig. 1). Furthermore, global diversity trends suggested that the taxonomic transition from the Paleozoic to the Modern fauna may instead have been trig-

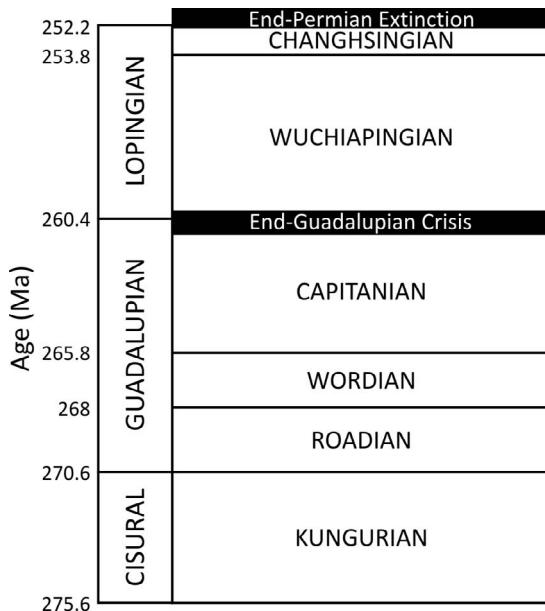


FIGURE 1. Timescale showing the Lopingian (Late Permian), Guadalupian (Middle Permian), and latest Cisuralian (Cisural; Early Permian) Kungurian Stages. The timing of the end-Guadalupian crisis and end-Permian extinction are shown at the end of the Capitanian and Changhsingian Stages, respectively.

gered by selective extinction at the Guadalupian/Lopingian (Middle/Late Permian) boundary, with members of the Modern fauna becoming more diverse than the Paleozoic fauna by the latest Permian Changhsingian Stage (Knoll et al. 1996).

Previous estimates of extinction severity during the end-Guadalupian crisis indicated that approximately 58% of marine invertebrate genera extant during the Capitanian (the last stage of the Guadalupian; Fig. 1) disappeared, a raw magnitude comparable to the end-Triassic or end-Cretaceous extinctions (Stanley and Yang 1994; Knoll et al. 1996), although that raw magnitude may have been elevated by backsmeared of Changhsingian extinctions (Foote 2007). The extinction was also particularly severe for fusulinid foraminifera, which suffered a highly selective taxonomic loss of genera with large and complex tests (Stanley and Yang 1994). Those data sets also suggest that standing marine invertebrate diversity decreased by more than 75% between the Capitanian and the Changhsingian (Knoll et al. 1996). The end-Guadalupian extinction

also may have been moderately selective; genera of the Paleozoic fauna such as rhynchonelliform brachiopods (58%) and stenolaemate bryozoans (61%) suffered greater extinctions than either bivalves (47%) or gastropods (42%) (Knoll et al. 1996). In addition to its potential taxonomic severity, the end-Guadalupian interval was also a time of important environmental and ecological change. Anoxic conditions are first observed in deep oceanic settings at this time, marking the onset of ocean stratification that would ultimately play a major role in the end-Changhsingian mass extinction (Isozaki 1997). These anoxic, and sometimes euxinic, conditions were also present in some deeper epicontinental basins in the early Lopingian (Nielsen and Shen 2004) and began to influence benthic animal communities living in deeper habitats. Molluscs were more abundant at the expense of rhynchonelliform brachiopods in some distal shelf assemblages (Clapham and Bottjer 2007b) while bryozoans became progressively restricted to inner and middle shelf habitats (Powers and Bottjer 2007), both beginning around the Guadalupian/Lopingian boundary.

But despite the apparently severe impact of the end-Guadalupian extinction and its potential influence on the demise of the Paleozoic fauna, the causes of the biotic crisis remain enigmatic. There is a broad plateau of positive carbon isotopic values in Capitanian strata, possibly indicating enhanced carbon burial and global cooling associated with the extinction of large photosymbiotic fusulinids and other tropical organisms (Isozaki et al. 2007a). The Guadalupian/Lopingian boundary itself is characterized by a relatively sharp negative carbon isotopic excursion (Wang et al. 2004; Kaiho et al. 2005) as well as a pronounced sea level fall that may have reduced shallow shelf habitat area (Hallam and Wignall 1999; Shen and Shi 2002). The Emeishan large igneous province, a minor flood basalt in south China, also erupted during the end-Guadalupian interval and may have contributed to the extinction (Wignall 2001; Zhou et al. 2002).

Part of the reason the end-Guadalupian crisis remains poorly understood is because of a lack of adequate data on the biogeographic

and taxonomic patterns of extinction. Previous estimates of global extinction severity typically undersampled the Late Permian record because of outdated biostratigraphy (considering several important Lopingian localities to be Guadalupian) and because many of the data are in foreign publications. Those studies have also not incorporated standardization methods to account for bias imparted by variable sampling, although rarefaction analysis has been used to assess brachiopod and rugose coral diversity patterns in South China (Shen et al. 2006; Wang et al. 2006). Taking advantage of recent advances in biostratigraphic correlation and increasing knowledge of important Late Permian fossil localities, we have assembled a new comprehensive Permian global diversity data set to (1) evaluate genus richness, extinction, and origination with sample standardized methods; (2) document taxonomic, ecological, and geographic selectivity; and (3) quantify changes in geographic range and geographic disparity in order to reassess the importance and potential causes of end-Guadalupian extinction.

### Methods

This study reassessed the severity, selectivity, and paleobiogeographic pattern of extinction during the end-Guadalupian interval, using a database of 53731 marine invertebrate fossil occurrences from 9790 Permian collections. Genus occurrences were tabulated from the primary literature (865 references, see online data at <http://dx.doi.org/10.1666/08033.s1>) and the China brachiopod database of Shen et al. (2006). The data set includes only collections that could be assigned to a single stage and excludes genera with questionable identifications, resulting in a total of 2066 genera based on 52301 occurrences from 9588 collections. Most analyses used the well-sampled Kungurian–Changhsingian interval (41,376 occurrences) encompassing the end-Guadalupian extinction (Fig. 1); each stage during that interval contains at least 5590 occurrences (Fig. 2A). In addition, it was also noted for each taxon whether it had a post-Paleozoic fossil record, so that extinction rates for the Changhsingian (traditional end-Permian extinction) could be calculated, although com-

plete stage-level occurrence data are not recorded for the Triassic. Shen personally revised taxonomic identifications for all Chinese brachiopods, and the synonymy and generic placement of all other species were updated where possible, using the most recent published opinions from the literature. Despite these efforts, there are likely some identifications, especially from older sources, that are incorrect and some species that are placed in the wrong genus. However, in a database of this size those errors are most likely randomly distributed (Adrain and Westrop 2000). The age assignment of each collection was also revised and aligned with the global Permian timescale (Jin et al. 1997) based on conodont, fusulinid, and/or ammonoid biostratigraphy.

The geographic coverage of the data is extensive, with records from all continents except Antarctica, although the locus of sampling shifted from North America to China between the Guadalupian and Lopingian owing to changes in the pattern of marine deposition (Fig. 2A,B). Sample distribution was quantified by calculating the paleoposition of each collection using the Point Tracker software (Scotese 2001) and counting the number of  $30^\circ \times 30^\circ$  paleolatitudinal and paleolongitudinal bins that contain fossil data. Fossil collections were present in 21 to 27 bins during the Kungurian–Wuchiapingian interval, with data coverage dropping to 17 bins in the latest Permian Changhsingian Stage (Fig. 2C). Aggregation of data within those bins was quantified with Green's coefficient of dispersion ( $G$ ), given by the equation

$$G = \frac{\frac{s^2}{\bar{x}} - 1}{\sum (x) - 1}$$

where  $s$  = standard deviation and  $x$  = number of collections or occurrences. It is essentially a variance-to-mean ratio with smaller values indicating more equitable distribution of samples among geographic bins (i.e., better sampling) and larger values indicating that the overall data set is strongly dominated by one or a few geographic bins (e.g., Kiessling et al. 2007). Data aggregation is greater in the Capitanian and is very low in the Roadian and

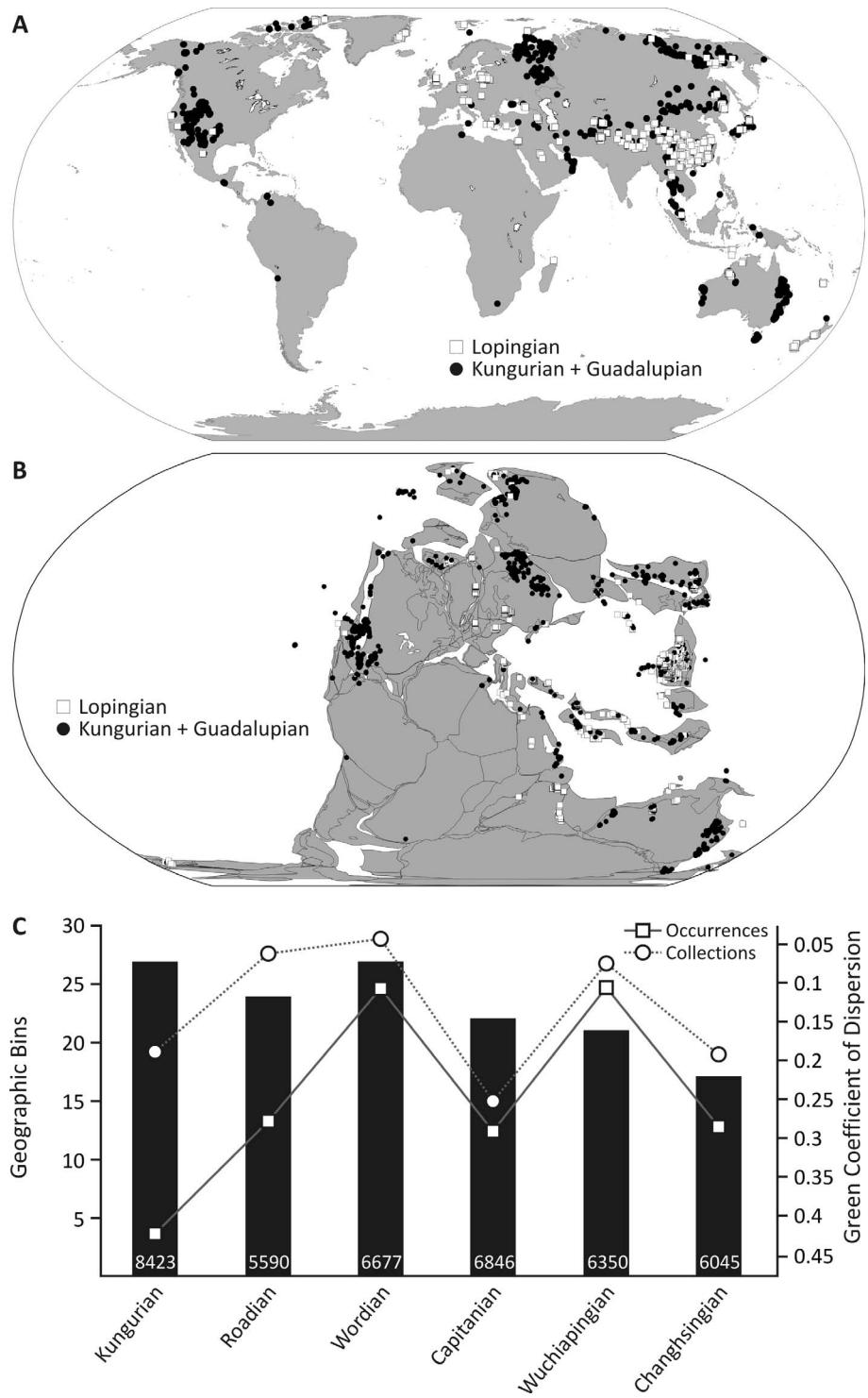


FIGURE 2. Intensity and geographic distribution of sampling during the Kungurian–Changhsingian interval. A, Geographic map with modern location of Kungurian and Guadalupian (filled circles) and Lopingian (open squares) fossil collections. B, Paleogeographic map (260 Ma reconstruction) with paleoposition of fossil collections. C, Number of  $30^\circ \times 30^\circ$  paleogeographic bins containing data in each stage and the Green coefficient of dispersion for occurrences (squares) and collections (circles). Because smaller values of the Green coefficient indicate less data aggregation, the axis is inverted to display smaller values at the top. Number of occurrences for each stage is indicated by the figure in each column.

Wordian, but Green coefficient values for occurrences are never extreme and there is no trend from the Guadalupian to Lopingian (Fig. 2C), suggesting that data aggregation is not a major bias.

Sampling-standardized generic diversity was calculated by repeatedly drawing a given quota of occurrences from each stage, excluding stratigraphic singletons (genera only found in a single stage), and ranging the subsampled genus occurrences through intermediate stages where they were not recorded. A quota of 5590 occurrences was applied, and randomization and subsampling were run for 30 iterations to generate mean extinction and origination rates. Although simple rarefaction may be less realistic than other standardization methods (Alroy et al. 2001; Bush et al. 2004), sampling is uniform enough throughout the Kungurian–Changhsingian interval (Fig. 2C) that extinction and origination rates are essentially unchanged, varying by no more than 2%, after standardization. Standardized extinction and origination metrics are presented for marine invertebrates as a whole, but the minimal effect of standardization allows unstandardized metrics to be used for individual groups, such as rhynchonelliform brachiopods or bivalves. The effects of standardization were tested for groups with sufficient data to fill a reasonable quota each stage (rhynchonelliform brachiopods, 3500 occurrences; bivalves, 460 occurrences; gastropods, 185 occurrences) but none of the standardized extinction or origination rates differed noticeably from the unstandardized results. In addition, application of a uniform occurrence threshold, when occurrences are used as proxies for abundance in rarefaction, is contingent on the actual abundance of a group remaining constant through the interval of study—an assumption that may not be valid for certain groups during the Guadalupian–Lopingian (Weidlich 2002; Clapham and Bottjer 2007a,b; Powers and Bottjer 2007). Furthermore, it is not possible to calculate sampling-standardized extinction and origination for the Changhsingian Stage because the database does not include complete Early Triassic occurrence data (Triassic records are collated for the Permian taxa, but they are com-

piled from the entire Triassic and do not include occurrence data).

Per-taxon extinction and origination rates are calculated as the number of genera with their last or first occurrence, respectively, within a stage relative to the number of boundary-crossing genera surviving into the next stage. Per-taxon rates are presented for the overall extinction and for select groups to allow comparison with previously published studies, but most analyses here use per capita extinction and origination metrics (Foote 2000). Because per-taxon metrics are a ratio of the number of extinct or new genera to all boundary-crossing genera within the interval, per-taxon extinction is also influenced by origination rates (i.e., boundary-crossers that appear within the stage and cross the top boundary) and per-taxon origination by extinction rates (Foote 2000). Per capita metrics disentangle the origination and extinction components of diversity and are used here, although the effects of pulsed versus continuous extinction within these time intervals are not addressed (Foote 2005). Per-taxon extinction is a simple percentage of genera, whereas per capita extinction or origination is measured in per lineage-million-years (per Lmy) (Foote 2000). Per capita extinction is calculated by  $-\ln(N_{bt}/N_b)/\Delta t$ , where  $N_{bt}$  is the number of taxa crossing both the bottom and top boundaries of a stage,  $N_b$  is the total number of taxa crossing the bottom boundary of a stage, and  $\Delta t$  is the duration of that interval (Foote 2000). Conversely, per capita origination is given by  $-\ln(N_{bt}/N_t)/\Delta t$ , where  $N_t$  is the total number of taxa crossing the top boundary of the stage. Extinction and origination rates are calculated for all marine invertebrate genera, for well-sampled and representative groups such as rhynchonelliform brachiopods, bivalves, gastropods, sponges, and corals, and for different ecological guilds such as epifaunal and infaunal bivalves and pelagic cephalopods.

The potential effect of Guadalupian–Lopingian climate change on extinction and origination (Isozaki et al. 2007a) was tested by comparing per capita metrics for tropical and extratropical genera. Tropical genera are defined as those with at least five occurrences confined to the range between 30°S and 30°N

paleolatitude, whereas extratropical genera are those with at least five occurrences only poleward of 45° paleolatitude (including boreal, natal, and anti-tropical genera). A genus's tropical or extratropical distribution was determined independently for each stage; for example, tropical genera in one stage are included even if they may have occurred outside of the Tropics at another time. However, extinction and origination patterns do not change substantially even if only those genera confined to the tropics throughout the entire Kungurian–Changhsingian interval, or even throughout the entire Permian, are included. Both of those criteria, however, result in small sample size for nontropical genera, so the less restrictive determination of tropical or nontropical distribution is used instead.

Because loss of habitat space and related changes in biogeography have previously been invoked as important contributors to the end-Guadalupian extinction (Shen and Shi 2002), we calculated the mean geographic range of marine invertebrate genera and quantified global geographic disparity for each interval (Miller et al. 2007). We measured the geographic range of each genus represented in at least three different localities by generating the convex hull that encompasses all occurrences of the genus and calculating the area of that polygon using the algorithm given by Bevis and Cambareri (1987). The convex hull does not take into account the continental configuration; as a result, the calculated range may extend across land barriers in Pangea rather than conforming to the shoreline. Geographic disparity, a measure of the pairwise compositional similarity between localities in relation to the distance separating them, was assessed by dividing the globe into 5° × 5° bins and calculating the percent similarity coefficient between all pairs of bins (the methodology of Miller et al. 2007). Geographic bins containing fewer than 40 genus occurrences were excluded from the calculation and all other bins were standardized by randomly selecting a quota of 40 occurrences. We calculated percent similarity for all pairwise comparisons (the proportional abundance of each shared genus is calculated, the minimum value is selected from either bin 1 or bin 2, and

those minimum values are summed) and repeated the process for 20 iterations, after which the data were binned into 2000 km size classes so we could calculate the mean percent similarity for all pairwise comparisons at distances less than 2000 km, 2000–4000 km, etc.

To assess geographic variations in extinction intensity we used a kernel density smoothing method in the program CrimeStat (Levine 2004) to calculate the density of extinctions using. The interpolation divides the globe into a series of reference cells (a cell size of 2° × 2° degrees was chosen), overlays a normal distribution to each data point (or kernel), calculates the distance from each kernel to the reference point, and sums all the individual kernel functions from each reference cell to produce an estimate of point density. Fixed distance bandwidth (which sets the standard deviation of the individual kernel functions and controls the smoothness of the resulting contours) was used with a distance metric of 3° degrees. For each stage we calculated the absolute densities of extinction occurrences and total occurrences. In order to account for large variations in the underlying distribution of occurrences, which will strongly influence the observed distribution of extinctions, a dual kernel density smoothing estimate was applied. The method calculates the ratio of the kernel density function for extinctions to the density function for all occurrences in each reference cell. Results were plotted in ArcGIS with an overlay showing the geographic locations of all extinctions. Dual kernel density estimates of extinction were culled from reference cells containing fewer than one occurrence per square degree because small values of the individual density functions (for either extinctions or occurrences) may affect the calculation of their ratio. Those cells typically occupy the tails of the kernel density functions and culling did not affect any cells or regions containing extinctions.

## Results

*Diversity, Extinction Rates, and Origination Rates.*—Genus richness of marine invertebrates decreased from its peak of 948 genera (ranged-through but excluding singletons) in the Wordian to 489 genera by the Changhsin-

gian (latest Permian) (Fig. 3A). At least part of this decline is a result of fewer Lazarus taxa (those ranging through but not occurring within a stage) in the Lopingian Stages, itself an edge effect of the severe extinction at the end of the Changhsingian, but sampled-in-bin diversity (excluding singletons) also decreased from 702 Wordian genera to 489 in the Changhsingian. Absolute generic richness in the Wordian–Changhsingian interval was slightly lower in all stages after sampling standardization but the decreasing trend is unchanged.

This gradual reduction in standing diversity is partially related to elevated raw extinctions in the Capitanian and, to a lesser degree, Wuchiapingian Stages. Unstandardized per-taxon extinction rates were moderately elevated during the Capitanian Stage (29% relative to 12% in the Roadian and 18% in the Wordian), and were virtually unchanged after sampling standardization, at 14% in the Roadian, 17% in the Wordian, and 32% in the Capitanian (Fig. 3B). However, they are much lower than previously published estimates for the end-Guadalupian extinction, which ranged as high as 58% at the genus level (e.g., Knoll et al. 1996). End-Guadalupian per-taxon extinction rates are much less severe than previously recognized because Lopingian diversity was underestimated in prior diversity compilations, partly because many of the data are in foreign language publications, but also because of increased publication in the past decade and improvements in Permian chronostratigraphic correlations. As a result, the database used here records 573 invertebrate genera in the Changhsingian (ranged-through, including singletons) compared to only 196 (also ranged-through, including singletons) in Sepkoski's database used by Knoll et al. (1996). In contrast, both data sets sample Guadalupian Stages well (e.g., 796 Capitanian genera in the Sepkoski database versus 880 in this database, both including singletons). In fact, many genera previously thought to have been lost during the end-Guadalupian “extinction” actually survived into the Lopingian and went extinct at the end of the Changhsingian (the end-Permian extinction sensu stricto). Per-genus extinction rates during the Changhsingian

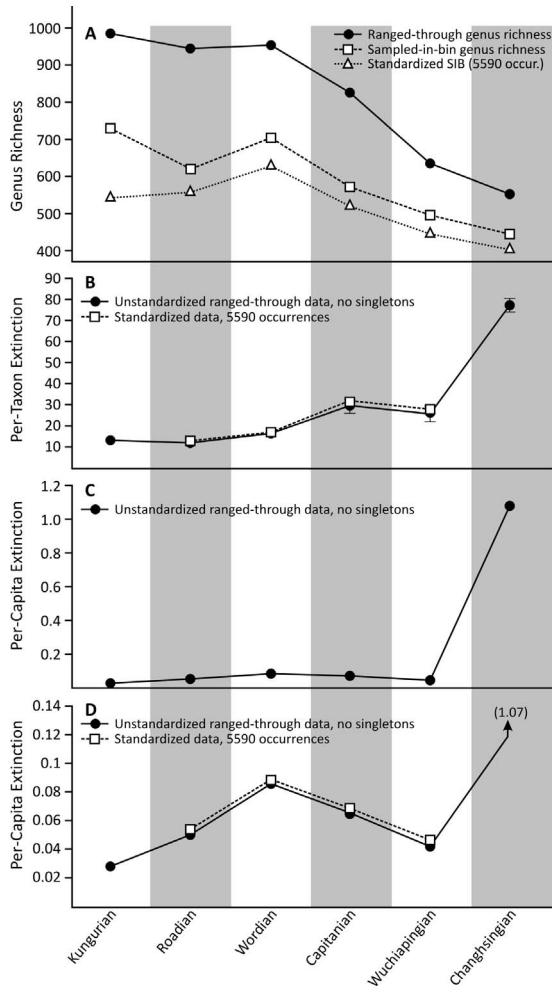


FIGURE 3. Diversity and extinction rate during the Kungurian–Changhsingian interval. A, Total genus richness including (1) ranged-through taxa but excluding singletons (filled circles), (2) unstandardized sampled-in-bin (SIB) richness, also excluding singletons (open squares), and (3) sampling standardized (simple rarefaction, subsampled at a quota of 5590 occurrences) sampled-in-bin richness excluding singletons (open triangles). Confidence intervals for the standardized richness are smaller than the size of the symbol. The standardized richness curve is systematically offset to lower values relative to unstandardized SIB richness because it is based only on Kungurian–Changhsingian data and therefore does not include singletons that also occur before the Kungurian. B, Per-taxon extinction rates for unstandardized (filled circles) and sampling-standardized (open squares) data. Binomial 95% confidence intervals are shown for the unstandardized data. Standardized rates do not include values for the Kungurian because earlier stages did not contain a sufficient number of occurrences or for the Changhsingian because the Triassic records do not contain occurrence data. C, Per capita extinction rates for unstandardized data. D, Enlargement showing per capita extinction rates for unstandardized (filled circles) and sampling-standardized (open squares) data. (1.07)

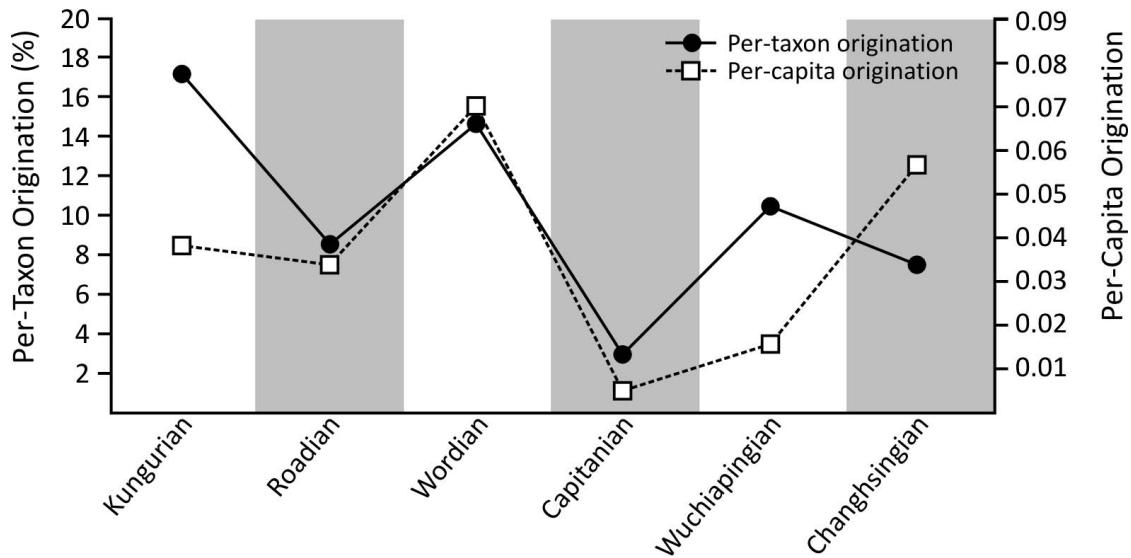


FIGURE 4. Per-taxon (filled circles) and per capita (open squares) origination rates for the Kungurian–Changhsingian interval.

reach 78%, far greater than any other Permian stage, confirming the extreme magnitude of the end-Permian mass extinction.

The severity of the end-Permian extinction is reinforced when per capita extinction rates (which are not influenced by origination within the stage, as in the case of per-taxon metrics) are calculated (Fig. 3C,D). The end-Guadalupian extinction peak recognized with per-taxon extinction estimates is not present in the per capita metric; Wordian (0.09 per Lmy) and Capitanian (0.06 per Lmy) per capita extinctions were very slightly higher than either the Roadian (0.05 per Lmy) or Wuchiapingian (0.05 per Lmy), but those variations fall well within normal background extinction variation and were minor compared to the Changhsingian Stage, which had per capita extinction rates of 1.07 per Lmy (Fig. 3C). There are two causes of the discrepancy between per-taxon and per capita extinctions during the Capitanian stage. The first is simply a function of the length of each stage; per capita extinctions are normalized to stage length and the Capitanian was approximately twice as long as the preceding Roadian or Wordian (Fig. 1). But more importantly, the per-taxon extinction rate during the Capitanian was artificially elevated by the low number of originations in that stage (Fig. 4). Per capita

origination rates were at their lowest in the Capitanian (0.006 per Lmy) and remain low in the Wuchiapingian (0.016 per Lmy).

The relationship between per capita extinction and origination rates demonstrates that the decrease in standing diversity during the end-Guadalupian interval resulted more from a lack of originations than from elevated extinctions (Fig. 4). Extinctions and originations were balanced in the Roadian and Wordian, but during the Capitanian and Wuchiapingian originations dropped sharply while extinctions remained unchanged. The end-Permian extinction (Changhsingian Stage) is a more conventional biotic crisis caused by a huge increase in the extinction rate.

*Taxonomic, Ecological, and Geographic Selectivity.*—This pattern of relatively stable per capita extinction but sharply decreased per capita origination during the end-Guadalupian is also observed in many individual taxonomic groups (Fig. 5). There was no consistent pattern among extinction rates in the Capitanian among well-represented groups in the database; per capita extinction may be higher (bivalves, Fig. 5B; sponges, Fig. 5D), lower (gastropods, Fig. 5C), or unchanged (rhynchonelliform brachiopods, Fig. 5A) relative to earlier stages. Moderately well represented groups, such as corals (Fig. 5E), bryozoans, and am-

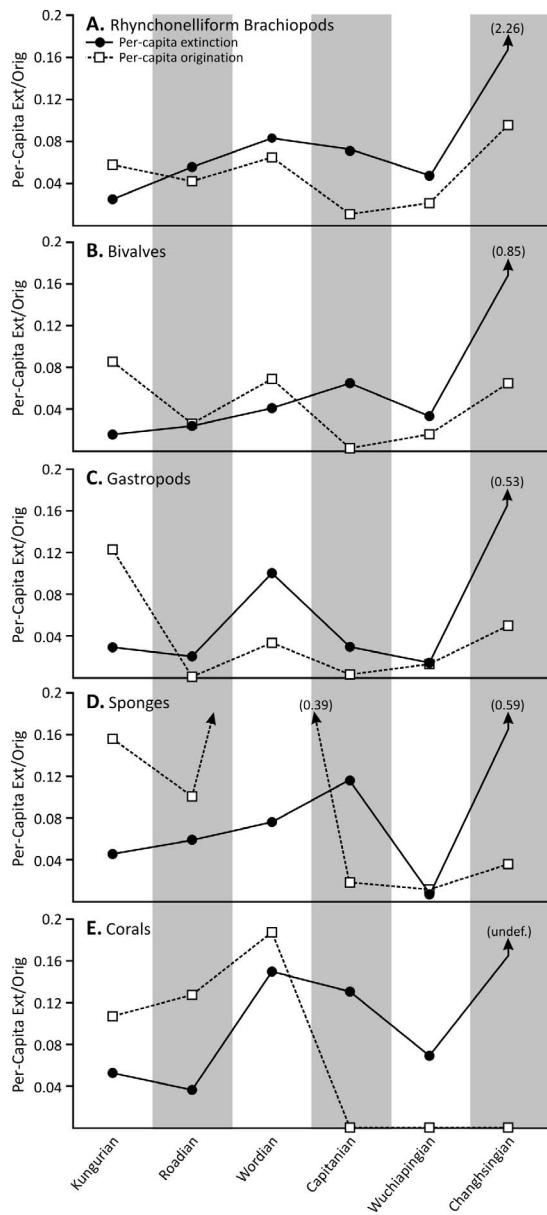


FIGURE 5. Per capita extinction rates (filled circles) and origination rates (open circles) based on unstandardized analyses for rhynchonelliform brachiopods (A), bivalves (B), gastropods (C), sponges (D), and corals (E).

monoids, also exhibited a similar range of extinction patterns. The pattern among corals, even based on moderately good sampling of the group, is consistent with a more comprehensive regional data set from South China, in which per-taxon extinction rates were high in the Capitanian but were comparable to the combined Roadian/Wordian or Asselian/

Sakmarian intervals in that region (Wang et al. 2006). Although Capitanian extinction rates were slightly elevated in a few groups, there is no consistent pattern and per capita values for the Changhsingian Stage were dramatically higher for all groups, indicating that any extinctions during the end-Guadalupian crisis were of minor importance. In contrast to the variable extinction patterns, the per capita origination rates for all taxa were depressed during the Capitanian (e.g., 0.01 per Lmy for rhynchonelliform brachiopods, 0.002 per Lmy for bivalves, and 0.003 per Lmy for gastropods) and were substantially lower than extinction rates during the same time (Fig. 5). Origination often remained unusually low in the Wuchiapingian but appears to have returned to typical levels in the Changhsingian among rhynchonelliform brachiopods, bivalves, gastropods, and sponges at least (but no new corals, bryozoans, or trilobites, other than singletypes, are recorded in the database). However, caution is needed when interpreting some Changhsingian origination rates because of low sample size of boundary-crossing genera; for example, per capita origination among rhynchonelliform brachiopods (0.10 per Lmy in the Changhsingian) appears greater than even the Roadian (0.08 per Lmy) or Wordian (0.07 per Lmy) Stages but results from one new genus appearing within the stage and crossing the Permian/Triassic boundary and only seven genera crossing both bottom and top boundaries (all eight genera ultimately went extinct soon after, in the earliest Triassic). However, regardless of Changhsingian origination rates, their consistent low in the Capitanian and Wuchiapingian confirms that decreased origination at the genus level, rather than increased extinction, caused end-Guadalupian diversity losses in all marine invertebrate groups examined.

Potential ecological selectivity was examined by quantifying extinction and origination rates for different bivalve guilds (epifaunal/semi-infaunal versus shallow/deep infaunal). Both ecological groups exhibited the typical pattern of markedly decreased per capita origination rates in the Capitanian (0.01 per Lmy for epifaunal and 0 per Lmy for infaunal) and, to a lesser degree, Wuchiapingian Stages (Fig.

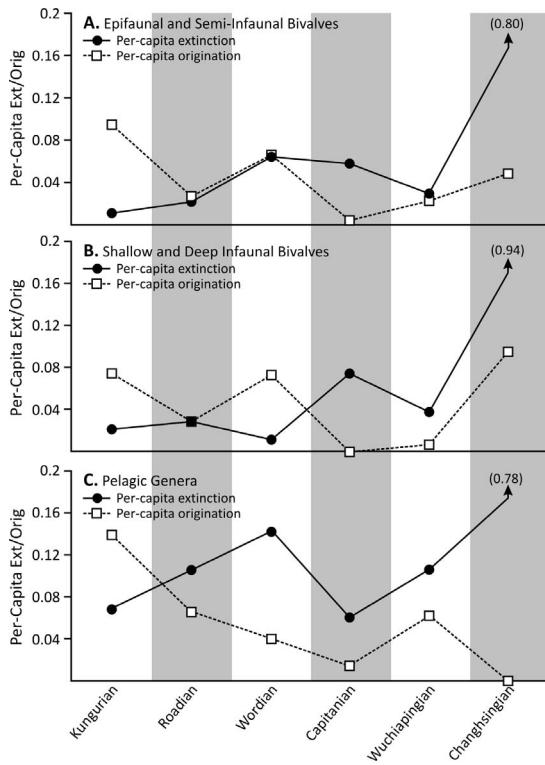


FIGURE 6. Per capita extinction rates (filled circles) and origination rates (open circles) based on unstandardized analyses for epifaunal and semi-infaunal bivalves (A), shallow and deep infaunal bivalves (B), and pelagic genera cephalopods (C).

6A,B). Extinction rates for epifaunal genera were slightly elevated in the Wordian (0.08 per Lmy) and Capitanian (0.07 per Lmy), but both were substantially lower than the Changhsingian end-Permian extinction (0.80 per Lmy). Infaunal bivalves had a minor extinction peak in the Capitanian, but again the per capita value (0.08 per Lmy) was much lower than in the Changhsingian (0.94 per Lmy). The pattern for other ecological guilds, such as pelagic cephalopods (Fig. 6C), was also similar—unchanged or minimally elevated per capita extinction accompanied by a larger drop in origination rates. Together, the absence of significant selectivity among different taxonomic groups or life habits implies that the factor(s) responsible for decreased origination rates affected all groups to approximately the same degree.

Extinction and origination rates were also independently assessed for tropical and extratropical taxa during the Kungurian–Chang-

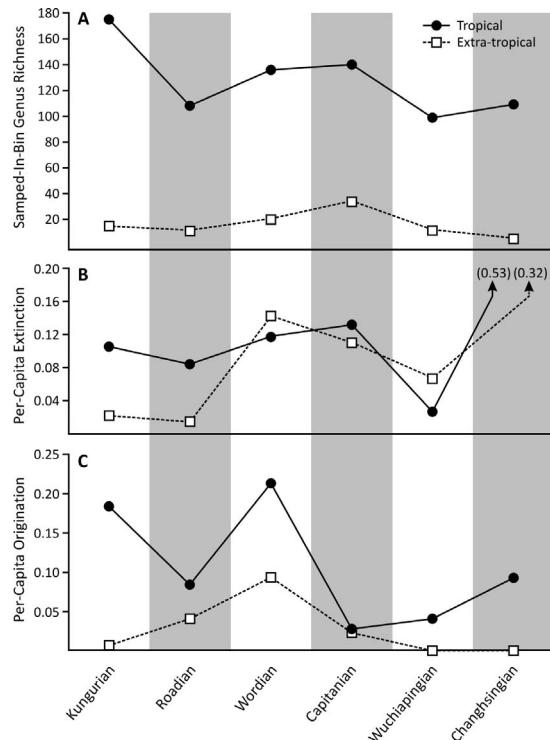


FIGURE 7. Tropical (filled circles) versus extratropical (open circles) extinction and origination. A, Sampled-in-bin genus richness. B, Per capita extinction rates. C, Per capita origination rates. Tropical genera are defined as those confined to within 30° of the paleoequator, whereas extratropical genera are those only found poleward of 45° paleolatitude.

singian interval (Fig. 7). Per capita extinction rates for tropical taxa, those confined to within 30° of the equator, increased slightly from the Roadian to Capitanian (from 0.08 to 0.13 per Lmy) but were substantially lower than the Changhsingian (0.53 per Lmy). Per capita extinction rates for extratropical taxa, those occurring poleward of 45° paleolatitude, were broadly similar during the studied interval, especially in the Wordian and Capitanian Stages (0.14 and 0.11 per Lmy). Both tropical and extratropical groups show the Capitanian–Wuchiapingian decrease in per capita origination observed in the whole fauna, most taxonomic groups, and ecological guilds. The decrease was greater in tropical regions than in extratropical; both had similar origination rates in the Capitanian (0.02 in nontropical versus 0.03 in tropical) yet tropical origination rates were otherwise consistently higher than non-tropical ones.

Although the total number of genus extinctions was high in the Capitanian, those extinctions were strongly clustered geographically (Fig. 8). Even after accounting for the underlying distribution of occurrences (which is strongly centered on western Laurentia in the Capitanian) through the use of a dual kernel density estimate, extinctions were still strongly clustered in western Laurentia, with secondary clusters in Tunisia, New Zealand, and northeastern Siberia (although there are few genera and occurrences in the latter two regions). In fact, the density of extinctions in other well-sampled regions, such as central and eastern Tethys and western Panthalassa, was largely unchanged relative to the Roadian or Wordian, suggesting that the greater number of extinct genera overall, and thus the elevated per-taxon extinction rate, in the Capitanian was strongly influenced by the western North American record. These concentrated extinctions may reflect geographic variability in actual extinction intensity, but are more likely an artifact of the near-complete loss of the preserved marine sedimentary record and its isolated and endemic marine fauna (21% of all genera are endemic to Laurentia in the Capitanian) due to Permo-Triassic tectonism in the western United States (e.g., Collinson et al. 1976).

*Changes in Geographic Range.*—In order to assess the influence of changes in habitat area on marine diversity during the end-Guadalupian interval (e.g., Hallam and Wignall 1999; Shen and Shi 2002), we quantified the latitudinal and geographic ranges of all genera in each stage. Most genera were confined to a single 20° paleolatitudinal bin (Fig. 9), and many of those were singletons occurring only at one locality. This pattern was essentially unchanged throughout the Middle and Late Permian, although the proportions of genera with latitudinal ranges less than 20° and with latitudinal ranges greater than 100° were slightly, but not significantly, lower in the Lopingian. Overall, the mean geographic range for all genera appears to have increased in the Lopingian (Fig. 10); the geometric mean range is  $7.3 \times 10^5 \text{ km}^2$  in the Wuchiapingian and  $3.5 \times 10^5 \text{ km}^2$  in the Changhsingian, much higher than the maximum value from the Kungurian–Capitanian

interval ( $1.9 \times 10^5 \text{ km}^2$  in the Wordian). The geometric mean (the mean of the logarithmic values of the data) was calculated instead of the arithmetic mean because the range data span nearly ten orders of magnitude, from less than  $0.1 \text{ km}^2$  to more than  $10^8 \text{ km}^2$ .

The broad shift toward larger ranges in the Lopingian does not appear correlated with sample distribution or aggregation, which decreases from 22 to 21 geographic bins containing data from the Capitanian to Wuchiapingian and is reduced further to 17 bins in the Changhsingian. In fact, sample distribution was at its maximum (27 sampled bins) and aggregation was minimal (Green coefficient for collections of 0.04) in the Wordian, yet the raw mean range was actually lower than in the Lopingian. Changes in sample distribution reflect a combination of the extent of shallow marine shelf area during the Permian and the modern distribution of preserved marine sedimentary rocks; their effects can be approximated by quantifying the maximum potential range of taxa recorded in each bin. Like the sample distribution, the maximum recorded geographic range is remarkably constant between the Kungurian and Wuchiapingian, varying from  $1.9 \times 10^8 \text{ km}^2$  to  $2.2 \times 10^8 \text{ km}^2$ , but it decreases to less than  $9 \times 10^7 \text{ km}^2$  in the Changhsingian. After normalizing the mean range to the maximum range recorded in each stage, the Late Permian increase in mean geographic range becomes even more dramatic, especially in the Changhsingian (Fig. 10B).

However, the timing of the pronounced increase in raw mean geographic range also coincides with a shift in regions sampled—most importantly, the loss of the marine fossil record from western Laurentia, and from the heavily sampled localities of west Texas in particular. Given that a genus must be recorded from three distinct collections in order for us to calculate a range, the intense sampling from a small geographic area in the Glass and Guadalupe Mountains in Texas would have recorded a large number of endemic genera with very small ranges in the Middle Permian but not in the Late Permian. The mean ranges of Kungurian and Middle Permian taxa endemic to Texas were indeed small (41 to 711  $\text{km}^2$ ) and those endemic taxa constituted a sig-

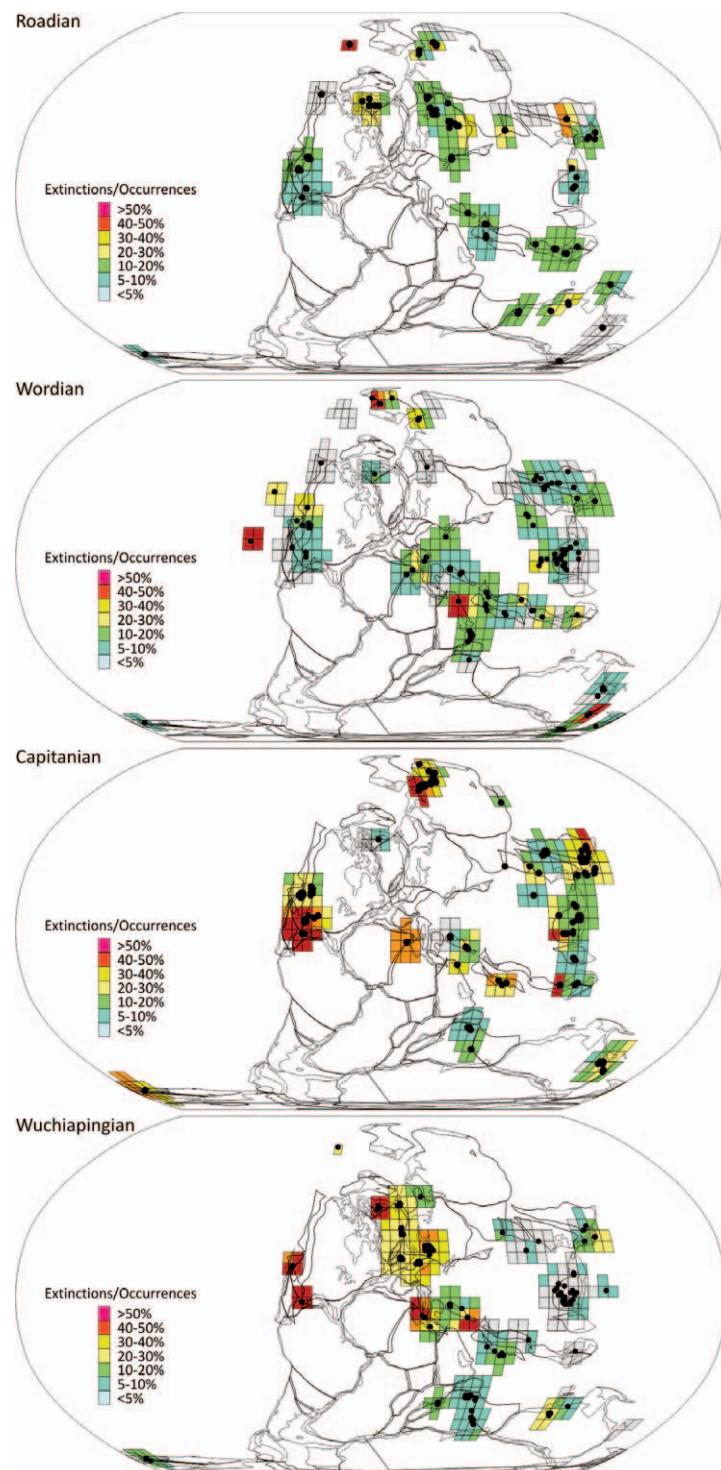


FIGURE 8. Maps showing paleogeographic distribution of extinctions during the Roadian, Wordian, Capitanian, and Wuchiapingian Stages (solid circles) and the contoured dual kernel density estimate for the geographic concentration of extinctions. Geographic concentration is measured as the ratio of the density kernel for extinction occurrences within the stage to the density kernel for all occurrences within that stage.

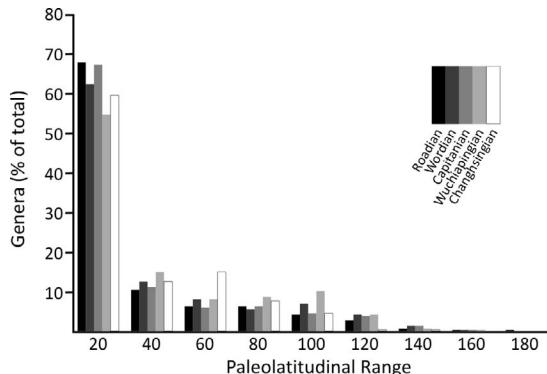


FIGURE 9. Histogram showing the number of genera in 20° paleolatitudinal bins for each Guadalupian and Lopingian stage.

nificant portion of all taxa with calculated ranges, especially in the Kungurian and Roadian (Fig. 11). However, the ranges of Texas endemics do not differ substantially from the typical range of endemic genera from other regions and it is not clear that Middle Permian localities are actually more finely sampled. Between 48.5% and 52.5% of Guadalupian genera occurred in at least three geographically distinct collections, and there was no change in the Wuchiapingian (51% of genera) and only a minor decrease in the Changhsingian (45.5% of genera). A more important effect seems to be the unusually large geographic ranges of taxa endemic to South China, which account for a substantial proportion of Lopingian occurrences (Fig. 11). In contrast to other Middle or Late Permian regions, the South China block was a continent-sized carbonate platform (with associated deeper basins) that has undergone minimal post-Paleozoic tectonic deformation and sediment cover. Thus, the shift from abundant endemics with small ranges from Texas to abundant Late Permian endemic taxa with much larger ranges from South China contributed to the apparent increase in geographic range, and when all genera with ranges less than 100 km<sup>2</sup> are conservatively excluded from the analysis the Late Permian increase in raw geographic range disappears and the increase in proportional geographic range is reduced to within error (Fig. 10A,B).

Although sampling effects make geographic range data difficult to interpret, those ef-

fects can be minimized when assessing the geographic selectivity of extinction by using a proportional range metric (the mean range of taxa that become extinct in a stage relative to the mean range of all taxa in that stage). The proportional mean range of extinct Capitanian genera was 3% of the mean range of all genera, consistent with values for the entire Kungurian–Wuchiapingian interval (Fig. 10C). That selectivity indicates that narrowly distributed genera were more likely to become extinct during the Capitanian (and through the entire Kungurian–Wuchiapingian), typical of background extinctions throughout the whole Phanerozoic (e.g., Jablonski 1986; Payne and Finnegan 2007). Although endemic genera from the western United States typically had small mean ranges, the loss of the sedimentary record from that region did not bias the mean range of extinct genera in the Capitanian, as western U.S. taxa constituted only 6% of all taxa with measured ranges, the mean range of Texas endemics was not smaller than that of endemics from other regions, and the selectivity for geographic range in the Capitanian was no different from background levels in other Permian stages. In contrast, geographic selectivity was significantly different during the Changhsingian (traditional end-Permian extinction) when the mean range of extinct genera was 67% of the overall mean range (Fig. 10C).

**Geographic Disparity.**—Although there is no strong evidence for changes in overall geographic range, decreasing global genus richness in the Lopingian may have been exacerbated by changes in geographic disparity (the degree of compositional disparity between marine biotas as a function of geographic distance; Miller et al. 2007). As expected, 5° × 5° cells separated by small distances were much more similar to one another than they were to distant cells during all time intervals (Fig. 12). There were no systematic differences in percent similarity between cells at moderate to large distances (greater than 6000 km), although there were no pairwise comparisons at distances greater than 14,000 km for the Capitanian, Wuchiapingian, or Changhsingian. Wuchiapingian and Changhsingian biotas were much less disparate than Guadalupian

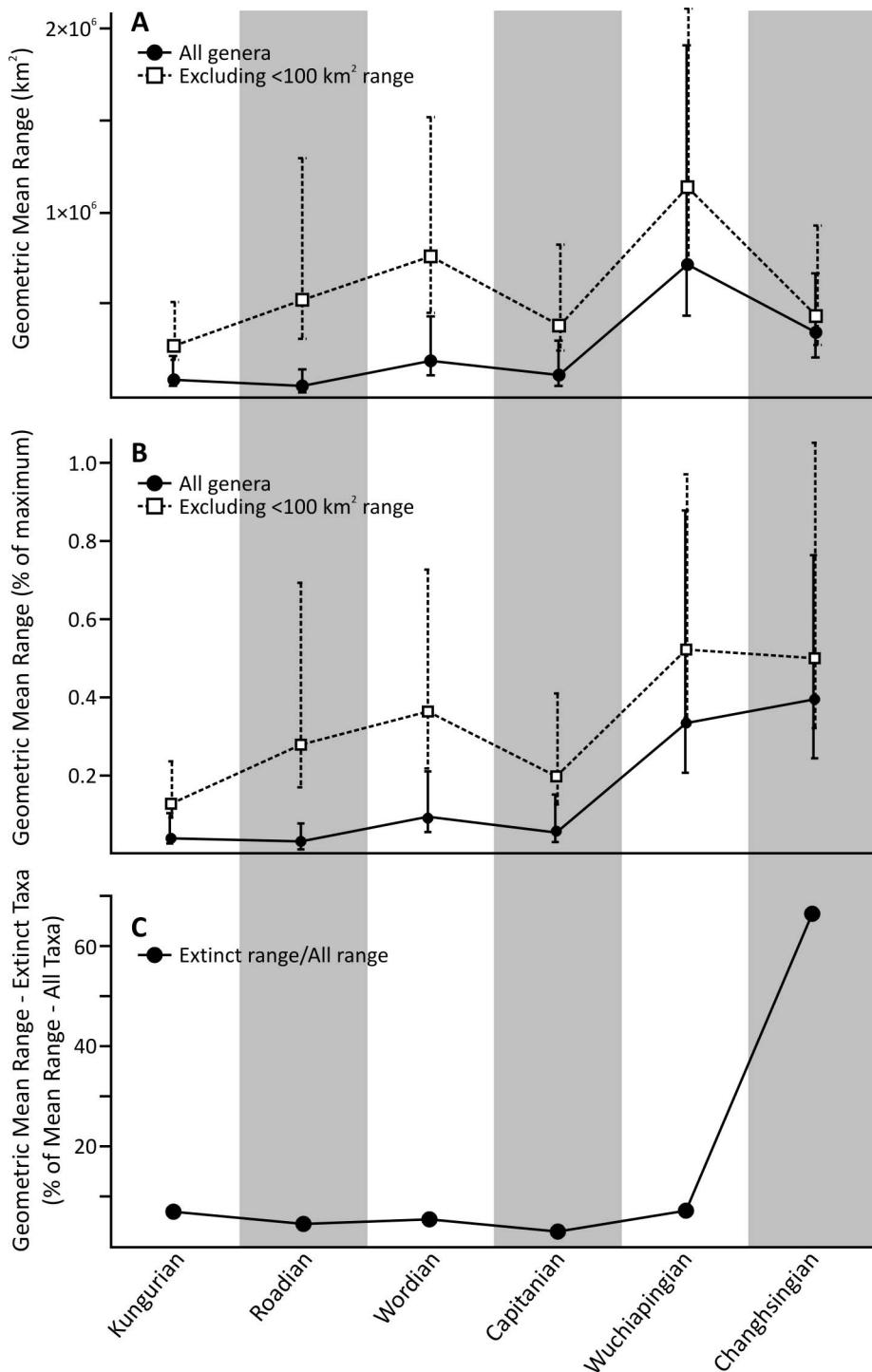


FIGURE 10. Mean geographic range of sampled-in-bin genera and extinct taxa during the Kungurian–Changhsingian. A, Geometric mean geographic range of all taxa (solid circles) and after excluding taxa with a range less than  $100 \text{ km}^2$  (open squares). B, Proportional geometric mean geographic range of all taxa (solid circles) and after excluding taxa with a range less than  $100 \text{ km}^2$  (open squares), both calculated relative to the maximum range recorded in each stage. C, Proportional geometric mean geographic range of taxa making their last appearance within a stage relative to the geometric mean range of all taxa within that stage. Error bars in A and B are bootstrap 95% confidence intervals.

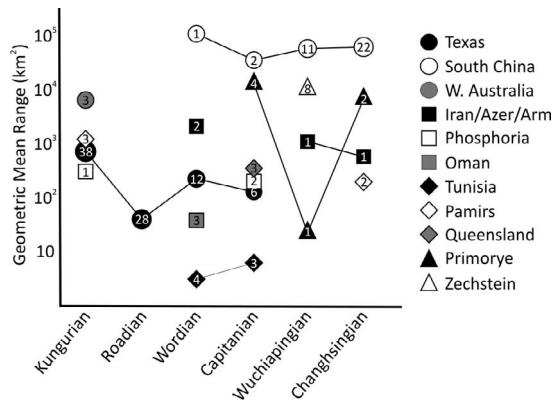


FIGURE 11. Geometric mean range of endemic genera from selected regions during the Kungurian–Changhsingian interval. Iran/Azer/Arm includes localities from northern Iran, Azerbaijan, and Armenia. Number inside each symbol indicates the percentage contribution of endemic taxa from that region to the total number of taxa with a calculated geographic range in the stage.

counterparts at small distances (less than 4000 km). This trend was not caused by sampling a greater variety of taxonomic groups in the Guadalupian, as similar changes in disparity occurred just among brachiopods. It was also not a function of shifting sampling localities, from Guadalupian faunas in the western United States (potentially recording more taxo-

nomic groups) to Lopingian faunas in Tethys, and China in particular. Guadalupian geographic disparity patterns were unchanged even after excluding western United States localities. At distances less than 2000 km, overall percent similarity increased from 0.10–0.15 in the Guadalupian Stages to 0.24 in the Wuchiapingian and 0.22 in the Changhsingian (Fig. 12). A similar pattern is observed at distances of 2000–4000 km; percent similarity was higher in the Lopingian than in the Roadian or Wordian, although the Capitanian also had decreased disparity.

#### Causes of the End-Guadalupian “Extinction”

Although there was no large extinction at the end of the Guadalupian, global standing diversity decreased by about 40% (and sampled-in-bin richness by about 25%) from the Capitanian to the Changhsingian (45% and 35%, respectively, from the Wordian to Changhsingian). This steady, gradual decrease in diversity was primarily caused by three proximate factors. First, origination rates were extremely low in the Capitanian and Wuchiapingian Stages, and contributed much more to the loss of diversity than the

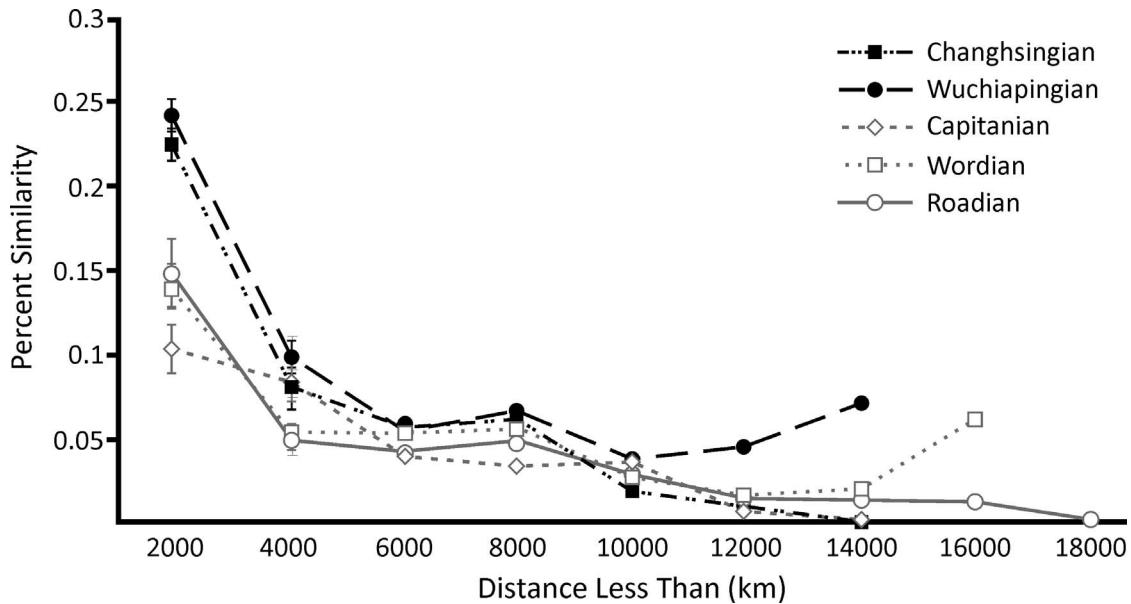


FIGURE 12. Graph showing changes in geographic disparity, as measured by the mean percent similarity of all pairwise comparisons between  $5^\circ \times 5^\circ$  paleogeographic bins, grouped by distance in 2000 km increments. Error bars, shown only for distances of 0–2000 and 2000–4000 km, are bootstrap 95% confidence intervals.

small increase in extinction. Second, the geographic distribution of sampled regions decreased from a maximum of 27 bins in the Wordian to a minimum of only 17 bins in the Changhsingian, with the resultant reduction in provinciality and loss of endemic faunas from isolated regions such as western North America (Shen and Shi 2002, 2004). The diverse and fairly endemic Grandian Province (Shen and Shi 2004) was nearly completely lost after the Capitanian. Reduced sampling and reduced provinciality were primarily caused by the lack of preservation of Lopingian marine sedimentary rocks in a number of regions, especially western North America, eastern Australia, and north China/Mongolia, due to tectonic and orogenic processes (Collinson et al. 1976; e.g., Collins 1991; Li 2006). Third, geographic disparity at smaller scales decreased significantly, indicating that the biotic composition within a region was much less variable in the Lopingian. Even though a similar number of collections and occurrences was recorded in each time interval, the fact that those collections were less disparate in the Lopingian contributed to overall lower global diversity.

Although it is possible to link the loss of isolated faunas and reduction in large-scale provincialism to tectonic causes (such as the Sonoma Orogeny in the western United States), the ultimate driver(s) of decreased geographic disparity over small distances and lower origination rates in the Capitanian and Wuchiapingian are less clear. The pronounced sea level regression at the Guadalupian/Lopingian boundary (Hallam and Wignall 1999) is unlikely to be a cause, as regression should fragment populations, increasing disparity and possibly promoting higher origination rates (e.g., Jackson 1974; Sepkoski 1998), although the link between geographic range and origination is not always clear (Jablonski and Roy 2003). Eruption of the Emeishan flood basalts spanned the Guadalupian/Lopingian boundary (Wignall 2001; Zhou et al. 2002), with the main pulse actually occurring during the mid-Capitanian *Jinogondolella altudaensis* and *J. prexuanhanensis* zones according to magnetostratigraphic correlation (Ali et al. 2002). However, the Emeishan basalts, with a volume of

about 300,000 km<sup>3</sup>, represent a very small large igneous province; significantly smaller than other provinces not associated with extinctions (Ali et al. 2005). Although environmental stress from the flood basalt eruption may have contributed to decreased origination rates, it should also have elevated extinction rates—and there is no indication of increased per capita extinctions during the Capitanian.

A potentially simple explanation for the decrease in geographic disparity could be that Wuchiapingian and Changhsingian collections are derived from a narrower range of lithologies or depositional environments. Although the data are predominantly from taxonomic papers that do not contain information on the sampled lithology or environment, it is unlikely that sampling was more uniform in the Late Permian given the large number of independent data sources. More than 1200 Wuchiapingian and 890 Changhsingian collections are included, and data from South China at least include samples from the siliciclastic Longtan and Dalong Formations and the carbonate Wujiaping and Changxing Formations, and from shelf, slope, and even basinal depositional environments.

The end-Guadalupian “extinction” also coincided with ecological changes between the Capitanian and Wuchiapingian, which led to increased dominance by molluscs in outer shelf settings (Clapham and Bottjer 2007b) and homogenized the onshore-offshore faunal gradient in terms of both abundance and diversity. In addition, increasing stress, likely from deep anoxic waters, in offshore habitats compressed the bathymetric range of sensitive invertebrate groups such as bryozoans, progressively restricting them to shallower shelf communities (Powers and Bottjer 2007). Bathymetric restriction and homogenization of the onshore-offshore faunal gradient would have altered the spatial structure of benthic communities, resulting in reduced small-scale geographic disparity among more similar mixed molluscan/brachiopod assemblages across and along the entire shelf. Although the environmental stress could have contributed to reduced origination rates, the effect of offshore anoxia began in the Wuchiapingian or

was at least minimal in the Capitanian (Clapham and Bottjer 2007b; Powers and Bottjer 2007).

Reduced origination rates in the Capitanian could instead have resulted from cooling (the Kamura Event) during the Capitanian-Wuchiapingian (Isozaki et al. 2007a), as origination rates are typically higher in warmer tropical regions than at cooler high latitudes (Flessa and Jablonski 1996; Powell 2007). In the late Paleozoic, brachiopod origination rates also tended to be higher during greenhouse climates and lower during the late Paleozoic ice age (Stanley and Powell 2003; Powell 2007). However, the overall extinction rate in the Tropics in the Capitanian was not elevated, except perhaps among specialized groups such as fusulinid foraminifera (Stanley and Yang 1994; Isozaki et al. 2007a; Isozaki et al. 2007b), suggesting that cooling may have been minimal. The degree of global cooling during the Kamura Event is also unknown. The advance of small ice sheets in eastern Australia is consistent with decreased temperatures (Fielding et al. 2008) but the Kamura cooling event has only been broadly inferred from a plateau of elevated carbon isotope values in some stratigraphic sections (possibly indicating enhanced carbon burial, although there are alternative explanations for positive excursions; Payne and Kump 2007). Tropical origination rates did decrease more than extratropical originations but it is not clear, however, if the moderate amount of cooling expected during the Kamura Event would have been sufficient to cause the dramatically lowered origination rates in the Capitanian (0.006 per Lmy) and Wuchiapingian (0.016 per Lmy). Origination rates were not as low even during the termination of the late Paleozoic ice age (0.03 per Lmy in the Sakmarian and Artinskian), when global climate was substantially colder than the Capitanian.

### Conclusion

The end-Guadalupian “extinction” was not an abrupt loss of taxonomic diversity, but rather was characterized by a gradual reduction in marine invertebrate genus richness from the Wordian to the end of the Permian. Per capita extinction rates were very slightly

higher in the Wordian and Capitanian but there is no actual end-Guadalupian extinction pulse among marine invertebrates (in contrast to the severe extinction of fusulinids). The diversity decrease was instead largely caused by sharply lower origination rates in the Capitanian and Wuchiapingian and by changes in beta diversity, most notably a reduction in provinciality (especially the loss of the isolated Grandian Province from western North America) and a reduction in geographic disparity over small distances. Those trends are consistently recorded by a wide variety of marine invertebrate clades, including rhynchonelliform brachiopods, bivalves, gastropods, sponges, corals, bryozoans, and cephalopods. Different ecological groups, such as epifaunal and infaunal bivalves or pelagic cephalopods, also exhibit the same pattern of extinction and origination, as do both tropical and extratropical genera. The only selectivity exhibited by extinctions during the Capitanian Stage was for small geographic range, although that selectivity was typical of background extinctions throughout the Kungurian–Wuchiapingian interval.

Although the Emeishan large igneous province and a major sea level regression occurred during the Guadalupian–Lopingian interval, their likely effects are not consistent with the observed changes in extinction, origination, and geographic disparity. The pronounced geographic concentration of extinctions during the Capitanian, and their spatial coincidence with regions where tectonism resulted in the disappearance of marine sedimentary deposition, suggest that some of the diversity reduction was caused by changes in marine habitat area and in the preserved rock record. The gradual decrease in marine invertebrate diversity can largely be explained by (1) possible cooling during the Capitanian Kamura event (if cooling actually occurred) or increased background stress from offshore anoxic waters, which did not increase extinction rates among invertebrate genera but may have reduced origination rates; (2) the onset and spread of anoxic deep water masses, which would have compressed the habitat range and homogenized onshore-offshore faunal gradients, contributing to decreased geographic

disparity over short to intermediate distances; and (3) reduction in marine habitat area and provinciality due to tectonic activity, especially in eastern Australia, northern China, and western North America.

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